The Great American Biotic Interchange in birds

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The sudden exchange of mammals over the land bridge between the previously isolated continents of North and South America is among the most celebrated events in the faunal history of the New World. This exchange resulted in the rapid merging of continental mammalian faunas that had evolved in almost complete isolation from each other for tens of millions of years. Yet, the wider importance of land bridge-mediated interchange to faunal mixing in other groups is poorly known because of the incompleteness of the fossil record. In particular, the ability of birds to fly may have rendered a land bridge unnecessary for faunal merging. Using molecular dating of the unique bird faunas of the two continents, we show that rates of interchange increased dramatically after land bridge completion in tropical forest-specializing groups, which rarely colonize oceanic islands and have poor dispersal abilities across water barriers, but not in groups comprised of habitat generalists. These results support the role of the land bridge in the merging of the tropical forest faunas of North and South America. In contrast to mammals, the direction of traffic across the land bridge in birds was primarily south to north. The event transformed the tropical avifauna of the New World.

land bridge | South America | biogeography | Neotropics

Following the mid-Cretaceous breakup of Gondwanaland and separation from Antarctica in the late Oligocene, South America was an island continent until joined by a land bridge to North America, between 3 and 4 Ma. During its island interval, the mammalian fauna of South America evolved in what has been coined "splendid isolation" (1). Land bridge completion is believed to have initiated the Great American Biotic Interchange (GABI), possibly one of the largest and most rapid episodes of interchange known between continental faunas (1–3). However, adequate appraisal of the role of land bridge formation in promoting a general interchange has been difficult because evidence has been overwhelmingly drawn from fossils for one taxon, the mammals (1, 3–5), and is unresolved to the species level. Interchange dynamics are largely unknown at tropical latitudes, where the majority of faunal and floral mixing occurred but where few fossils have been excavated.

To understand the contribution of a completed land bridge to faunal and floral mixing between North and South America, we need a detailed analysis of the timing of interchange events at tropical latitudes. Here we provide such an analysis of interchange events in several families of passerine birds, a group that inhabits both temperate and tropical regions of the New World and makes up the bulk of avian species diversity. Like most terrestrial groups, birds lack a good fossil record, especially from tropical latitudes, and so the effects of land bridge formation on avian interchange between the continents is poorly understood (6). We used molecular phylogenetic data to overcome this limitation, and maximum-likelihood estimation to compare rates of avian interchange before and after land bridge completion. Faster rates of avian interchange between North and South America after ≈3.5 Ma, compared with before 3.5 Ma, would support the view that land bridge formation initiated an abrupt mixing of the faunas of North and South America. In contrast, a finding of similarly high interchange rates before and after land bridge completion would support a more protracted history of interchange. We compare differences in the timing of interchange in passerine families that are believed to cross water barriers frequently with tropical forest-specialized clades, which rarely do so.

Results and Discussion

To measure exchange rates, we focused on four passerine families that straddle the two continents and exhibit some of the greatest numbers of interchange events: antbirds (Thamnophilidae), woodcreepers (Dendrocolaptidae), tanagers (Thraupidae), and blackbirds (Icteridae). We chose these families because they are highly diverse in tropical regions of both North and South America and jointly account for 30% of all passerine species in the New World. These families also represent a range of degrees of habitat specialization and dispersal abilities. The antbirds and woodcreepers are restricted to tropical forest, whereas many blackbirds and tanagers are more generalist (7, 8). This difference is likely to affect the propensity of these groups to cross open-water gaps. For example, of the four families analyzed only the blackbirds and tanagers have representatives on Caribbean islands (Table 1), and many species of antbirds and woodcreepers and other tropical forest-restricted species are reluctant to fly across open-water gaps of as little as 100 m (9). We sampled 457 of the 734 species belonging to these families, and in each family included all clades occurring in both North and South America. We sampled populations from both sides of the land bridge in almost all lineages straddling the divide, and subsampled species from clades exhibiting no interchange events. A dated molecular phylogeny was generated for each family. In our analysis of interchange events between North and South America, the data at the tips of each phylogeny are the landmasses on which each species resides. Some interchange events are represented by the same species in both continents, and in such cases local populations within each continent were sampled from either side of the land bridge and were similarly coded according to landmass (see *SI Text*, Figs. S1–S3, Tables S1–S3, and Dataset S1). North America is here considered to include all of Middle America south to central Panama, and South America includes the Darien region of the Panamanian and Colombian borders southward. The land bridge was completed between central Panama and the Darien.

