Biological evidence supports an early and complex emergence of the Isthmus of Panama

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The linking of North and South America by the Isthmus of Panama had major impacts on global climate, oceanic and atmospheric currents, and biodiversity, yet the timing of this critical event remains contentious. The Isthmus is traditionally understood to have fully closed by ca. 3.5 million years ago (Ma), and this date has been used as a benchmark for oceanographic, climatic, and evolutionary research, but recent evidence suggests a more complex geological formation. Here, we analyze both molecular and fossil data to evaluate the tempo of biotic exchange across the Americas in light of geological evidence. We demonstrate significant waves of dispersal of terrestrial organisms at approximately ca. 20 and 6 Ma and corresponding events separating marine organisms in the Atlantic and Pacific oceans at ca. 23 and 7 Ma. The direction of dispersal and their rates were symmetrical until the last ca. 6 Ma, when northern migration of South American lineages increased significantly. Variability among taxa in their timing of dispersal or vicariance across the Isthmus is not explained by the ecological factors tested in these analyses, including biome type, dispersal ability, and elevation preference. Migration was therefore not generally regulated by intrinsic traits but more likely reflects the presence of emergent terrain several millions of years earlier than commonly assumed. These results indicate that the dramatic biotic turnover associated with the Great American Biotic Interchange was a long and complex process that began as early as the Oligocene–Miocene transition.

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The Isthmus of Panama is the narrow strip of land that connects North and South America and divides the Atlantic and Pacific oceans. The emergence of the Isthmus initiated one of the largest episodes of biological migration between previously disconnected landmasses, the Great American Biotic Interchange (GABI) (1–5), one of the best natural experiments on invasive species. The closure of the Central American Seaway (CAS, the oceanic pathway along the tectonic boundary between South America and the Panama Block) and rise of the Isthmus have been linked to the onset of both thermohaline oceanic circulation and northern hemisphere glaciation (6–8). Despite its broad importance, the formation of the Isthmus and its impact on the rich biodiversity of the Americas remains contentious (9). Therefore, a better understanding of when the formation of the Isthmus of Panama occurred has important implications in several scientific fields across multiple disciplines.

The timing of Isthmus formation has been assessed through different proxies. Previous studies have long suggested full closure by 3.5 Ma (7, 8, 10–16). More recent geological work has suggested a longer and more complex formation, where the initial collision between South America and the Panama Block occurred between 25 and 23 Ma (17). By 20 Ma the Panama Block is suggested to have been connected to North America (18–21) and the width of the CAS to be 200 km (19, 20). Full closure of the CAS occurred by 10 Ma, ending the exchange of

deep and intermediate waters between the Caribbean and the Pacific (11, 19, 20, 22–24). However, the exchange of shallow waters between these oceans likely continued along pathways other than the CAS for many millions of years (7, 8, 10–16, 25).

Over the past two decades, hundreds of studies have assumed the Isthmus of Panama to have closed at 3.5 Ma (SI Appendix), causing the separation of widespread marine populations into distinct Pacific and Caribbean groups (vicariance) and the first possible dispersals between North and South America (with the exception of stochastic long-distance dispersals). Here, we address the following questions: Given the complexities and the recent evidence of a much older geological history of the Isthmus of Panama, is 3.5 Ma an adequate age for those events? Were the suggested water corridors across the Isthmus—even if shallow and narrow—indeed effective barriers against both dispersal of terrestrial organisms and conduits of marine ones until a full closure at 3.5 Ma? We address these questions using comprehensive biological data from living and fossil organisms, where the assumption is that any well-developed terrestrial corridor would lead to both more frequent biotic dispersal between North and South America as well as a division of widespread marine organisms into distinct Caribbean and Pacific lineages (26). Biological data provide a powerful tool for this purpose compared with geological evidence, which cannot inform on the subtle

Significance

The formation of the Isthmus of Panama, which linked North and South America, is key to understanding the biodiversity, oceanography, atmosphere, and climate in the region. Despite its importance across multiple disciplines, the timing of formation and emergence of the Isthmus and the biological patterns it created have been controversial. Here, we analyze molecular and fossil data, including terrestrial and marine organisms, to show that biotic migrations across the Isthmus of Panama began several million years earlier than commonly assumed. An earlier evolution of the Isthmus has broad implications for the mechanisms driving global climate (e.g., Pleistocene glaciations, thermohaline circulation) as well as the rich biodiversity of the Americas.

Table 1.   Migration models estimated from analysis of phylogenetic data

Dataset, sample size	Model	Time of rate shift, Ma				Log-likelihood	AICc	Delta AICc
		First	Second	Third	Fourth			
All taxa, 426	Free model (five rates)	41.14	23.70	8.76	5.26	943.96	−1,869.48	0
	Standard model	3.5				670.72	−1,337.42	532.06
	Miocene model	20	10			876.85	−1,735.54	133.94
NA→SA, 144	Free model (three rates)	23.87	7.54			145.682	−280.928	0
	Standard model	3.5				78.94	−153.79	127.14
	Miocene model	20	10			128.66	−251.15	29.78
SA→NA, 154	Free model (three rates)	23.14	6.13			199.958	−389.511	0
	Standard model	3.5				102.85	−201.62	187.90
	Miocene model	20	10			128.66	−251.15	138.36
Marine, 86	Free model (four rates)	23.73	7.96	2.06		51.81	−88.17	0
	Standard model	3.5				5.41	−6.68	81.49
	Miocene model	20	10			41.07	−75.85	12.33

The results of migration rate analyses are shown for the full dataset, for the terrestrial taxa split by the direction of migration (North to South and South to North), and for the marine taxa. The free model—that is, the best-fitting model after optimizing the number and temporal position of the rate shifts—is compared against models with fixed times of shifts according to the "Standard" and the "Miocene" models. Rate estimates under the best model confidence intervals are provided in the MRTT plots (Fig. 2 and *SI Appendix,* Figs. S1–S4).

differences between exposed land and shallow waters that can be crucial to the dispersal of organisms.

Recent attempts to synthesize dispersal patterns across the Isthmus of Panama are based on dated phylogenies (27–29) that have included data that used a 3.5 Ma Isthmus closure as a calibration point (e.g., in calculating mutation rate). These assumptions lead to circularity if the goal is to examine timing of dispersal or vicariance across the Isthmus. Our molecular analyses differ from previous studies both qualitatively (by the elimination of the timing of the emergence of the Isthmus of Panama and the contrast between patterns in marine and terrestrial taxa) and quantitatively (735% more data points than a previous cross-taxonomic analysis) (27) and serve as a comparison with a comprehensive fossil dataset.

Another crucial aspect of the formation of the Isthmus of Panama and its impact on biological diversity entails the direction of terrestrial dispersal (e.g., north to south) and the ecology of dispersing organisms. In his seminal work on the GABI, Simpson (1) used the mammal fossil record to suggest that North American taxa had a competitive advantage over the South American fauna in that more North American taxa dispersed, survived, and diversified in southern ranges. Recent studies have suggested that ecological barriers to dispersal, such as dry savanna-like environments (30) or reduced rain forest cover (31), also prevented tropical South American taxa from migrating successfully to the north.

To explicitly address the timing of the formation of the Isthmus of Panama and its effect on geographical distributions of biota, we develop a Migration Rates Through Time (MRTT) model. Using this approach, in which migration is defined as dispersal and vicariance events collectively, we conduct an analysis of over 400 data points (*SI Appendix, 1.2*) of molecular divergence dates conferring dispersal events between North and South America or vicariance between the eastern Pacific and the Caribbean Sea. We compare results from extant data with over 23,000 records of American fossil mammals. Our results corroborate recent geological evidence that rather than a Pliocene, time-limited, single event, the formation of the Isthmus of Panama and the GABI were long and complex processes that began as early as the Oligocene–Miocene transition. We also show incongruent patterns in the direction of migration when comparing the molecular and fossil data, possibly reflecting differential diversification rates following dispersal. None of the ecological factors measured in the analyses can explain the statistical differences

in the timing of migration across the Isthmus region among different taxa, and together with the MRTT results, this suggests that rather than intrinsic (biological) traits, extrinsic factors such as the presence of emergent land likely drove these patterns.

Results

Biological Data Reject a 3.5 Ma Assumption of Closure. The most likely migration model for the molecular dataset as a whole demonstrates four statistically significant migration rate shifts. These are estimated at 41.1 Ma (95% confidence interval, 35.9–46.2), 23.7 (19.9–26.2), 8.7 (7.2–10.0), and 5.2 (5.1–6.0). The first shift at 41.1 Ma shows a sixfold rate increase from a negligible 0.001 (0–0.007) to 0.006 (0.003–0.008) migrations per family per million years, the shift at 23.7 Ma is a significant rate increase from 0.006 to 0.036 (0.029–0.044), whereas the shifts at 8.0 and 5.1 Ma represent drastic rate increases to 0.142 (0.106–0.207) and 0.371 (0.351–0.386) migrations per million years, respectively (Table 1 and *SI Appendix,* Table S1). All of the inferred migration rate shifts predate 3.5 Ma.

To assess the effect of molecular data and uncertainty in divergence times on the estimated MRTT, the ages of the biogeographic events were randomized to simulate different proportions of error (*SI Appendix, 1.7*). The dynamics of the MRTT obtained from the datasets with simulated errors were strikingly consistent with those estimated from the events' mean ages, even when the relative error was more than twice as large as that observed from the data (50%; *SI Appendix,* Fig. S1). This indicates that our findings are robust even in the face of considerable amounts of potential error in the data, including ascertainment bias in taxonomic sampling, molecular clock calibration, and topological and branch length estimations (Fig. 1 and *SI Appendix,* Fig. S1).

We compared the Akaike Information Criterion (AIC) scores (32) of two migration models, one containing a single rate shift fixed arbitrarily at 3.5 Ma, consistent with the traditional interpretation of the formation of the Isthmus of Panama, and one encompassing two shifts, as recently suggested by Montes et al. (19, 20), at 25 Ma (initial collision of the Panama block and South America) and 10 Ma (closure of the CAS) (*SI Appendix* and Table 1). In this explicit test of geological models for the emergence of the Isthmus, we found that although neither of the constrained migration models were as likely as those obtained under the best, unconstrained model, Miocene rate shifts were preferred over the previously accepted 3.5 Ma Pliocene shift.

Fig. 1. MRTT estimated from molecular data. The plots show rescaled migration rate for dispersal (*A–C*) and vicariance (*D*) events across the Isthmus of Panama. The rates and their temporal dynamics were estimated using maximum likelihood and 1,000 randomizations to infer 95% confidence intervals of MRTT (shaded areas) (see also *SI Appendix*, Fig. S1 for a sensitivity analysis) and the time of each rate shift with their confidence intervals (circles and bars at the bottom of each panel). Dispersal between North and South America was calculated for (*A*) the entire dataset, (*B*) major taxonomic groups, and (*C*) direction of dispersal. (*D*) Comparison between vicariant events separating marine organisms in the Caribbean and the Pacific and the dispersal of terrestrial vertebrates (mammals, amphibians, nonavian reptiles, and birds) between North and South America. The number of rate shifts was selected by model testing via AICc (Table 1 and *SI Appendix*, Table S10). The dashed line indicates the generally accepted emergence of the Isthmus of Panama at 3.5 Ma.

This is shown by an improvement in the second-order AIC by several orders of magnitude (Table 1). Results from these tests demonstrate that cross-Isthmian migrations occurred in incremental pulses over a long time period, presumably correlated with the stepwise formation and emergence of the Isthmus of Panama and in stark contrast to the assumption that a majority of events occurred at, or shortly after, a 3.5 Ma closure (dashed line in Fig. 1).

We split the molecular data to compare terrestrial dispersal patterns with those of marine vicariance events. We found that terrestrial migration exhibited significant increases at ~20.23 (19.4–22.81) and 6.12 (5.1–7.89) Ma, whereas corresponding events separating marine organisms occurred at 23.73 (19.9–27.41) and 7.96 (7.75–8.96). Migration rates in marine organisms decreased by 50% after the third inferred shift at 2.06 (1.03–4.35) Ma.

We further compared our molecular results with inferences from fossil mammals, which provide the most abundant and best-studied fossil record. Although the number of fossil occurrences varies considerably through time due to differential sampling efforts and preservation rates (Fig. 2*A*), there is no bias toward particular time periods at the species level, except for fossils 1 million years or younger (*SI Appendix*, Table S2). The plots of the fossil data (Fig. 2 *B* and *C*) show that migration events occurred with increasing frequency since ca. 10 Ma and a drastic increase in North American taxa migrating south occurred over the last 3 Ma. The common explanation of this pattern is complete closure of the Isthmus and a competitive advantage of North American mammals over South American counterparts (1). However, we consider equally possible the scenario that the major drop in global temperatures in the last 3 Ma (Fig. 2*C*, blue curve) acted as the triggering mechanism driving North American mammals southwards, as well as leading to the onset of northern hemisphere glaciations and rapid vegetation changes in North America. Dropping sea levels in the same period (Fig. 2*C*, yellow curve) likely increased land exposure along coastal plains, which should have further facilitated migration.

Asymmetry in the Direction of Dispersal Events. The directionality of migrations has long been an intriguing aspect of the GABI (2). In our analyses based on phylogenetic data, the asymmetric model (where migration rates and times of shift were considered as independent parameters) strongly outperformed the symmetric model [corrected ΔAIC (ΔAICc) = 13.96; *SI Appendix*, Table S3]. This suggests that the migrations from South America to North America and in the opposite direction followed different dynamics. However, the estimated rates through time and the respective confidence intervals show that the rates in the two directions were largely overlapping across the long geological time and both underwent a similar rate shift around the transition between the Oligocene and Miocene (ca. 23 Ma; *SI Appendix*, Table S3 and Fig. 1*B*). Migration rates only started to differ significantly after the most recent rate shift (around 6–7 Ma). During this time frame, lasting until the present, the overall migration rate from South America to North America is found to be around 30% higher than the rate from North America to South America.

Our analyses of the fossil mammal data recover a similar number of migrant lineages in South and North America between 11 and 3 Ma; however, these represent a higher fraction of the sampled diversity in South America (Fig. 2 *B* and *C* and *SI Appendix*, Table S2). A large increase in the proportion of North American lineages in South America is observed over the last 3 Ma, resulting in about 45% of the sampled diversity of South American species (Fig. 2*C*). This diversity is likely affected by our definition of migrant lineages and reflects the combined effects of migration and in situ diversification.

The asymmetry detected in the fossil record contrasts with the cross-taxonomic results from molecular phylogenies, where migrations in either direction were not found to be significantly different until ca. 6 Ma, when the migration rate from South to North America exceeds that in the opposite direction (Fig. 1*B* and *SI Appendix*, Table S3). The causes for this discrepancy are still uncertain. The fossil record of South American mammals is mostly derived from temperate latitudes and is heavily biased toward large body-sized grazer/browser animals, whereas the extant mammal data primarily include taxa inhabiting tropical

Fig. 2. Mammal fossil record in the Americas. The bar plots show mammal diversity through time based on fossil occurrences identified to the species level (reduced for clarity to the past 25 Ma, using time bins of 1 Ma) (see *SI Appendix, 1.4 and Table S2* for more details). (*A*) Total number of fossil occurrences. (*B*) Diversity trajectories based on the first and last appearances of species (the thickness of curves reflects 95% confidence intervals of ages) (see also *SI Appendix, Table S6*) for North and South America. (*C*) Mean fraction of immigrant lineages—that is, North American lineages found in South America and vice versa (see *SI Appendix, 1.4* for their definition)—plotted through time as a proportion of the total diversity sampled within each 1 Ma bin on each continent (confidence intervals are given in *SI Appendix, Table S2*). Approximate curves for global mean temperature (38) and eustatic sea level down-sampled ca. 0.1 Ma resolution (39) are plotted for reference.

regions. Perhaps fossil and molecular rates indicate the migration of two different biomes, temperate and tropical, respectively.

The Role of Ecology in Dispersal. Organisms have different dispersal traits and life history strategies. Our results (*SI Appendix, Fig. S2*) support the view that plants, which have generally higher dispersal abilities compared with many animals, were the first organisms to migrate between North and South America (27, 33, 34). Freshwater fishes and amphibians, despite their requirements for survival, suggesting restricted dispersal ability, migrated relatively early compared with other organisms (*SI Appendix, Figs. S2 and S3*). Birds began dispersing much later in the Pliocene, even though many are typically considered good dispersers (*SI Appendix, Fig. S4*). The terrestrial vertebrate and marine data are highly congruent in their increase and decrease in the rate of exchange, respectively, between ca. 10 and 6 Ma (Fig. 1*D*), suggesting that as the CAS closed and vicariance led to the split of species into distinct lineages in the Caribbean and the Pacific oceans, the Isthmus was formed and dispersal increased with connectivity between North and South America.

Despite the general trends detected among taxonomic groups, the Generalized Linear Mixed Model (GLMM) results showed that the variability in migration times is poorly explained by the metrics of dispersal and natural history we quantified (*SI Appendix, Fig. S5 and Tables S2–S5*), and therefore the driving dynamics and mechanisms of migration remain elusive. Our results thus imply that migration events across the Isthmus of Panama were primarily determined not by intrinsic biological variables but potentially by extrinsic factors—including the availability of land, and sea and freshwater corridors, and the establishment of suitable climates and environments.

Discussion

The patterns inferred from the migration analyses of both molecular and fossil data (Figs. 1 and 2) are strikingly consistent and robust to uncertainties associated with age estimations (see confidence intervals in Figs. 1 and 2 and sensitivity analysis in *SI Appendix, Fig. S1*). Our results support an initial collision of the Panama Block and South America at 25–23 Ma with development of extensive terrestrial (although not necessarily fully connected) landscapes in Panama by 20 Ma, at least some 17 Ma earlier than generally assumed. Our results further imply that over the past 10 Ma there has been substantial dispersal and vicariance across the Isthmus and that pulses of dispersal of terrestrial organisms occurred over at least three periods during the last 30 Ma. The underlying causes for these discrete migration pulses remain elusive but may be associated with landscape formation, volcanism, climate change, and/or sea level fluctuations (25, 35).

North American taxa may have been preadapted to dispersal in that many of the successful lineages had migrated from Europe and Asia across northern land bridges, before their movement into South America. Despite this, our results on the North-to-South asymmetry detected in the fossil record contrast with the cross-taxonomic results from molecular phylogenies, where migrations in either direction were not found to be significantly different until ca. 6 Ma, when the migration rate from South to North America exceeds that in the opposite direction (Fig. 1*B* and *SI Appendix, Table S1*).

In summary, can we assume that "no vicariant date [3.5 Ma] is better dated than the Isthmus" (26)? Our results indicate that we cannot. We show that the GABI occurred over a much longer time period than previously proposed and comprised several distinct migrational pulses. Marine and terrestrial clades exhibit similar dispersal/vicariance pulses, occurring between ca. 23–20 Ma and 8–6 Ma. An earlier connection with North America, together with evidence of a southern connection with Antarctica until 30 Ma (36), challenges the long-standing idea of South America being an island continent that evolved in "splendid isolation" (1). These realizations impact our understanding of the temporal evolution and assembly of the American biota and urge a reevaluation of how the formation and emergence of the Isthmus of Panama impacted biological exchange, oceanic currents, atmospheric circulation, and global climate change.

Materials and Methods

Phylogenetic Data. We performed an analysis of available molecular phylogenies with broad representation across taxonomic groups and habitats. We excluded studies that incorporated any assumption of the timing of the closure of the Isthmus (calibrations in dated phylogenies were directly or indirectly derived from this event). We included phylogenetic studies with at least one unambiguous instance of dispersal across the Isthmus of Panama, for instance an ancestor with a North American distribution that had a descendant lineage in South America, as well as marine studies of sister species between the Caribbean and Pacific oceans. The dataset included 424 dated dispersal or vicariance events across the Isthmus of Panama (collectively referred to here as migration events). The data were compiled from 169 dated molecular phylogenies from across the tree of life and published in 29 peer-reviewed journals (*SI Appendix, Tables S8 and S9*, respectively). For each

biogeographic event, we also recorded mean crown age, the lower and upper confidence intervals of ages, and direction of dispersal, as well as the taxon's altitudinal range, dispersal capability, and biome of occurrence.

MRTT Analyses. Biogeographic events with associated age uncertainties were analyzed in a maximum likelihood framework to estimate rates of migration (*SI Appendix*, Table S10) and their variation through time. Although, ideally, such migration rates should be estimated on a per-capita basis (as for other macroevolutionary rates), their estimation in this context would be affected by unobserved extinct lineages and further biases would likely arise from combining data from multiple independent phylogenies. We therefore modeled migrations as random events resulting from a stochastic Poisson process, with a rate parameter that describes the expected waiting time between successive events. As a mean to standardize the migration rates across datasets, we rescaled the estimated absolute Poisson rates by the number of families considered in each analysis. Thus, the migration rates shown in the MRTT plots indicate the expected number of migration events per Ma per family. We emphasize that this standardization is not intended as a correction for temporal biases within each dataset but rather as a tool to facilitate comparisons across different analyses. To account for deviations from a constant rate (homogeneous) process, we tested different non-homogeneous Poisson processes with time-varying rates, including a model with exponentially increasing rates, which might capture potential biases owed to the exponential increase of lineages in extant-taxa phylogenies. To allow for temporal changes in the migration rates, we implemented a non-homogenous Poisson process, in which rate shifts can occur through time. Our maximum likelihood algorithm involved (*i*) assessing the best-fitting number of rate shifts by a stepwise AICc procedure, (*ii*) the optimization of their temporal placement, and (*iii*) the estimation of the migration rates between shifts (*SI Appendix, 1.7*). We used simulations to assess the most appropriate AICc thresholds, thus minimizing the risk of false positives in our analyses (*SI Appendix, 1.6*). We generated and analyzed 1,000 datasets resampled from the uncertainty intervals for migration dates to generate the MRTT plots and calculate 95% confidence intervals.

In addition to jointly analyzing the full molecular dataset, we repeated the analyses on 14 subsets based on different criteria considering geographical, ecological, and taxonomic aspects. These tests allowed us to investigate the differential patterns of migrations linked to direction of migration and environment (terrestrial or marine) and to compare different taxonomic groups and their dispersal ability (Fig. 1*B* and *SI Appendix*, Figs. S2–S4 and *1.8*). Additionally, we compared the AIC scores of two migration models with a model containing a single rate shift fixed at 3.5 Ma and a model containing two shifts in the Miocene, at 25 Ma (initial collision of the Panama block and South America) and 10 Ma (closure of the CAS) (*SI Appendix, 1.8* and Table 1).

GLMM Analyses. We used a GLMM approach on the molecular datasets of terrestrial/freshwater and marine taxa to test for intrinsic (biological, ecological) factors driving the differential timing of dispersal or vicariance. Ecological and biological variables (biome type, dispersal ability, dispersal direction, and elevation preference as derived from the literature and consultation with specialists) were treated as fixed effects, and we included a phylogenetic correction by treating taxonomic rank as a nested random effect (*SI Appendix*, Tables S4–S7). Because the molecular dates in the dataset were calibrated using a range of approaches (e.g., fossils, molecular clocks), we included calibration type as an additional variable in the model to account for any potential bias associated with how the phylogenies were time-calibrated.

Fossil Data. We compiled fossil occurrence data from all available publications of South American mammalian fossils and reviewed the Cenozoic American mammal fossil record in the Paleobiology Database (https://paleobiodb.org/#/), synthesizing data from across the entire American continent. The vetted dataset comprised 23,090 fossil records from 112 families and 3,589 species. Based on first and last appearances of each species in the fossil record, we plotted diversity trajectories through time, by counting the number of species within 1 Ma bins. To explicitly incorporate dating uncertainty of fossils, we randomized the age of each fossil 1,000 times within the temporal boundaries of the geological formation in which they were found (Fig. 2*B* and *SI Appendix, 1.4*). We classified each fossil occurrence as North or South American if the taxon or its ancestor was in either North or South America before 10 Ma, following Carillo et al. (37). We then plotted the amount of immigrant species as a proportion of the total diversity in each continent within 1 Ma time bins (Fig. 2*C*).

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EVOLUTION

Supporting Information:

Materials and Methods, Results and Discussion

Figures S1-S4

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SUPPORTING INFORMATION

1. SUPPORTING MATERIALS AND METHODS

1.1 Assumptions about the Isthmus of Panama

Hundreds of researchers have assumed a closure date for the Isthmus of Panama between 3.5 and 3.0 Ma over the last two decades. The papers most cited for this geological date are essentially from two research groups, Coates (1-5) and Haug (6, 7). Taken together, these papers alone have been cited 2092 times, according to Google Scholar (accessed March 4, 2015).