We used maximum likelihood to test the effect of land bridge formation on the rate of interchange between the continents (10). We compared two probabilistic models of interchange along the phylogeny for each family separately. In the single-rate model, the per-lineage crossing rate between continents was constrained to be constant through time, before and after land bridge completion (3.5 Ma). Under the two-rate model (10), the

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Table 1. Maximum likelihood estimates of interchange rates

Family	n	q_b	q_a	q_a / q_b	Mean log-likelihood	LR	P
Antbird							
1 rate	1	0.13			−82.12		
2 rate	3	0.025 ± 0.00105 (SE)	0.579 ± 0.00778 (SE)	31.96 ± 2.5 (SE)	−61.506 ± 0.467 (SE)	41.23	1.11 × 10⁻⁹
Woodcreeper							
1 rate	1	0.158			−54.02		
2 rate	3	0.043 ± 0.0017 (SE)	0.394 ± 0.005 (SE)	11.48 ± 0.696 (SE)	−47.2 ± 0.206 (SE)	13.64	0.00111
Tanager							
1 rate	1	0.11			−152.55		
2 rate	3	0.012 ± 0.00062 (SE)	0.167 ± 0.00050 (SE)	24.508 ± 2.84 (SE)	−139.648 ± 0.246 (SE)	25.8	2.50 × 10⁻⁶
Blackbird							
1 rate	1	0.18			−70.57		
2 rate	3	0.11 ± 0.0012 (SE)	0.298 ± 0.00274 (SE)	2.76 ± 0.0509 (SE)	−68.4 ± 0.078 (SE)	4.34	0.114

Values estimated from 100 randomly chosen posterior trees. Parameters estimated are as follows: q, rate parameter under one-rate model; q_b and q_a, rates before and after the best fit breakpoint under two-rate model (as shown in Fig. 1 A). Standard errors reflect uncertainty in node age estimates. Abbreviations as follows: LR, likelihood ratio; n, number of free parameters; P, P-value for likelihood ratio test.

rates of crossing were free to differ before and after a specific time point that was also estimated from the data. Comparison of the two models tests whether a GABI occurred, and whether its start coincided with land bridge completion or was initiated sooner (e.g., along the proto-land bridge, consisting of a string of islands) or later, in association with events long after land bridge completion. With this approach it is not necessary to reconstruct the continent on which the ancestors occurred. Rather, crossing rates are estimated over all possible ancestor reconstructions, weighting each by its likelihood support (10–12). The two-rate model gave a significantly better fit than the one-rate model in woodcreepers, antbirds, and tanagers. In each of these families, the estimated rate was significantly higher after the breakpoint than before (see Table 1). In the two tropical forest-restricted families, antbirds and woodcreepers, the best-fit breakpoint occurred within an estimated several hundred thousand years after land bridge completion (Fig. 1), strongly supporting the role of land bridge completion in increasing interchange rates. In contrast, a breakpoint of 6.5 Ma gave the best fit to the tanager data, suggesting an initiation of GABI during the proto-land bridge period, although a breakpoint between 3.5 and 4 Ma gave almost equal support (see Fig. 1). The best-fit breakpoint in blackbirds at 2.9 Ma is also associated with land bridge completion, but support for the two-rate model was weak and we cannot rule out the possibility that interchange rates before and after land bridge completion were similar in this habitat generalist family.

Maximum-likelihood ancestor reconstructions were used to visualize these results (see *SI Text*, Section B). Based on this analysis, a total of 113 crossing events between continents were reconstructed (see *Materials and Methods*) (18 in woodcreepers, 25 in antbirds, 45 in tanagers, and 25 in blackbirds). We were able to approximate a date for 88 of these interchange events, of which 72 postdated land bridge completion (3.5 Ma; an additional 14 crossing events postdated 3.5 Ma but could not be dated more precisely). We used these reconstructions to estimate the rate of crossing during 0.5- or 1.0-million-year time intervals by dividing the number of reconstructed crossing events in the interval by the sum of evolutionary time (i.e., summed branch lengths in each interval) (see Fig. 1). These rates control for the possibility that some crossing events went extinct leaving no descendants to the present (see *Materials and Methods*). For the antbirds and woodcreepers, a high dispersal rate from South America into North America became established at or soon after the completion of the land bridge and has continued to the present. In contrast, in the tanagers, which are also of South American ancestry, a number of pre-land bridge dispersal events