1.2 Molecular data compilation and analyses

We used molecular phylogenetic studies that included extant New World species published or in press until May 2013 in 29 journals (Tables S8 and S9). We identified 424 divergence time estimates in 169 phylogenies that represented unambiguous instances of dispersal across the Isthmus of Panama or vicariance events of marine taxa across the Caribbean and Pacific oceans. Our proxy for dispersal time, mean crown ages

and the confidence intervals around them, were gleaned from each phylogeny. Crown groups are defined as the least inclusive monophyletic group that contains all the extant members of a clade (sensu 8). We adopted the approach of Hoorn et al. (9) for data mining and included studies that were directly or indirectly dated with fossil calibration or known rates of nucleotide substitution and excluded studies with calibrations based on geologic events, such as the closure of the Panama Isthmus.

1.3 Fossil data generation

To compile fossil mammal data, searches were conducted in Web of Knowledge (http://wokinfo.com) and Georef (http://www.agiweb.org/georef/). The key terms used in the searches included: fossil mammal(s), South America, geological epochs from the Paleocene to the Pleistocene, and the names of all South American countries. New fossil occurrences were added to the Paleobiology Database (PBDB; http://paleodb.org/). From this database, a total of 32,342 fossil mammal records were gathered for this study. We assigned the origin of each fossil mammal occurrence to its respective family or order using information from the fossil record and the literature.

1.4 Fossil data analysis

All undetermined fossil occurrences and all records that had not been identified to species level were removed, leaving 23,090 occurrences in the analyses. The final data set (available from http://datadryad.org) included 3,589 species, of which 2,657 (21,104 occurrences) were found in North America and 958 (1,986 occurrences) in South America (Fig. 2A). We classified each fossil occurrence as North or South American if

the taxon or its ancestor(s) were in either North or South America before 10 Ma

following Carillo et al. ([10](#)) and identified 50 South American clades in North America

(494 occurrences) and 182 North American lineages in South America (439 occurrences).

All fossil occurrences were provided with minimum and maximum ages, derived from

the temporal ranges of the respective geological units and reflecting the degree of

uncertainty in their dating. These were treated as confidence intervals and used as

uniform ranges from which the ages of the occurrences were randomly drawn ([11](#)). The

ages of the fossil occurrences of each species were randomly resampled 1,000 times from

the respective ranges and used to determine the first and last appearances of species,

while accounting for the dating uncertainties of the fossil record. Based on the first and

last appearances, we calculated the raw number of species in North and South America

within time bins of 1 Myr and plotted diversity trajectories through time with 95%

confidence intervals obtained from the 1,000 randomized samples (Fig. 3B, Table S2).

Based on these counts the proportions of migrant species in the two continents were also

quantified for each time bin (Fig. 2C, Table S2).

1.5 Re-estimation of divergence times

A number of marine lineages exhibit trans-Isthmian divergences that are assumed to have

taken place concomitantly with the final closure of the Isthmus of Panama ([reviewed in](#)

[12](#)). The genetic distances among these geminate species pairs have been used to

calibrate molecular clocks based on a closure of the Isthmus of Panama between 3.5 and

3.0 Ma. This molecular clock has then been used to estimate the divergence times of

sister pairs that occur in the marine ecosystems on each side of the Isthmus (e.g. 13, 14, 15). Because we did not include molecular dates calibrated with any estimate of Isthmus closure, we had to estimate divergence dates for marine taxa using an independent rate in order to include these taxa in our study.

We obtained genetic distances (Kimura's two-parameter distance) for trans-isthmian species pairs from Lessios (25) and applied a standard molecular clock rate of 2% mitochondrial sequence divergence per million years to convert values to absolute time. This molecular clock has substantial uncertainty surrounding it, thus divergence times for these species pairs should thus be considered as coarse approximations. Although molecular dating based on secondary rate calibrations is prone to potential caveats (e.g. 16, 17), re-estimation allowed for a comprehensive synthesis on trans-isthmian divergences in both marine and terrestrial systems.

1.6 Estimating migration rates from dated migration events

Migration events (dispersals and vicariances) extracted from dated phylogenies were used to estimate rates of migrations and their variation through time. Migrations were treated as independent events occurring through time according to a random Poisson process. In our notation, the ages of all events are measured as time before the present. For a number K of migration events, we define a vector of times of migration $\mathbf{t} = t_1, t_2, ... t_K, t_{K+1}$, where t_1 and t_K represent the oldest and most recent events respectively, and $t_{K+1} = 0$ represents time 0, i.e. the present. Assuming that the rate parameter changes over time according to a function $\lambda(t)$, the likelihood of $\mathbf{t}$ based on a non-homogeneous Poisson process is:

$$P(t_1, ... t_K | \lambda) = \prod_{j=1}^{K} \exp\left(-\int_{t_j}^{t_{j+1}} \lambda(u) \; du\right) \prod_{j=1}^{K} \lambda(t_j)$$
(1)

where the first product describes the probability of the waiting times between events and the second product accounts for each migration events based on the variable rate λ. Note that t_{K+1} appears in the first product where it accounts for the waiting time between the last migration event and the present (i.e. $t_K - t_{K+1}$), whereas it is not included amongst the migration events in the second product.

Several Poisson models were implemented, the simplest of which had one constant rate through time, i.e. $\lambda(t) = \lambda$, for $t_1 \leq t \leq 0$, that is a single free parameter estimated from the data (degrees of freedom, d.f. = 1). A model with exponentially distributed rate was generated using the following function:

$$\lambda(t) = q + l \exp(-lt)$$
(2)

where $q \geq 0$ is a minimum baseline rate and l is the rate parameter of the exponential distribution. Both q and l were estimated from the data as two independent free parameters (d.f. = 2). Because the times of migration are expressed as time before present ($t = 0$ being the present), this function models a rate that exponentially increases towards the present. To allow for more complex patterns of rate variation, models with rate shifts through time were additionally implemented. These assumed that rate changes occurred

at times of shift τ defining time frames, while the rates were assumed to be constant within each time frame. For a set of T times of shift defining $T+1$ time frames, a vector of rates $\lambda_1, \dots \lambda_{T+1}$ was defined and used to calculate the probability of Equation (1). Each rate shift introduces two additional parameters in the model, i.e. the time of shift and the migration rate following the shift. For instance, a model with one rate shift has two rate parameters $\{ \lambda_1, \lambda_2 \}$ and one time of shift $\{ \tau_1 \}$ (d.f. = 3).

Implementation - The fit of alternative models of migration were compared in a maximum likelihood framework. Because the sample size in several of the data sets was comparatively small (Table S10), we used the second-order Akaike Information Criterion (AICc; [18], [19]) in all model comparisons, and AICc thresholds determined through simulations (see below) as indicators of significant support for a more parameter-rich model against a simpler model. We used a stepwise procedure that starts with a constant rate model and subsequently adds rate shifts to determine the best number of rate shifts supported by the data (e.g., [20], [21]). At every step, the algorithm adds a rate shift in the model, estimates the parameters (migration rates and times of shift) by likelihood optimization, and computes the AICc score. If the AICc for this model is significantly lower (i.e. better) than the previous score, based on the AICc threshold, the model is retained and one additional rate shift is tested. The procedure is stopped when an additional rate shift does not yield a significant improvement of AICc score, in which case the previous (simpler) model is retained ([20]). For model comparison, we also ran maximum likelihood optimizations under two models with fixed times of rate shift, which we named the 'Standard' and the 'Miocene' models following Coates and Stallard

(5). The Standard model assumed a shift at 3.5 Ma and two rate parameters (before and after the shift; d.f. = 2) and the Miocene Model had shifts at 25 and 15 Ma and three rate parameters (d.f. = 3).

The migration models were implemented in a Python (www.python.org) script (available from the authors) to optimize the parameters using maximum likelihood. To reduce the risk of finding local optima, likelihood optimizations were repeated 500 times from different random starting parameter values. Under each model, starting times of shift were proposed as random values from a uniform distribution spanning the age of the data set and then optimized as a free parameter.

Determining AICc significance thresholds - We carried out simulations in order to assess AICc thresholds indicating significant support for a parameter rich model against a simpler model. Following the procedure recently employed by Pennel et al. ([22](#)), we simulated data sets of sizes N = {10, 25, 50, 75, 100, 150, 200, 250, 300, 400} under a constant-rate Poisson process, i.e. drawing N times of migration from uniform distributions. The number of simulations totaled 10,000 (i.e. 1,000 of each size). The simulated migrations spanned a time frame ranging from 0 to a maximum age randomly sampled between 65 and 15 Ma. These sample sizes and time frames reflected the ranges observed in our empirical data sets. We analyzed each simulated data set and recorded the difference in AICc values (ΔAICc) between the (true) constant rate model and best (incorrect) model with one rate shift. We then determined AICc threshold for each data size as the 95th ΔAICc percentile and fitted an *x*-shifted power function ([22](#)) to draw

AICc thresholds for any data size. Based on the best fitting function the AICc threshold

for a data set of size N can be obtained from the following equation:

$$\Delta AICc_{threshold}(N) = -59.587 \times (N \times 0.573)^{-1.399} + 6.108 \qquad (3)$$

Given the range of sample sizes in our empirical analyses, the AICc thresholds used here

ranged between 2.87 and 6.08 log-units (Table S10).

1.7 Analysis of the migration events (molecular data)

Analyses of migration rates were performed on the full data set (see above) and on

different subsets based on different biogeographic, ecologic, and taxonomic criteria. The

definition of subsets was also conditioned on including at least 10 migration events, in

order to avoid an exceeding loss of analytical power due to sample size.

The following data sets were analyzed (sample size in parentheses):

1. All data (424): all sampled plants and animals (terrestrial and aquatic)

2. Dispersal direction of terrestrial taxa: North to South (144), South to North (154), defined as explained below

3. Terrestrial vertebrates (59) and marine taxa (86), the latter distributed either in the Caribbean Sea or in the Pacific Ocean

4. Taxonomic groups: arthropods (35), mammals (24), birds (158), non-avian reptiles (17), amphibians (18), plants (74), and freshwater fishes (14)

5. Dispersal ability (as defined below): low (61), medium (78), high (287).

Model selection was performed independently on each data set based on the mean ages of migration events (Table S8). After testing the migration models with a constant rate and an exponentially distributed rate, we used the stepwise AICc procedure described above to assess the number rate shifts (Table S10). Maximum likelihood estimations of the parameters (rates and times of rate shifts) were performed under the model selected by stepwise AICc and repeated on 1,000 replicates after randomizing the age of the migration events uniformly within the respective confidence intervals (Table S8). The rate estimates were used to calculate mean and 95% confidence interval of the migration rate within time bins of 1 Myr and to construct migration rates through time plots (MRTT, Figs. 2 and S2). 95% confidence intervals were also calculated for the times of rate shifts.

Rate standardization - The migration rates estimated through Equations (1,2) represent the absolute rate of the fitted Poisson process, and represent the expected number of migration events per time unit (1 Myr) in a given data set. While ideally, such rates should be estimated on a per-lineage basis [as for other macroevolutionary rates (e.g. 23)], their estimation would be likely affected by unobserved extinct lineages and further biases might arise form combining data from different phylogenies. Thus, we preferred the estimation of absolute Poisson rates, and assumed that the model with exponentially increasing rates might capture potential biases owed to the exponential increase of lineages in extant-taxa phylogenies.

As a mean to approximately standardize the migration rates across data sets, we rescaled the estimated absolute Poisson rates by the number of families considered in each analysis. Thus the migration rates showed in the MRTT plots indicate the expected number of migration events per Myr per family. We emphasize that this standardization is not intended as a correction for temporal biases within each data set (as rates are simply rescaled), but rather as tool to facilitate comparisons across different analyses. Number of families included is provided for each data set in Table S10.

An additional test was performed using the two data sets of terrestrial taxa defined by dispersal direction (see point 2 above) to assess whether significant asymmetries in migration rates could be detected between North American taxa migrating southward and South American taxa migrating northward. The likelihoods of different migration models were therefore optimized on a data set that included both subsets. We first tested three-rate models, i.e. the model selected by stepwise AICc for both subsets analyzed independently (Table S3). Secondly a symmetric model (identical rates and shift times) was compared with an asymmetric four-rate model in which rates and times of shifts were independently estimated for the two directions of migration and their AICs scores were compared. Finally to assess when were most different, we looked at the amount of overlap in the respective migration rates (and 95% confidence intervals) through different time frames.