into North America occurred (one of which produced the only endemic North America tanager genus, *Acanthidops*), and crossings have continued up to the present, with one inferred recent back-colonization. Unlike the other three families, North America is the inferred ancestral continent for the blackbirds (see Fig. S2). The reconstructions suggest a pre-land bridge burst of dispersal from North to South America between 7 and 10 Ma, when representatives of several major clades colonized the continent (see Fig. 1). Blackbird interchange from north to south has continued up to the present. However, the results suggest that back-colonization from south to north occurred primarily after land bridge completion in this group (see Fig. 1). Significantly, most of these south-to-north blackbird taxa (five of seven, three species of *Psarocolius* and two of *Cacicus*) are primarily associated with tropical forest.

To further test the association between tropical forest habitat specialization, dispersal ability, and the impact of the land bridge, we estimated earliest dates of crossing of 14 of the 26 passerine bird families involved in the biotic interchange using dated molecular phylogenies (Table 2). This process added a third primarily tropical forest-specialized family to the previous two, the tapaculos (Rhinocryptidae), added five families without tropical forest specialists, and brought to six the number of families with a mixture of the two. It was not possible to analyze these additional families in the same way as the woodcreepers, antbirds, tanagers, and blackbirds because the number of crossing events was too few or the level of phylogenetic detail was too sparse to allow us to compare crossing rate before and after land bridge completion. Earliest reconstructed crossing events in the three forest-specializing families all date between 3.0 and 4.0 Ma, when the land bridge was completed. In contrast, earliest reconstructed crossing events predated the land bridge in 10 of the 11 families not specialized exclusively in tropical forest ($P = 0.011$, Fisher's exact test). Across passerine families (see Table 2), tropical forest specialization is also tightly associated with absence on Caribbean islands ($P = 0.0019$) and with an absence of long-distance migrants ($P = 0.0006$). These results strengthen the conclusion that tropical forest-inhabiting families required a completed land bridge to cross between the continents, while habitat-generalist families did not. Because the remaining unsampled tropical forest-specializing families (Conophagidae, Cotingidae, Formicariidae, Grallariidae, and Pipridae) also lack migratory ability and do not occur on Caribbean islands, we predict that they too will be found to have crossed only after land bridge formation. Considering that all eight of these tropical forest-specializing passerine families (which added 80 species to the North American fauna) (see Table 1) originated in South

Fig. 1. Analysis of avian crossing between North and South America. (*A*) The likelihood of a range of times for the breakpoint (time of rate change) in the two-rate analysis. The date of the best-fit breakpoint is shown by a triangle. Breakpoints within 1.92 log-likelihood units of the maximum log-likelihood (all values above *dashed red line*) are considered not significantly different from the best-fit value at a 95% level of confidence. (*B*) Crossing dates and rates of crossing between North and South America estimated in 1-million-year intervals, obtained by dividing the number of crossing events in each interval by the total branch length in the tree that falls within that interval. Crossings from North to South America are indicated with yellow bars and those from South to North America are in black. Crossing rates from North to South America are shown by a blue line and those from South to North America by a red line. Rates corrected for missing lineages in phylogenies are shown by dashed lines. Rates are shown for the time span in which each continent was occupied. Completion of the land bridge between 3 and 4 Ma is shown by gray shading.

America and spread north (see Table 2), the evidence indicates that land bridge completion precipitated a massive wave of South American tropical forest lineages to southern North America. Floral makeup of tropical rainforests in Central America is largely comprised of South American elements (13, 14), suggesting that the rainforest flora and avifauna of South America may have invaded North America together in a post-land-bridge wave.