Sensitivity to dating errors - To further assess the effect of data uncertainty on the estimated dynamics of migration rates, the ages of the biogeographic events were

randomized to simulate different proportions of error. For a given relative error r, the ages of all biogeographic events were randomly redrawn from normal distributions centered in their mean value and with standard deviation equal to a fraction r of their mean. Thus, for an event i of mean age m_i new values were randomly resampled from:

$$m_i' = |\mathcal{N}(\mu = m_i, \sigma^2 = rm_i)|, \qquad (4)$$

where the absolute value is used to avoid negative ages. Based on Equation (4), 100 randomized data sets with relative errors of 10, 20, and 50 % (obtained from $r = \{0.1, 0.2, 0.5\}$, respectively) were simulated and analyzed by the stepwise AICc algorithm described above. To assess whether our choice of simulated errors were comparable with those observed in the data we calculated the mean relative error in our molecular data. We used the available 95 % confidence intervals around the age estimates (Table S2) and assumed normal distributed errors, so that the boundaries of the confidence interval equal the mean age +/- 1.96 σ^2. Based on Equation 3, we calculated the relative error for all events for which a confidence interval was available (46 % of the data) and obtained an average relative error in our data equal to 21.04 % ($r = 0.21$), thus falling well within the range of simulated errors. The dynamics of the migration rates through time obtained from the data sets with simulated errors were strikingly consistent with those estimated from the events' mean ages, even when the relative error was more than twice as large as that observed from the data (50 %; Fig. S1). This indicates that our findings are robust even against considerable amounts of potential error in the data (Figs. 1, S1).

1.8 Assessing the impact of taxon biology on dispersal time

The taxa that migrated across the Isthmus of Panama exhibit variability in ecology and evolutionary history. Because taxon ecology and evolutionary history has been shown to impact genetic differentiation and dispersal across the landscape (27, 24), the variance in the observed dispersal times across the Isthmus of Panama may be attributable to taxon-specific factors.

To test this hypothesis, we employed a Generalized Linear Mixed (GLMM) model approach to assess the effect of elevational preference, biome type, dispersal ability, and dispersal direction on the timing of dispersal. We also included the molecular-dating calibration type used by the original studies in the model to account for potential variance in migration times associated with a particular calibration method (e.g. molecular clock vs. fossil calibration). For example, dates obtained using a molecular clock may yield more recent divergence events if the substitution rates tended to be faster than dates obtained from phylogenies calibrated with fossils. A complete description of the ecological and biological variables is listed below. We fit the data to models using the lme4 v. 0.9975-12 package in the R programming language (25).

For the models examining taxa that inhabit terrestrial and freshwater biomes we treated the variables (biome, elevational preference, dispersal ability, dispersal direction, and calibration type) as fixed effects. We were unable to identify dispersal direction for some taxa because there is inadequate information in their phylogenies. We also could not

obtain sufficiently detailed information on the elevational preferences or biome for

particular taxa to accurately assign them to a category. Thus, we removed the points

classified as missing or equivocal data. Because some taxa had missing data in multiple

categories, the final data set analyzed was reduced from 341 to 280 points. Finally, we

included a phylogenetic correction by treating taxonomy as a nested random effect to

account for the non-independence of the data in each model. We started with 'Class',

'Order', and 'Family' as a nested random effect, but 'Order' was removed because the

estimated variance around the parameter was 0 due to the strong correlation between

'Order' and 'Class'. We obtained similar results if we removed 'Class' instead of

'Order'. Irrespective of the random effect chosen, the results from our model

comparisons were similar between models retaining all three taxonomic levels. The full

model for taxa that inhabit the terrestrial and freshwater biomes was structured as

follows:

glmer(log(Dispersal.Time) ~ Elevational.Preference + Dispersal.Direction + Dispersal.Ability +

Biome + Calibration +(1|Order/Family), family="gaussian")

For the model examining the marine taxa, we did not include habitat type or altitude

because the majority of taxa inhabited shallow waters and there were inadequate sample

sizes for the different levels in the 'Biome' category. We included all of the compiled

dispersal times for marine taxa in the model (n=80). For the phylogenetic correction, we

used 'Class', 'Order', and 'Family' as a nested random effect. The 0 estimated variance

in 'Order' observed in the terrestrial and freshwater taxa model was not observed in the

marine taxa models (Table S5). The full model for marine was structured as follows:

glmer(log(Dispersal.Time) ~ Dispersal.Ability + Calibration + (1|Class/Order/Family),

family="gaussian")

For all models, we specified a Gaussian error distribution and we log-transformed dispersal time to reduce the residual variance. The outputs for full and reduced models are available in Tables S4 and S6.

We evaluated the importance of each fixed effect by comparing the full model versus a model where the variable was removed using the R function anova(full.model, reduced.model, test="chisq"). The idea being that if a variable was important in explaining the variance in dispersal times the model would be significantly worse when it was excluded (Tables S5 and S7).

We found that the biological variables could not significantly explain the variance in dispersal times across the Isthmus of Panama (Tables S5 and S7). By comparing full and reduced models in the terrestrial and freshwater taxa we found that excluding the variables elevational preference (Pr>ChiSq = 0.60), dispersal direction (Pr>ChiSq = 0.30), dispersal ability (Pr>ChiSq = 0.54), or biome type (Pr>ChiSq = 0.20) did not yield significantly different models. In the marine taxa the removal of dispersal ability (Pr>ChiSq = 0.83) from the model did not have a significant effect. One of the confounding issues in assessing the significance of these variables was the association between biological differences and the taxonomic groups. For example, the taxa

identified as good dispersers exhibit much more recent dispersal times across the Isthmus of Panama, but the majority of the good dispersers were birds.

We found that the inclusion of calibration type improved the model, which suggests that some of the variance in dispersal times may be associated with how molecular dating was done in the original studies. In the terrestrial and freshwater taxa model calibration type was only marginally significant (Pr>ChiSq = 0.09), whereas in the marine taxa, calibration type was significant (Pr>ChiSq) = 6.19E-5).

Biomes - We used World Wildlife Fund (WWF) biomes to assign taxa to broad-scale habitats that represent their climatic envelopes (26). Biome types are as follows: TSMBF – Tropical & Subtropical Moist Broadleaf Forest; TSDBF – Tropical & Subtropical Dry Broadleaf Forest; TSGSS – Tropical & Subtropical Grasslands, Savannas, and Shrublands; DXS – Deserts & Xeric Shrublands; TSCF – Tropical & Subtropical Coniferous Forests; TGSS – Temperate Grasslands, Savannas, and Shrublands; BFT – Boreal Forests/Taiga; MGS – Mangroves; and Aquatic). Marine habits include: Tropical Coral, Tropical Upwelling, Pelagic Marine (open-water dispersers), and Intertidal (for nearshore, generally sessile aquatic organisms). We condensed our variables into humid forest (TSMBF), dry forest (TSDBF), forest (multiple forest types or non-tropical forest), nonforest (TGSS, DXS TSGSS), multiple biomes (eurybiomic), or aquatic (separating freshwater and salt water).

Elevational range - We assigned clades to their elevational preference: Lowland (0 – 500 m), Montane (500-2500), and Highland (>2500 m). There were only five taxa assigned to the highland category, so for the purposes of the analyses we merged Montane and Highland taxa. For clades that were distributed in multiple elevational zones, we assigned them to two broad elevation categories Lowland-Montane and Lowland-Highland.

Dispersal direction - Dispersal direction was obtained from original publications. The three dispersal categories assigned were 1) North to South – represents a dispersal event where a lineage started north of the Isthmus of Panama and went south into South America, and 2) South to North – represents a dispersal event where a lineage started in South America and dispersed north of the Isthmus of Panama.

Dispersal ability - We assigned taxa to three categories, which reflect coarse-scale differences in dispersal abilities. Dispersal categories were defined as Category 1 – poor; Category 2 – moderate; and Category 3 – good.

Aquatic Organisms Category 1) Obligatory freshwater organisms. In general these species are restricted to freshwater habitats and are incapable of crossing a marine barrier causing them to have limited ability to disperse. Category 2) Viviparous, clonal, or nesting marine species were assumed to be relatively good dispersers but not as high as broadcast spawners. Category 3) Marine organisms whose reproductive life history traits include having pelagic eggs or larvae (i.e., early-stage young are released to be dispersed by the ocean).

Terrestrial Animals Category 1) Organisms that are constrained to aquatic habitats on land during any stage of life. Category 2) Organisms that spend the majority of their lives on terrestrial habitats (not aquatic), and are incapable of flight. Category 3) Organisms that are capable of flying.

Plants Category 1) Plants possessing heavy fruits or seeds, passive fruit dispersal, or narrow distribution. Category 2) Because of the lack of information on natural history of many tropical plant groups this category was scored as anything in between categories 1 and 2. Category 3) Plants producing spores; small or winged seeds; or dispersed by birds, usually producing berries.

Molecular dating calibration - The published phylogenies used to extract dispersal events across the Isthmus of Panama were calibrated using molecular clocks, fossils, and secondary calibrations based on dating events from external phylogenies, or a "mixed" calibration, which used more than one type of calibration. Because the calibration type may influence divergence time estimates, we included a calibration type in our GLM models to account for any potential biases.

SUPPORTING FIGURE AND TABLE CAPTIONS

Figure S1. Migration rates through time estimated on the full data set (426 biogeographic events) after introducing 10, 20, and 50 % of random error in the data. The black dashed

line indicates the rate estimate obtained from the analysis of the mean ages of the biogeographic events.

Figure S2. Estimated rates of dispersal across the Isthmus of Panama through time for non-avian reptiles and amphibians, birds, and mammals. The rates and their temporal dynamics were estimated using maximum likelihood and 1,000 randomizations to infer 95% confidence intervals (CI; shaded areas). Circles and bars at the bottom indicate the mean and 95% CI for times of rate shift.

Figure S3. Estimated rates of dispersal across the Isthmus of Panama through time for freshwater fish, arthropods, and plants. The rates and their temporal dynamics were estimated using maximum likelihood and 1,000 randomizations to infer 95% confidence intervals (CI; shaded areas). Circles and bars at the bottom indicate the mean and 95% CI for times of rate shift.

Figure S4. Estimated rates of dispersal across the Isthmus of Panama through time for taxa divided by low, medium, and high dispersal ability. The rates and their temporal dynamics were estimated using maximum likelihood and 1,000 randomizations to infer 95% confidence intervals (CI; shaded areas). Circles and bars at the bottom indicate the mean and 95% CI for times of rate shift.

Table S1. Migration rates and times of rate shifts, estimated from the analysis of phylogenetic data.

Table S2. Mean and 95% confidence intervals of sampled species through time based on the fossil record, and proportion of immigrant species in North and South America.

Table S3. Migration models estimated from analysis of phylogenetic data.

Table S4a-f. Generalized Linear Mixed Model output for full and reduced models examining the effects of ecological and historical variables on cross-Isthmus of Panama dispersal times in terrestrial and freshwater taxa; a) full model; b) model with elevational preference variable removed; c) model with dispersal direction variable removed; d) model with dispersal ability variable removed; e) model with biome type variable removed; and f) model with calibration type variable removed.

Table S5. Generalized Linear Mixed Model comparison between full and reduced models, computed to examine the effects of ecological and historical variables on dispersal times across the Isthmus of Panama for terrestrial and freshwater taxa.

Table S6a-c. Generalized Linear Mixed Model output for full and reduced models examining the effects of ecological and historical variables on dispersal times across the Isthmus of Panama for marine taxa: a) full model; b) model with dispersal ability variable removed; and c) model with calibration type variable removed.

Table S7. Generalized Linear Mixed Model comparison for full and reduced models examining the effects of ecological and historical variables on dispersal times across the Isthmus of Panama for marine taxa.

Table S8. Survey of approximate ages of extant taxa reported from published phylogenies. The complete data is deposited at Dryad (http://datadryad.org).

Table S9. List of journals surveyed for the present study, in which we searched for suitable dated phylogenies.

Table S10. Migration models estimated over the phylogenetic data for terrestrial taxa, partitioned by the direction of migration.

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Reptiles and Amphibians
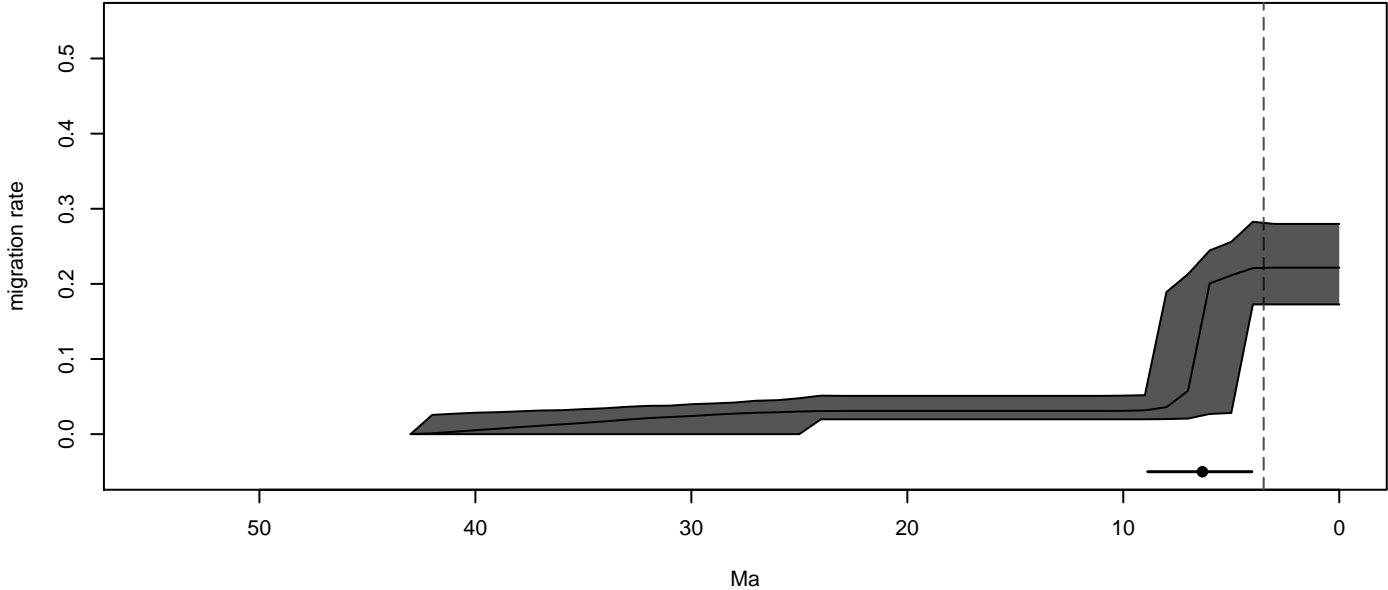
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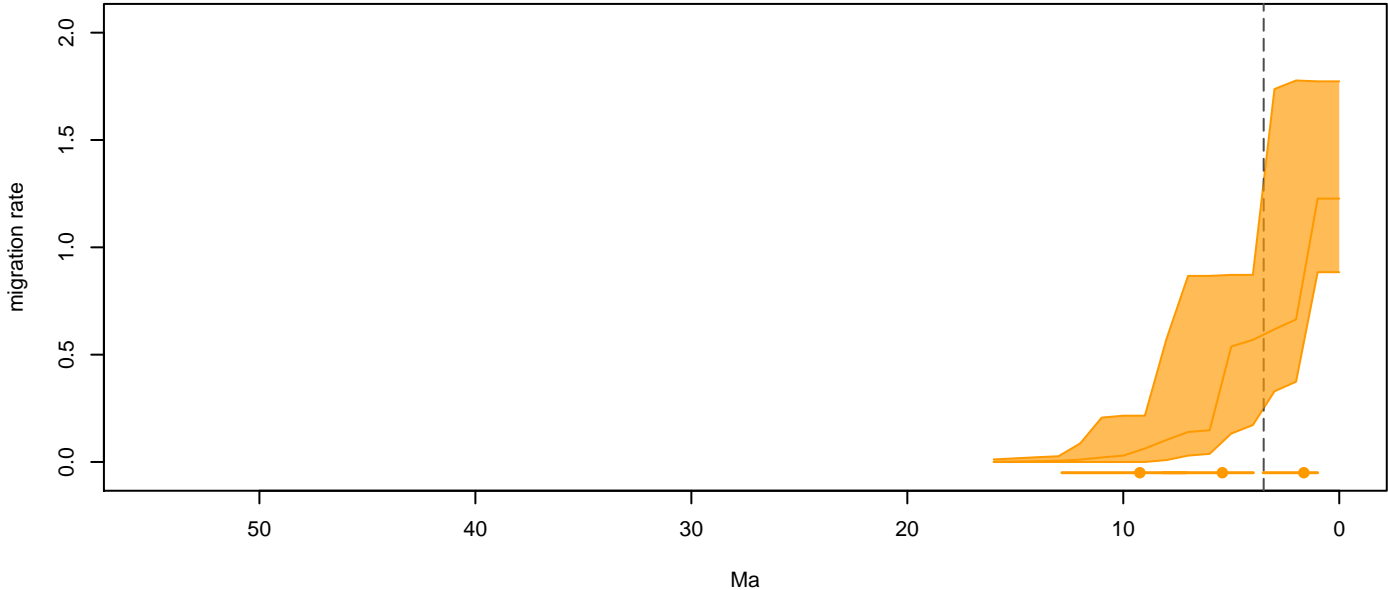
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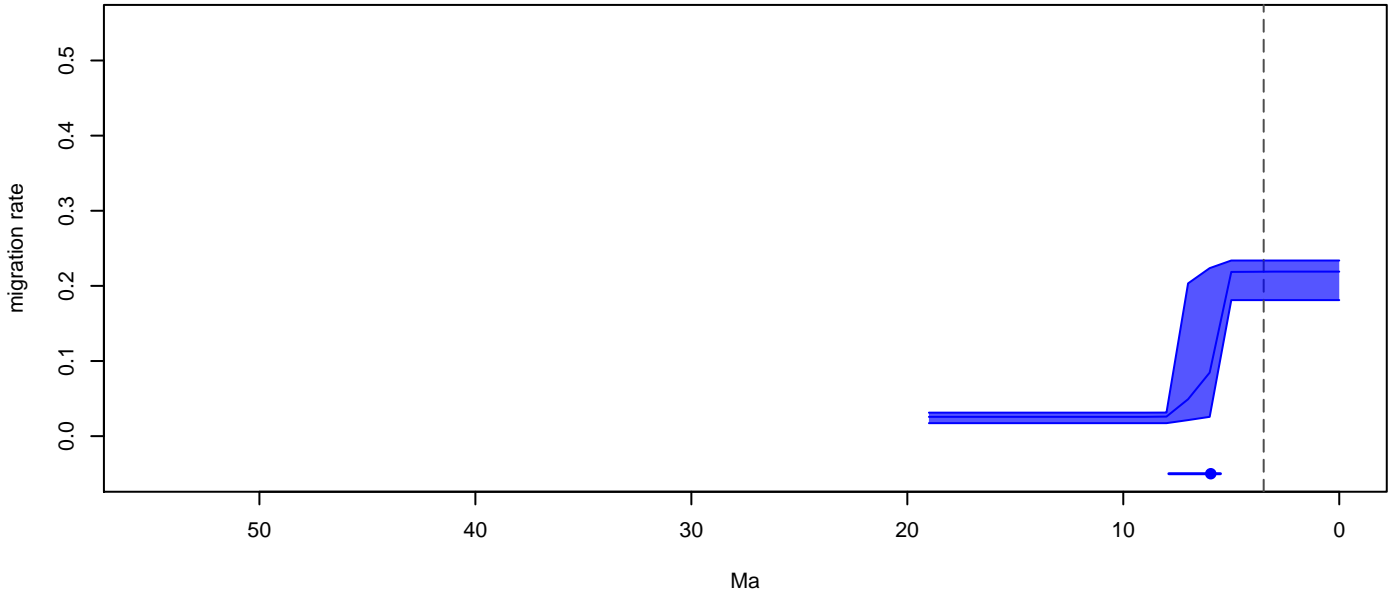
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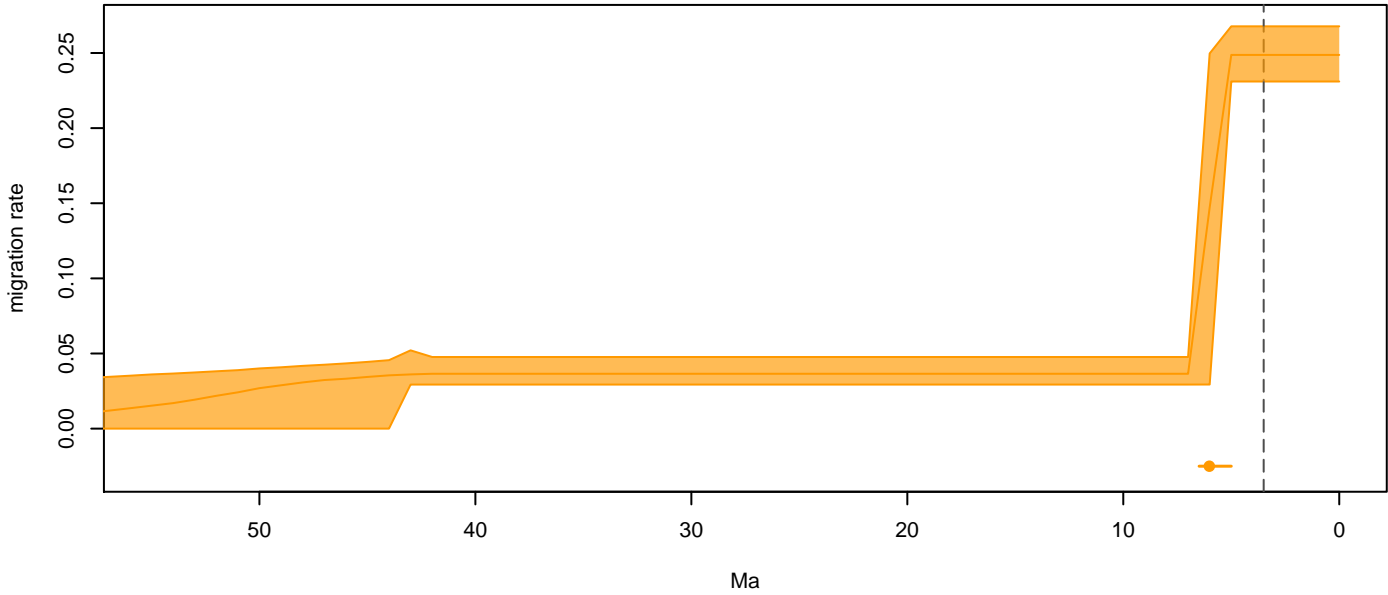
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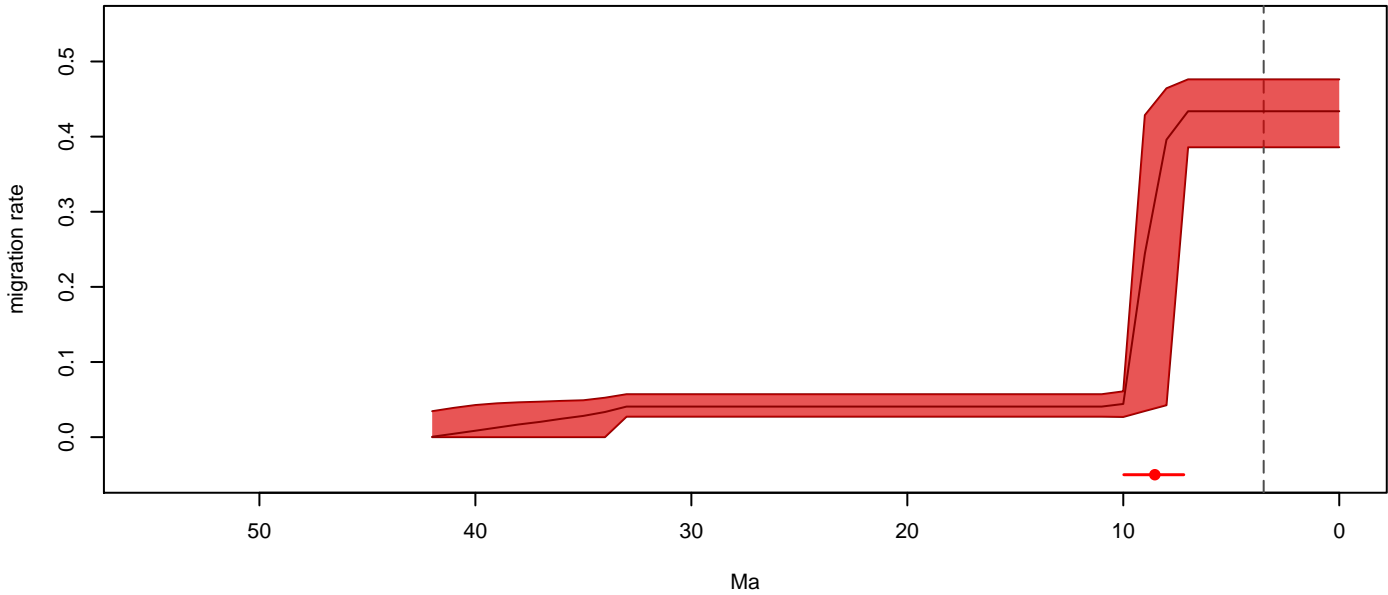
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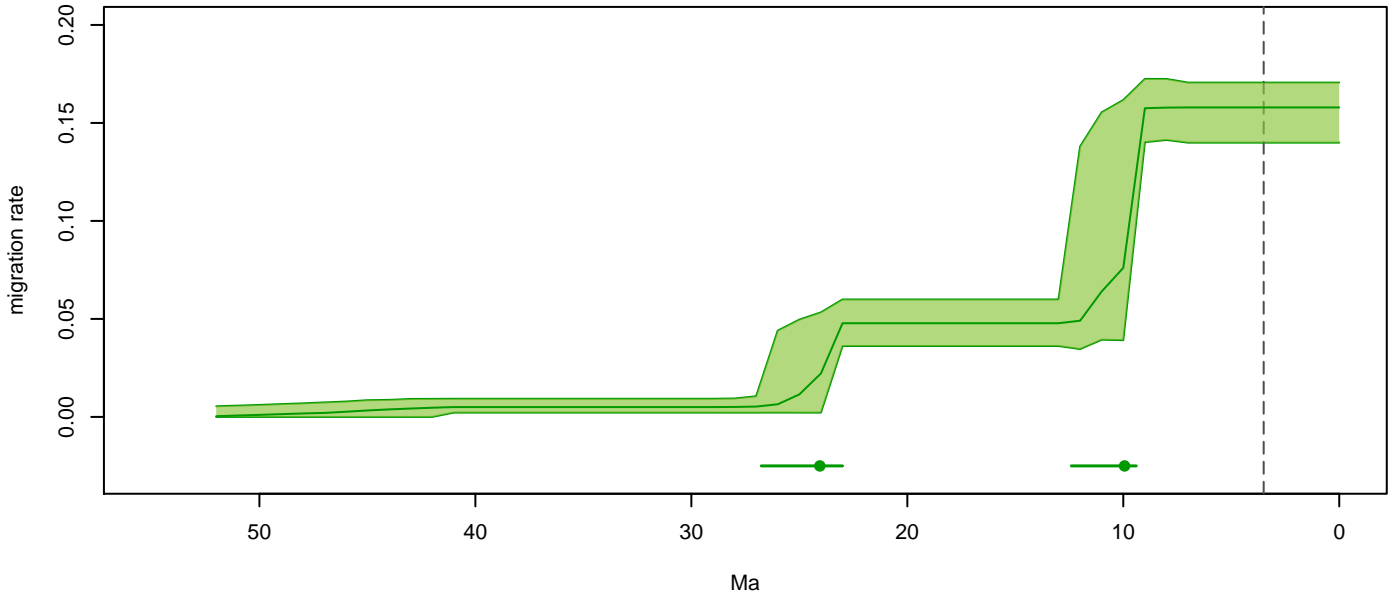
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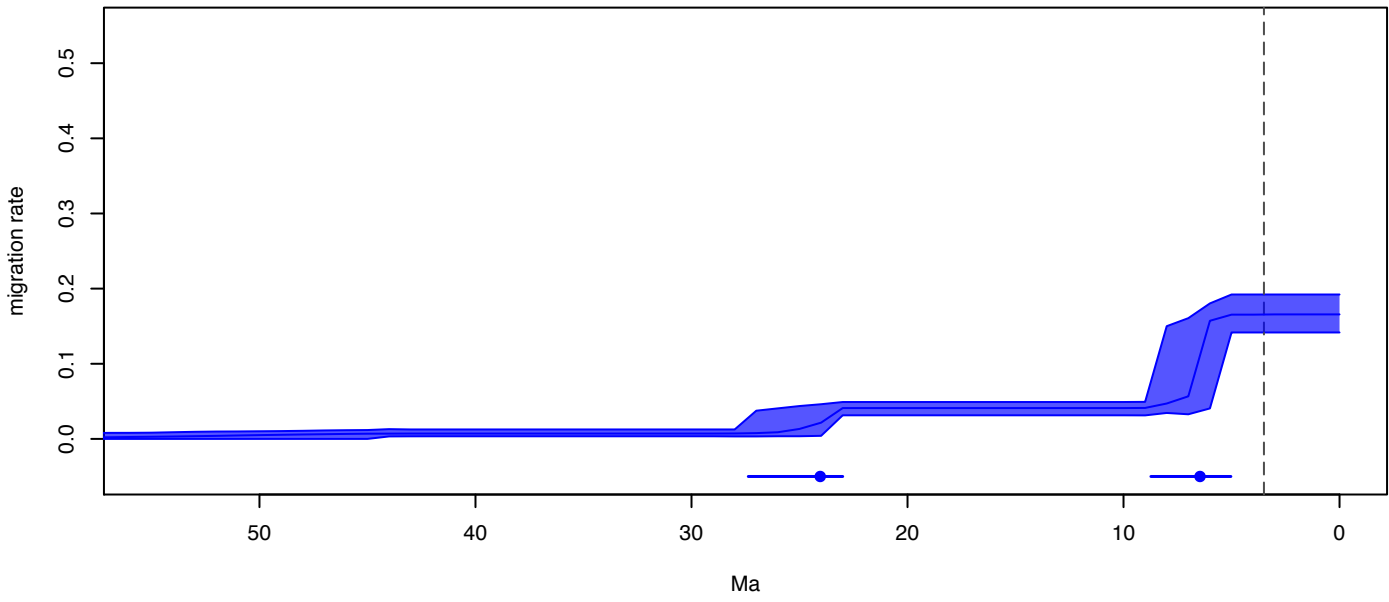
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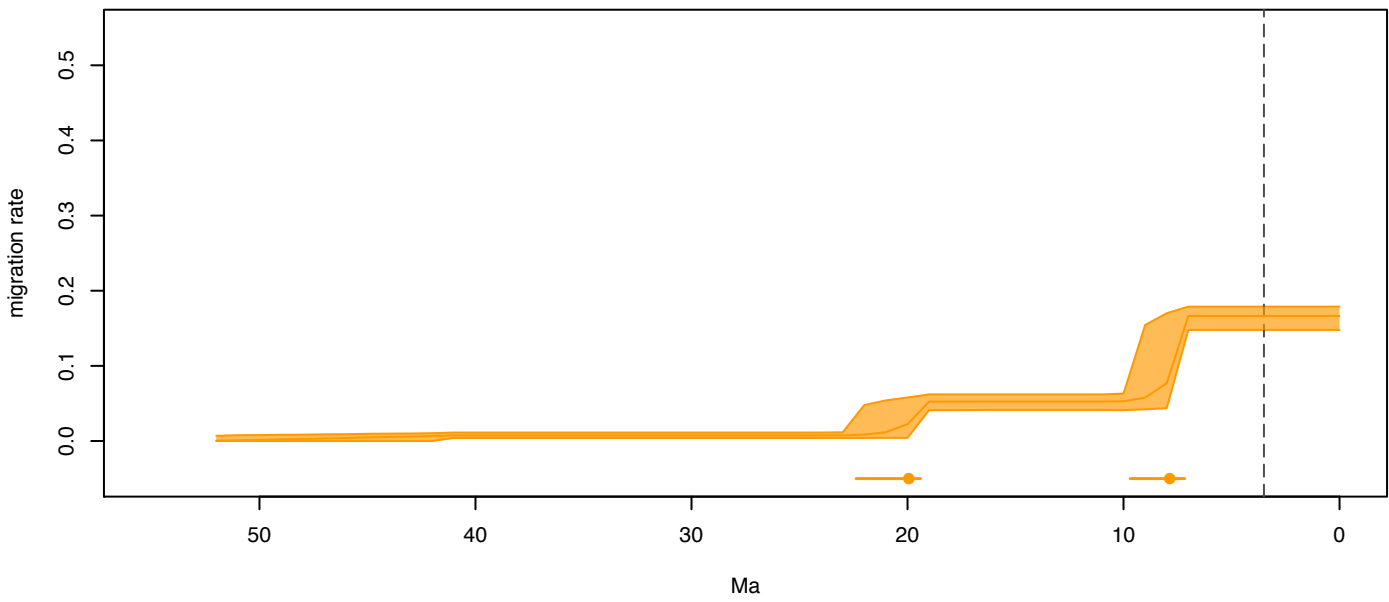
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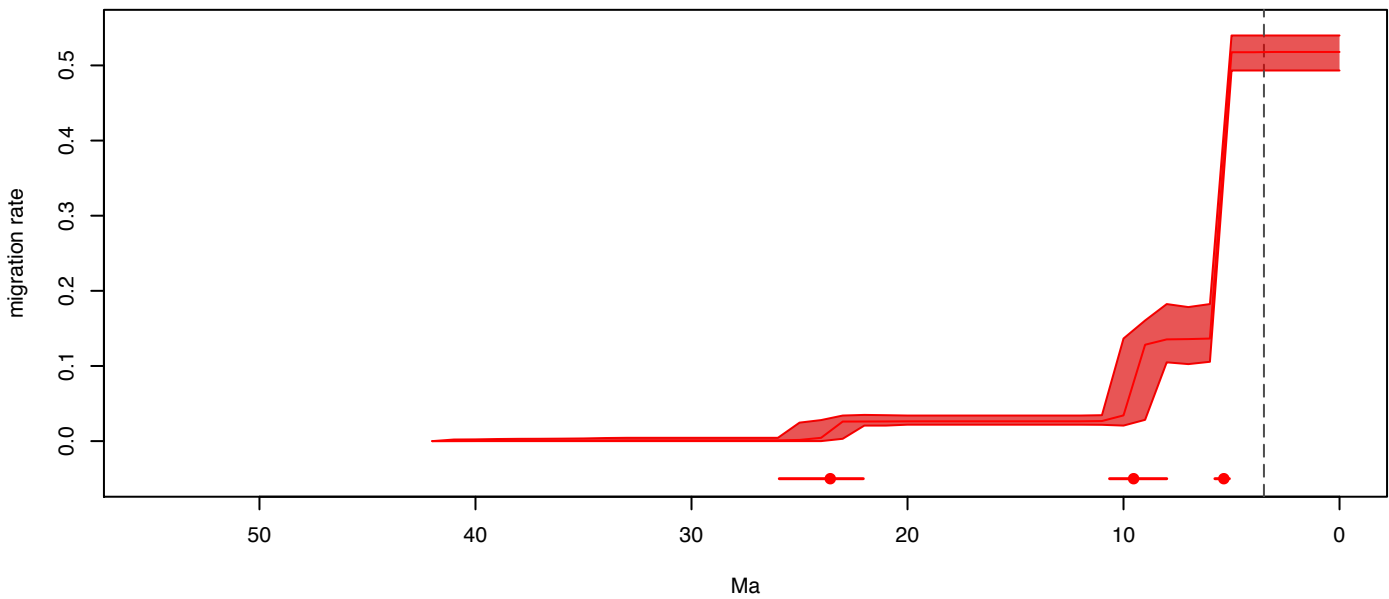
Table S1. Migration rates and times of rate shifts from analysis of phylogenetic data.