Results for birds and mammals differ importantly in the estimated primary direction of movement across the land bridge. Fossil mammals suggest a primarily north-to-south movement (Fig. 2). In contrast, molecular evidence from birds indicates mainly a south-to-north transfer after land bridge completion (although most interchange before completion occurred from north to south). However, the mammal record is derived almost entirely from temperate-latitude fossils and includes few fossils from tropical forests, which may bias estimates of the direction of traffic between the continents. The phylogenetic methods

used here could be used to expand the record for tropical mammals and other groups, and provide a more complete evaluation of movement trends following land bridge formation.

Dates of interchange in birds nevertheless agree closely with those in mammals, despite being based on molecules rather than fossils (see Fig. 2). In both groups, a limited number of interchange events occurred in the late Miocene, before land bridge completion. At this time, tanagers and flycatchers (see Table 2), as well as four genera of ground sloth and armadillos, moved north, whereas early representatives of blackbirds and most other passerine families of North American origin (see Table 2) (15), racoons, camels, tapirs, peccaries, and proboscideans, moved south (3–5) (see Fig. 2). Dispersal by several other vertebrate groups is also believed to date to this time period (16, 17). These early dispersal events are presumed to have occurred either over open ocean or along the proto-land bridge, consisting of a string of islands (18, 19) or as an ephemeral peninsula (20). In tropical forest-specializing bird families and mammals, accelerated interchange was initiated shortly after land bridge completion and has continued to the present (see Figs. 1 and 2).

Global diversity of birds, mammals, plants and most other groups is highest in the New World tropical wet forests that extend from the Amazon to southern Mexico (21–23). A number of historical events (i.e., uplift of the Andes and Amazon River formation), and possibly low tropical extinction rates (24), are believed to have contributed to this high diversity. The timing of interchange in tropical birds indicates that land bridge completion may have also contributed to the extraordinary diversity in this region by recently merging the faunas and floras long confined to separate continents. Within the land bridge itself, this merging produced a contemporary avian fauna composed almost equally of species belonging to families of North and South American origin, demonstrating substantial faunal merging. (The North/South ratio in Costa Rica is 0.98 and in Panama is 0.85 for passerines; this ratio increases northwards and declines southwards. Ratios are determined from species lists for each country.) Whether this merging resulted in a net increase in species diversity remains unknown, but low estimates of avian extinction rates from tropical latitudes (present study: see *SI Text*) (24) supports this possibility.

Our results demonstrate that despite their ability to fly, interchange of tropical forest-specializing birds between the continents was greatly enhanced by land bridge completion, while habitat-generalist families were less affected. The results are unique in providing a detailed understanding of interchange dynamics at tropical latitudes that have been neglected in fossil analysis of mammals. The results complement those from mammals, despite being based on entirely different methods, and suggest that the so-called "Great American Biotic Interchange" was a general biogeographic event, reshaping patterns of biodiversity across a wide taxonomic spectrum.

Materials and Methods

Taxon Sampling. Published molecular phylogenies with a large proportion of genera sampled were available for antbirds (25, 26), woodcreepers (27, 28), tanagers (29–33), and blackbirds (34–38). These previous phylogenetic studies demonstrated that antbirds, woodcreepers, and blackbirds represent monophyletic groups. However, current taxonomic boundaries of tanagers are poorly defined. To define a monophyletic tanager radiation, we generated a large phylogenetic tree, including almost all genera traditionally assigned to the tanagers and a large proportion of genera in related families (see *SI Text*, Section A).

Genetic samples (see Dataset S1 of tissue samples used) representing the North American side of the isthmus were collected primarily by J.T.W. over a 3-month period in western Panama (west of the Canal Zone), mostly in the provinces near the Costa Rican border. The South American side was represented by samples collected in Darien Province near the Panama–Colombia border. The sampling design was augmented with a large number of samples obtained from throughout Mesoamerica and South America from a variety of

Table 2. Earliest reconstructed dispersal dates for 14 of 26 passerine families involved in the GABI