Data set	Time of rate shift (Ma)				Migration rates between shifts				
All	5.263 (5.1–6.092)	8.756 (7.2–10.047)	23.696 (19.9–26.271)	41.14 (35.917–46.239)	0.371 (0.351–0.386)	0.142 (0.106–0.207)	0.036 (0.029–0.044)	0.006 (0.003–0.008)	0.001 (0–0.002)
N to S America	7.541 (5.172–9.704)	23.873 (22–26.415)			0.227 (0.192–0.281)	0.036 (0.025–0.048)	0.004 (0.002–0.007)		
S to N America	6.132 (5.1–7.048)	23.142 (20.5–26.576)			0.304 (0.274–0.345)	0.031 (0.024–0.04)	0.003 (0–0.005)		
Marine	2.061 (1.028–4.35)	7.959 (7.75–8.955)	23.733 (19.9–27.411)		0.13 (0.121–0.2)	0.292 (0.205–0.312)	0.045 (0.035–0.059)	0.006 (0–0.019)	
Terrestrial tetrapods	6.12 (5.1–7.89)	20.225 (19.4–22.813)			0.216 (0.181–0.245)	0.043 (0.033–0.054)	0.004 (0–0.01)		
Reptiles and amphibians	6.335 (4.046–8.864)				0.222 (0.173–0.28)	0.031 (0.02–0.051)			
Fresh water fish	6.016 (5–6.49)				0.249 (0.231–0.268)	0.037 (0.029–0.048)			
Arthropods	8.54 (7.2–9.975)				0.434 (0.386–0.476)	0.041 (0.027–0.057)			
Plants	9.941 (9.4–12.405)	24.051 (23–26.762)			0.158 (0.14–0.171)	0.048 (0.036–0.06)	0.005 (0.002–0.009)		
Birds	1.64 (1–3.524)	5.414 (3.977–8.177)	9.234 (7.071–12.843)		1.227 (0.884–1.773)	0.618 (0.329–1.737)	0.148 (0.038–0.867)	0.011 (0–0.086)	
Mammals	5.95 (5.5–7.89)				0.219 (0.181–0.234)	0.026 (0.017–0.031)			
Low dispersal ability	6.458 (5.03–8.733)	24.04 (23–27.37)			0.166 (0.142–0.192)	0.041 (0.031–0.049)	0.007 (0.003–0.013)		
Medium dispersal ability	7.86 (7.17–9.694)	19.943 (19.4–22.38)			0.166 (0.148–0.179)	0.053 (0.041–0.062)	0.007 (0.004–0.011)		
High dispersal ability	5.357 (5.1–5.769)	9.534 (8–10.647)	23.576 (22.047–25.937)		0.518 (0.493–0.54)	0.137 (0.106–0.182)	0.026 (0.022–0.034)	0.001 (0–0.004)	

The results of migration rate analyses are shown for the full dataset and several subsets defined by the direction of migration, taxonomic group, and dispersal ability. Maximum likelihood estimates of the times of rate shift (in Ma) and migration rates (dispersals/family/Myr) are reported based on the best fitting model selected by AICc (see text). Reported migration rates refer to the mid-point between times of shift. 95% confidence intervals are provided in parentheses for both shift times and migration rates.