Family	Common name	Continent of origin	Number of continental species (NA/ SA)	Number of reconstructed dispersal events	Earliest reconstructed interchange date (Ma)	Migratory	Colonized Caribbean	Tropical forest specialist
Dendrocolaptidae	Woodcreepers	SA	19/46	18	3.6	No	No	Yes
Rhinocryptidae	Tapaculos	SA	1/54	1	3.8	No	No	Yes
Thamnophillidae	Antbirds	SA	26/218	25	3.0	No	No	Yes
Tyrannidae	Flycatchers	SA	125/374	Many	12.7	Yes	Yes	Mixed
Cinclidae	Dippers	NA	1/2	1	≈3.5	No	No	No
Emberizidae	Sparrows	NA	74/48	Many	> 4.8	Yes	Yes	Mixed
Hirundinidae	Swallows	NA	15/20	10	13.1	Yes	Yes	No
Icteridae	Blackbirds	NA	46/60	25	8.4	Yes	Yes	Mixed
Megaluridae	Donacobius	SA	0/1	1	14.7	No	No	No
Mimidae	Mockingbirds	NA	16/7	3	6.4 or 7.5	Yes	Yes	No
Motacillidae	Pipits	?	5/7	2 or 3	4.7 or 8.2	Yes	No	No
Thraupidae	Tanagers	SA	50/334	46	8.4	No	Yes	Mixed
Troglodytidae	Wrens	NA	44/46	> 23	15.6	Yes	Yes	Mixed
Turdidae	Thrushes	?	38/32	Many	13.3	Yes	Yes	Mixed

See Section D in the *SI Text* for additional details, ancestor state reconstructions, and dated phylogenies. Earliest dispersal dates were not available for the following passerine families of South American origin [Conophagidae (1 species NA/10 species SA), Cotingidae (10/59), Formicariidae (3/11), Grallariidae (4/49), Furnariidae (24/234), Pipridae (11/47)] or North America origin [Alaudidae (1/1), Cardinalidae (34/19), Corvidae (32/15), Fringillidae (32/34), Parulidae (74/40), Polioptilidae (8/9), Vireonidae (29/23)]. None of these South American-derived families have colonized the Caribbean or possess long-distance migrants and all but Furnariidae specialize in tropical forest. None of these North American-derived families specialize solely in tropical forest. The following North American-derived families have also colonized the Caribbean: Corvidae, Fringillidae, Parulidae, Polioptilidae, and Vireonidae. The following North American-derived families also possess long-distant migrants: Alaudidae, Cardinalidae, Fringillidae, Parulidae, Polioptilidae, Vireonidae. Earliest reconstructed dates in Turdidae, Emberizidae, and Tyrannidae were obtained from well-sampled clades within those families and sampling of additional clades may reveal even older dates. Dates within the remainder of families are from detailed analysis for the entire family. Tapaculos are primarily associated with tropical forest, although a small number of species occur in southern temperate forest and bushland.

museums (see Dataset S1). We sampled 44 of 51 woodcreeper, 100 of 219 antbird, 85 of 100 blackbird, and 228 of 364 tanager species.

DNA Sequencing and Phylogenetic Analysis. The woodcreeper, antbird, tanager, and blackbird phylogenies were generated from a combination of Gen-Bank sequences and a large number of additional sequences generated specifically for the present study (Fig. S2). Partial (≈1000 bp) or complete (1143

Fig. 2. Comparison of crossing dates and rates of crossing of North and South American birds (woodcreepers, antbirds, tanagers, and blackbirds) and mammals. Mammal dates are based on fossil information provided in refs. 3 to 5. Bird dates are based on molecular estimates. Crossings from North to South America are indicated with yellow bars and those from South to North America are in black. Crossing rates from North to South America are shown by a blue line and those from South to North America by a red line.

bp) sequences of the mitochondrial cytochrome *b* (*cyt b*) gene were sequenced for all individuals using standard protocols (24). The complete mitochondrial NADH dehydrogenase subunit 2 gene (*ND2*: 1041 bp) was sequenced using primers L5215 (39) and H6313 (40) for a subset of individuals representing most of the major lineages included in each phylogeny. *ND2* was also sequenced for one or more individuals for most lineages that occur in both North and South America. Partial sequences of the nuclear recombination activating protein 1 (*RAG1*) gene and c-myc exon 3 were sequenced (for protocols see ref. 41) for major woodcreeper lineages to better resolve basal nodes. This sequencing effort was augmented with other mitochondrial genes and nuclear introns available from GenBank (see Dataset S1) (woodcreepers: *myoglobin*; antbirds: *myoglobin*, *NADPH*, *ND3*, *NADPH*, *B-fibrinogen*; tanagers: *ATPase*, *COI*, *12s*, *myoglobin*, *RAG1*, *cmyc*; blackbirds: *COI*, *12s*).