Table S2. Mean number of sampled species and 95% confidence intervals through time based on the fossil record.

Time bin (Ma)	Species in NA	Immigrants spp. In NA	Species in SA	Immigrants spp. In SA
1-0	451.541 (438-462)	31.018 (26-34)	265.643 (256-274)	132.196 (126-139)
2-1	345.403 (326-361)	29.307 (25-32)	144.823 (134-154)	72.567 (66-79)
3-2	290.129 (273-308)	23.681 (19-27)	88.737 (76-100)	40.388 (31-48)
4-3	261.813 (245-279)	15.058 (11-19)	41.736 (35-48)	5.48 (4-8)
5-4	202.087 (183-217)	8.349 (3-12)	54.962 (48-62)	3.665 (0-6)
6-5	146.069 (132-161)	2.855 (0-5)	61.98 (53-71)	3.353 (1-5)
7-6	197.235 (179-214)	3.967 (1-6)	81.165 (68-92)	3.48 (1-5)
8-7	232.0 (215-252)	4.601 (3-7)	145.899 (132-157)	4.875 (2-7)
9-8	248.387 (229-267)	4.739 (3-7)	145.056 (133-158)	4.124 (2-6)
10-9	245.849 (225-263)	4.285 (1-6)	76.743 (67-87)	1.687 (1-3)
11-10	251.042 (231-269)	3.116 (1-4)	58.861 (48-68)	0.414 (0-1)
12-11	275.948 (260-294)	2.179 (0-3)	40.467 (31-48)	0.123 (0-1)
13-12	286.671 (269-301)	1.517 (0-3)	32.88 (26-38)	0
14-13	303.987 (286-321)	0.852 (0-2)	37.235 (30-43)	0
15-14	341.303 (326-357)	0.457 (0-1)	33.742 (28-40)	0
16-15	323.656 (305-341)	0.399 (0-1)	49.2 (42-57)	0
17-16	272.66 (255-290)	0.354 (0-1)	62.221 (52-70)	0
18-17	276.298 (255-294)	0.307 (0-1)	56.887 (47-66)	0
19-18	259.082 (238-277)	0.273 (0-1)	47.093 (37-54)	0
20-19	221.165 (203-239)	0.218 (0-1)	48.407 (41-57)	0
21-20	192.9 (173-211)	0.166 (0-1)	42.753 (34-51)	0
22-21	194.115 (175-211)	0.115 (0-1)	46.916 (36-57)	0
23-22	194.932 (177-212)	0.054 (0-0)	48.79 (38-59)	0
24-23	177.211 (162-191)	0.003 (0-0)	43.093 (34-51)	0
25-24	170.026 (155-185)	0	48.921 (40-57)	0

26-25	154.27 (141-166)	0	48.633 (40-56)	0
27-26	144.085 (130-156)	0	44.551 (37-53)	0
28-27	132.027 (119-144)	0	35.645 (27-44)	0
29-28	116.989 (105-129)	0	26.871 (17-34)	0
30-29	96.625 (84-108)	0	16.876 (11-22)	0
31-30	75.878 (65-85)	0	21.885 (15-27)	0
32-31	71.742 (64-78)	0	24.128 (18-29)	0
33-32	75.734 (69-82)	0	23.91 (18-29)	0
34-33	149.921 (143-156)	0	21.012 (15-26)	0
35-34	131.024 (120-142)	0	19.08 (14-24)	0
36-35	145.614 (132-156)	0	18.583 (13-23)	0
37-36	122.66 (109-133)	0	15.726 (10-20)	0
38-37	87.016 (76-97)	0	10.44 (7-14)	0
39-38	87.623 (78-97)	0	9.534 (6-13)	0
40-39	87.321 (77-96)	0	9.844 (6-13)	0
41-40	89.524 (78-99)	0	10.667 (6-14)	0
42-41	104.63 (93-116)	0	13.203 (9-17)	0
43-42	116.778 (105-129)	0	10.548 (7-14)	0
44-43	117.049 (102-128)	0	10.868 (6-14)	0
45-44	104.33 (90-116)	0	10.933 (6-14)	0
46-45	79.049 (66-90)	0	10.893 (6-14)	0
47-46	67.289 (58-78)	0	10.633 (6-14)	0
48-47	80.434 (70-89)	0	10.215 (6-14)	0
49-48	90.497 (81-101)	0	13.779 (8-18)	0
50-49	91.143 (79-101)	0	20.152 (14-26)	0
51-50	97.343 (84-108)	0	24.872 (17-31)	0
52-51	114.26 (101-126)	0	27.678 (20-34)	0
53-52	123.66 (109-135)	0	28.63 (22-36)	0
54-53	118.126 (106-131)	0	27.578 (20-34)	0

55-54	97.919 (85-110)	0	24.717 (19-32)	0
56-55	70.031 (58-80)	0	23.169 (17-30)	0
57-56	48.671 (44-53)	0	25.768 (20-31)	0
58-57	30.39 (24-36)	0	14.043 (9-18)	0
59-58	34.334 (28-41)	0	7.318 (3-11)	0
60-59	34.671 (27-40)	0	1.246 (0-2)	0
61-60	32.541 (26-38)	0	1.119 (0-2)	0
62-61	33.173 (27-39)	0	2.402 (0-5)	0
63-62	35.209 (32-39)	0	6.508 (3-10)	0
64-63	25.364 (18-32)	0	8.921 (6-12)	0
65-64	23.625 (19-27)	0	8.482 (5-11)	0
66-65	17.378 (12-22)	0	5.256 (2-8)	0

The number of species in each North America (NA) and South America (SA) were counted within 1 Myr time bins and averaged after 1,000 randomizations to account for the uncertainty of the ages of the occurrences, 95% confidence intervals are provided in parentheses. The number of immigrant lineages (see definition in the text) shows a significant increase of migrant species in both continents over the past 15–10 Myrs (Fig. 2).

Table S3. Migration models estimated over the terrestrial taxa phylogenetic data, partitioned by the direction of the migration.

Model	Subset	d.f.	Time of rate shift (Ma)		Rescaled rates between shifts			log-likelihood	AICc
					2 Ma	15 Ma	30 Ma		
Asymmetric	NA->SA	10	7.54 (5.63–9.71)	23.87 (22.00–25.86)	**0.227 (0.192–0.265)**	0.036 (0.032–0.038)	0.004 (0.003–0.003)	345.64	-670.51
	SA->NA		6.13 (5.10–6.72)	23.14 (20.50–24.93)	**0.304 (0.279–0.335)**	0.026 (0.026–0.029)	0.002 (0.002–0.002)		
Symmetric		5	6.01 (5.1–7.24)	23.54 (22.00–25.18)	0.173 (0.153–0.190)	0.027 (0.023–0.026)	0.004 (0.003–0.003)	333.38	-656.55

Different constraints on the times of shift and rates between shifts were applied to assess the presence of significant asymmetry of the rates through time. The preferred model is the asymmetric, in which rates and their variation are estimated independently in the two directions (North to South, South to North). Times of rate shift and rescaled rates between shifts are given as mean and 95% confidence intervals (CI). The estimated rate following the most recent shift (~ 6–8 Ma) is significantly higher in direction S to N as compared with the rate estimated in the opposite direction, as suggested by the lack of overlap between the respective CI.

Table S4a Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores using all ecological and biological variables (full model)

Formula: log(Dispersal.Time) ~ elevation + Disperal.Direction + Dispersal.Ability + Biome + Calibration + (1 |Class/Family)

AIC	logLik	deviance	REMLdev
810.6	-386.3	754.9	772.6

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.40901	0.63954
Class	(Intercept)	0.17929	0.42342
Residual		0.66961	0.8183

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	14.774913	0.543804	27.17
elevation-Lowland	0.198281	0.159263	1.245
elevation-Lowland.Highland	0.149247	0.258569	0.577
elevation-Lowland.Montane	0.030644	0.181332	0.169
Dispersal.Direction-south.to.l	-0.142801	0.139666	-1.022
Dispersal.Ability-moderate	0.079662	0.296096	0.269
Dispersal.Ability-poor	0.334834	0.335246	0.999
Biome-dryforest	-0.461085	0.564123	-0.817
Biome-eurybiomic	0.451573	0.496146	0.91
Biome-forest	0.026395	0.476824	0.055
Biome-humidforest	0.004105	0.473582	0.009
Biome-nonforest	0.131791	0.54127	0.243
Calibration-fossil	0.56672	0.289524	1.957
Calibration-geology	0.427819	0.468079	0.914
Calibration-mixed	0.734744	0.281032	2.614
Calibration-secondary	0.403461	0.312215	1.292

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.
The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S4b Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable elevational preference removed

Formula: log(Dispersal.Time) ~Dispersal.Direction + Dispersal.Ability + Biome + Calibration + (1 | Class/Family)

AIC	logLik	deviance	REMLdev
801.7	-384.9	756.7	769.7

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.39599	0.62928
Class	(Intercept)	0.16355	0.40441
Residual		0.67166	0.81955

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	14.95854	0.51094	29.276
Dispersal.Direction-south.to.ı	-0.10233	0.1353	-0.756
Dispersal.Ability-moderate	0.09552	0.29188	0.327
Dispersal.Ability-poor	0.28682	0.32874	0.872
Biome-dryforest	-0.6241	0.5399	-1.156
Biome-eurybiomic	0.31085	0.47817	0.65
Biome-forest	-0.11818	0.45846	-0.258
Biome-humidforest	-0.12928	0.45668	-0.283
Biome-nonforest	-0.04054	0.52019	-0.078
Calibration-fossil	0.62278	0.28356	2.196
Calibration-geology	0.4487	0.46506	0.965
Calibration-mixed	0.82416	0.27171	3.033
Calibration-secondary	0.43267	0.30397	1.423

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.
The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S4

Table S4c Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable dispersal direction removed

Formula: log(Dispersal.Time) ~ elevation+Dispersal.Ability+Biome+Calibration+(1 | Class/Family)

AIC	logLik	deviance	REMLdev
807.5	-385.8	755.9	771.5

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.43447	0.65915
Class	(Intercept)	0.17128	0.41386
Residual		0.66192	0.81358

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	14.75308	0.5447	27.085
elevation-Lowland	0.16729	0.15539	1.077
elevation-Lowland.Highland	0.10896	0.25495	0.427
elevation-Lowland.Montane	0.01871	0.18061	0.104
Dispersal.Ability-moderate	0.08889	0.29766	0.299
Dispersal.Ability-poor	0.31293	0.33473	0.935
Biome-dryforest	-0.45371	0.56532	-0.803
Biome-eurybiomic	0.40915	0.49592	0.825
Biome-forest	-0.01219	0.47627	-0.026
Biome-humidforest	-0.0581	0.47051	-0.123
Biome-nonforest	0.10947	0.54142	0.202
Calibration-fossil	0.58433	0.29018	2.014
Calibration-geology	0.42563	0.46812	0.909
Calibration-mixed	0.74345	0.28134	2.643
Calibration-secondary	0.42094	0.3129	1.345

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.
The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S4d Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable dispersal ability removed

Formula: log(Dispersal.Time) ~ elevation +Dispersal.Direction + Biome + Calibration + (1 | Class/Family)

AIC	logLik	deviance	REMLdev
806.4	-386.2	756.1	772.4

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.39985	0.63234
Class	(Intercept)	0.20901	0.45717
Residual		0.66759	0.81706

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. error	t value
(Intercept)	15.10824	0.45332	33.33
elevation-Lowland	0.17656	0.15664	1.13
elevation-Lowland.Highland	0.12935	0.25679	0.5
elevation-Lowland.Montane	0.02369	0.18021	0.13
Dispersal.Direction-south.to.ı	-0.13141	0.13849	-0.95
Biome-dryforest	-0.6845	0.52201	-1.31
Biome-eurybiomic	0.24346	0.45265	0.54
Biome-forest	-0.17631	0.43577	-0.4
Biome-humidforest	-0.21213	0.42617	-0.5
Biome-nonforest	-0.08196	0.50138	-0.16
Calibration-fossil	0.56295	0.28979	1.94
Calibration-geology	0.44944	0.46611	0.96
Calibration-mixed	0.76649	0.27579	2.78
Calibration-secondary	0.39702	0.31114	1.28

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.