Dated phylogenetic trees were generated in three steps. First, Bayesian topology estimates were obtained in MrBayes v3.7 (42) using the GTR-gamma model and a full dataset of mitochondrial and nuclear genes for all individuals. In many cases, species occurring in both Central and South America were represented by several samples from different geographic localities. To make phylogenetic reconstruction computationally feasible for these large datasets, many redundant samples and localities within each continent were excluded. Analyses were run for a minimum of 5-million generations and were sampled every 5,000 generations after an initial burn-in of at least 1-million generations. Sampled Bayesian trees were used to construct majority-rule consensus cladograms with strong posterior support for most nodes. Second, ultrametric estimates of branch-lengths along the consensus topology were generated under a Bayesian framework in BEAST v1.4.2 (43, 44) using only the cytochrome *b* dataset and fewer intraspecific samples (redundant samples within populations were excluded). This two-stage process was necessary because the multigene dataset provided more robust topologies, but we estimated node ages only with cytochrome *b* for which we have a robust molecular clock. The uncorrelated lognormal relaxed-clock model [with Yule prior for branch lengths (44)], which does not rely on the assumption of molecular rate constancy throughout the tree, was used in combination with the GTR-gamma model of sequence evolution. The duration, sampling frequency, and burn-in were the same as in tree construction. Mean consensus branch lengths were obtained from the Bayesian samples. In addition, for each family, 100 randomly selected posterior trees from the BEAST analysis were used to determine the effect of error associated with node age estimates on the parameter estimates in Table 1. Because posterior trees are each
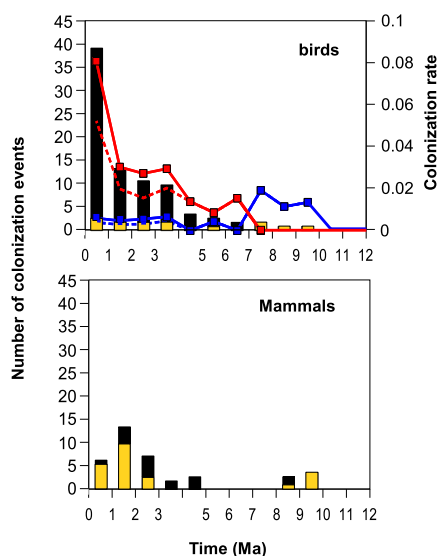
constrained to the consensus topology, they may underestimate the range of node ages, but mean estimates of node ages should be unaffected.

To date trees, we used a molecular clock of 2.1% sequence divergence per million years (1.05% per lineage), a rate strongly supported by an extensive avian-clock calibration dataset for cytochrome *b* (45).

Identical methods were used to construct dated phylogenies for an additional 11 passerine families involved in the GABI (see Table 2). Sampling of species was sufficiently complete in seven of these families to allow us to reconstruct the earliest date of crossing. In the remaining four families (Tyrannidae, Emberizidae, Troglodytidae, and Turdidae) detailed phylogenies were available only for one or a few key clades, but this provided sufficient information to demonstrate pre-land bridge dispersal between the continents (for additional details, ancestor state reconstructions and dated phylogenies see *SI Text*, Section D). It is possible that further sampling of the remaining clades within these four families would reveal even earlier dispersal dates than the ones reported here. Cyt b sequences were used to construct phylogenies for each family, except cyt b and ND2 sequences were used for Turdidae and cyt b; ND2 and ATPase 6 and 8 were used for Emberizidae.

Biogeographic Methods. Interchange rates before and after a breakpoint were calculated using maximum-likelihood models of character evolution along phylogenetic trees (9–11, 46) implemented in the R package GEIGER (47). Breakpoints were tested every 0.1 million years back to 8 Ma to determine whether a change in interchange rates between the continents coincided with land bridge completion (see Fig. 1). Species and population data at each tip of the phylogeny is the land mass on which the taxon resides. We assumed that interchange events coincided with nodes on the phylogeny rather than occurred along branches. Further tests support this assumption over an alternative that allows transitions to occur along branches (48) (see *SI Text*, Section B). However, if the source population of a crossing event went extinct after leaving descendants, then the corresponding node would be lacking from our phylogenetic trees, with the result that the next deepest node would estimate the crossing date. In such cases, the date of crossing will be overestimated. Our approach to dating interchange events is thus conservative because extinctions would favor the null hypothesis of no change in interchange rate before and after the land bridge. We constrained crossing events to occur at nodes in the one-rate model by ignoring branch lengths (accomplished by setting all branch lengths in the phylogeny to 1). We achieved this in the two-rate model by setting all branches immediately descending from nodes predating the breakpoint to 1 and postdating the breakpoint to a value *f*. In the two-rate model we incorporated node-age uncertainty in the estimates using a random sample of 100 posterior trees from our analysis in BEAST. Some nodes occur before or after the breakpoint in different posterior trees, generating varying parameter estimates under the two-rate model.

Maximum likelihood was used to estimate the home continent of ancestors at interior nodes of the tree using Mesquite v2.6 (49) (see Fig. S2). Branch-length information was not used in this analysis (all branch lengths were set to 1). Samples from western Panama northward through North America were coded as North American, and those from near the Panama–Colombian border and throughout South America were coded as South American. In a small number of cases (a few blackbird clades only), it appears that interchange between North and South America occurred via islands in the Caribbean rather than via the Panama land bridge. In such cases, Caribbean taxa were coded as belonging to the continent from which the Caribbean was inferred to have been colonized. Most nodes received strong support for either a North or South American ancestry. Parsimony reconstructions were also generated for comparison and yielded almost identical results to the maximum-likelihood reconstructions (see Fig. S2). Given the concordance

between these methods, we considered only the most likely state at each node in our analysis.

We were not able to obtain precise dates for 22 crossing events (8 in tanagers, 6 in blackbirds, 3 in woodcreepers, and 5 in antbirds) because in each case, we lacked the necessary sequence data from one side of the Isthmus of Panama. Seventeen of these were represented by interchange events in which the same species occurs on either side of the isthmus, and are expected to date to the post-land-bridge period. The remaining four (all tanagers) are represented by closely related sister-species pairs in which one species occurs in Central America and the other in South America. For purposes of ancestor-state reconstruction and maximum-likelihood model testing, we added each missing lineage as sister to the sampled lineage to which it is most closely related. For the 17 crossing events represented by populations of the same species on either side of the land bridge, the missing population was added as sister to its conspecific sample obtained from the opposite side of the land bridge. The four missing species were treated similarly, but were joined to their sister species from the other side of the land bridge. These are shown and discussed with reference to reconstructions included in the *SI Text*.

In analyses involving ancestor-state reconstructions and rate estimation under the one-rate model, branch lengths were set to 1 and so crossing events lacking dates do not present a problem. However, in analyses based on the two-rate model, it is necessary to specify whether a crossing event occurred before or after the breakpoint when the rate change occurred. For crossing events lacking dates, if the most closely related out-group lineage diverged after the breakpoint, then the node represented by the missing lineage was dated after the breakpoint. If out-group taxa predated the breakpoint, then it remains unknown whether crossing events with missing dates occurred before or after the breakpoint. In such cases, crossing events were assumed to predate the breakpoint. This assumption increases rate estimates before the breakpoint and, thus, is conservative as it favors the null hypothesis of no change in crossing rates before and after land bridge formation.

Finally, rates of interchange within narrow time intervals were calculated by dividing the sum of interchange events by the sum of branch lengths (evolutionary time) during each time interval (see Fig. 1*B*). This method assumes complete species sampling to estimate correctly the sum of branch length for each time interval. We corrected for missing branch lengths in these phylogenies by assuming that each missing species contributed to branch-length estimates in each time interval following land bridge completion, but not to those predating the land bridge. This is a conservative correction because it reduces the estimate of crossing rate only after land bridge completion. Branch lengths represented by multiple genetically differentiated lineages within species were not included in these calculations because it is unlikely that more than a single population within each species would be in a position to colonize between the continents (i.e., the one closest to the land bridge). The method also assumes that per-lineage extinction rates are the same for lineages that crossed and lineages that remained behind within the same clade (an assumption which further analysis appears to support; see *SI Text*, Section E). While other molecular-based studies have provided dates of interchange events [e.g., trogons (16) and wrens (15)], this study is unique in providing per capita rates that correct for extinction.

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