The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S4e Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable biome type removed

Formula: log(Dispersal.Time) ~ elevation+Origin+Dispersal.Ability+Calibration+ (1 | Class/Family)

AIC	logLik	deviance	REMLdev
803.8	-387.9	762.1	775.8

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.4325	0.65765
Class	(Intercept)	0.16893	0.41101
Residual		0.66874	0.81777

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. error	t value
(Intercept)	14.8175	0.3123	47.44
elevation-Lowland	0.1743	0.156	1.12
elevation-Lowland.Highland	0.174	0.2575	0.68
elevation-Lowland.Montane	-0.0144	0.1756	-0.08
Dispersal.Direction-south.to.n	-0.1198	0.1358	-0.88
Dispersal.Ability-moderate	0.1346	0.2963	0.45
Dispersal.Ability-poor	0.3585	0.306	1.17
Calibration-fossil	0.5657	0.2891	1.96
Calibration-geology	0.3044	0.4601	0.66
Calibration-mixed	0.7906	0.2768	2.86
Calibration-secondary	0.4207	0.3076	1.37

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.
The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S4f Terrestrial and freshwater taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable calibration type removed

Formula: log(Dispersal.Time) ~ elevation+Origin+Dispersal.Ability+Biome+(1 | Class/Family)

AIC	logLik	deviance	REMLdev
807.2	-388.6	763	777.2

Random effects:

Groups	Name	Variance	Std.Dev.
Family:Class	(Intercept)	0.39996	0.63242
Class	(Intercept)	0.25192	0.50192
Residual		0.67837	0.82363

Number of obs: 279, groups: Family:Class, 92; Class, 10

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	14.93755	0.52779	28.302
Elevation-Lowland	0.29634	0.15432	1.92
elevation-Lowland.Highland	0.22591	0.25659	0.88
elevation-Lowland.Montane	0.04615	0.17813	0.259
Dispersal.Direction-south.to.r	-0.15094	0.13991	-1.079
Dispersal.Ability-moderate	0.16087	0.2982	0.539
Dispersal.Ability-poor	0.4534	0.33726	1.344
Biome-dryforest	-0.26803	0.57214	-0.468
Biome-eurybiomic	0.66184	0.49669	1.332
Biome-forest	0.16838	0.48349	0.348
Biome-humidforest	0.15971	0.48017	0.333
Biome-nonforest	0.27619	0.5463	0.506

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables.
The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S5 Terrestrial and freshwater taxa GLMM model comparison
Model comparison of full model containing all variables vs a model with a variable removed

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Elevational Preference Removed	16	788.73	-378.36			
Full Model	19	792.87	-377.43	1.856	3	0.6029

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Dispersal Direction Removed	18	791.93	-377.97			
Full Model	19	792.87	-377.43	1.063	1	0.3026

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Dispersal Ability Removed	17	790.12	-378.06			
Full Model	19	792.87	-377.43	1.25	2	0.5353

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Biome Type Removed	14	790.15	-381.07			
Full Model	19	792.87	-377.43	7.28	5	0.2006

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Calibration Type Removed	15	792.99	-381.5			
Full Model	19	792.87	-377.43	8.123	4	0.08717

Table S5 Terrestrial and freshwater taxa GLMM model comparison
Model comparison of full model containing all variables vs a model with a variable removed

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Elevational Preference Removed	16	788.73	-378.36			
Full Model	19	792.87	-377.43	1.856	3	0.6029

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Dispersal Direction Removed	18	791.93	-377.97			
Full Model	19	792.87	-377.43	1.063	1	0.3026

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Dispersal Ability Removed	17	790.12	-378.06			
Full Model	19	792.87	-377.43	1.25	2	0.5353

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Biome Type Removed	14	790.15	-381.07			
Full Model	19	792.87	-377.43	7.28	5	0.2006

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Calibration Type Removed	15	792.99	-381.5			
Full Model	19	792.87	-377.43	8.123	4	0.08717

Table S6a Marine taxa - Generalized linear mixed model parameter estimates and likelihood scores using the variables dispersal ability and calibration type (full model)

Formula: log(Dispersal.Time) ~ Dispersal.Ability + Calibration + (1 | Class/Order/Family)

AIC	logLik	deviance	REMLdev
171.6	78.8	157.1	169.6

Random effects:

Groups	Name	Variance	Std.Dev.
Family:(Order:Class)	(Intercept)	0.12478	0.35324
Order:Class	(Intercept)	0.36113	0.60094
Class		0.25324	0.50323
Residual		0.26122	0.5111

Number of obs: 80, groups: Family:(Order:Class), 29; Order:Class, 17; Class, 7

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	1.1059	0.3293	3.358
Dispersal.Ability-moderate	-0.2902	0.6096	-0.476
Calibration-fossil	1.3776	0.295	4.669

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables. The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S6b Marine taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable dispersal ability removed

Formula: log(Dispersal.Time) ~ Calibration + (1 | Class/Order/Family)

AIC	logLik	deviance	REMLdev
170.6	-79.31	157.1	158.6

Random effects:

Groups	Name	Variance	Std.Dev.
Family:(Order:Class)	(Intercept)	0.1227	0.35029
Order:Class	(Intercept)	0.34852	0.59036
Class		0.19805	0.44502
Residual		0.26186	0.51172

Number of obs: 80, groups: Family:(Order:Class), 29; Order:Class, 17; Class, 7

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	1.0566	0.2915	3.625
Calibration-fossil	1.3469	0.2854	4.72

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables. The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S6c Marine taxa - Generalized linear mixed model parameter estimates and likelihood scores for the model with the variable calibration type removed

Formula: log(Dispersal.Time) ~ Dispersal.Ability + (1 | Class/Order/Family)

		AIC	logLik	deviance	REMLdev
		184.5	-86.25	173.1	172.5

Random effects:

Groups	Name	Variance	Std.Dev.
Family:(Order:Class)	(Intercept)	0.43065	0.65624
Order:Class	(Intercept)	0.50772	0.71255
Class		0.19064	0.43662
Residual		0.26078	0.51067

Number of obs: 80, groups: Family:(Order:Class), 29; Order:Class, 17; Class, 7

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	1.4704	0.347	4.237
Dispersal.Ability-moderate	0.4676	0.7062	0.662

Note: categorical variables with K levels are entered in the model as a sequence of K-1 variables. The coefficients correspond to the comparison of the reference level for each categorical variable.

Table S7 Marine taxa GLMM model comparison

Model comparison of full model containing all variables vs a model with a variable removed

	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Dispersal Ability Removed	6	169.13	-78.563			
Full Model	7	171.08	-78.54	0.0465	1	0.8293
	Df	AIC	logLik	Chisq	Chi Df	Pr(>Chisq)
Calibration Type Removed	6	185.12	-86.561			
Full Model	7	171.08	-78.54	16.043	1	<0.0000

Table S8. Survey of approximate ages of extant taxa reported from published phylogenies, the complete data is deposited at Dryad (http://datadryad.org).

Class : Order : Family	Taxon / clade (constituent species)	Crown age (MA)	Reference
Marine organisms			
Actinopterygii : Mugiliformes : Mugilidae	*Agonostomous monticola*	20.7	1
Actinopterygii : Perciformes : Carangidae	*Trachurus*	7.7	2
Actinopterygii : Perciformes : Chaetodontidae	*Chaetodon humeralis vs. C. ocellatus*	3.4	3
Actinopterygii : Perciformes : Cichlidae	*Andinoacara coeruleopunctatus*	5	4
Actinopterygii : Perciformes : Cichlidae	*Caquetaia umbrifera (Central America)*	33.89	5
Actinopterygii : Perciformes : Cichlidae	*Cichlasoma facetus*	19.56	5
Actinopterygii : Perciformes : Cichlidae	*'Heros' atromaculatus*	3.6	6
Actinopterygii : Perciformes : Cichlidae	Central American Heroini	54.15	6
Actinopterygii : Perciformes : Cichlidae	*Heros' festae* group	41.39	6
Actinopterygii : Perciformes : Gerridae	*Gerres cinereus vs. G. cinereus*	2.55	7
Actinopterygii : Perciformes : Haemulidae	*Anisotremus interruptus vs. A. surinamensis*	0.8	7
Actinopterygii : Perciformes : Haemulidae	*Anisotremus taeniatus vs. A. virginicus*	2.2	7
Actinopterygii : Perciformes : Lutjanidae	*Lutjanus argentiventris vs. L. apodus*	1.75	7
Actinopterygii : Perciformes : Mulloidichthys	*Mulloidichthys dentatus vs. M. martinicus*	0.65	7
Actinopterygii : Perciformes : Poeciliidae	*Pseudopeocillia festae*	22	4
Actinopterygii : Perciformes : Poeciliidae	*Neoheterandria elegans +N. tridentiger*	22	4
Actinopterygii : Perciformes : Poeciliidae	*Poecilia reticulata*	3	4
Actinopterygii : Perciformes : Poeciliidae	*Poecillia spp.*	27.8	8
Actinopterygii : Perciformes : Pomacanthidae	*Centropyge aurantonota + (C. loriculus, C. potteri)*	13.9	9
Actinopterygii : Perciformes : Pomacanthidae	*Pomacanthus zonipectus, P. parularcuatus*	19.9	9
Actinopterygii : Perciformes : Pomacanthidae	*Holacanthus passer + (H. bermudensis, H. ciliaris)*	5	9
Actinopterygii : Perciformes : Pomacentridae	*Abudefduf concolor vs. A. taurus*	0.7	7
Actinopterygii : Perciformes : Pomacentridae	*Abudefduf troshelii vs. A. saxatilis*	2.25	7
Actinopterygii : Perciformes : Serranidae	*Rypticus bicolor vs. R. saponaceus*	1.6	7

Actinopterygii : Perciformes : Serranidae	*Paranthias colonus vs. P. furcifer*	2.4	7
Actinopterygii : Perciformes :Labridae	*Halichoeres nicholsi vs. H. bivittatus clade*	3.55	7
Actinopterygii : Perciformes :Labridae	*Halichoeres dispilus vs. H. pictus*	5.1	7
Actinopterygii : Perciformes :Pomacentridae	*Chromis atrilobata vs. C. multilineata*	4.7	7
Actinopterygii : Perciformes :Priacanthidae	*Heteropriacanthus cruentatus vs. H. cruentatus*	5.35	7
Actinopterygii : Siluriformes : Heptapteridae	*Pimelodella chagresi*	3.5	10
Actinopterygii : Siluriformes : Heptapteridae	*Pimelodella chagresi*	1	10
Actinopterygii : Siluriformes : Heptapteridae	*Rhamdia guatemalensis, R. laticauda, R. cinerascens*	6.05	11
Actinopterygii :Tetraodontiformes: Balistidae	*Melichthys niger vs. M. niger*	0.1	7
Actinopterygii :Tetraodontiformes: Balistidae	*Diodon hystrix vs. D. hystrix*	0.3	7
Actinopterygii :Tetraodontiformes: Monocanthidae	*Alutera scripta vs. A. scripta*	0.45	7
Actinopterygii: Scorpaeniformes: Scorpaenidae	*Scorpaena mystes vs. S. plumieri*	2.75	7
Bivalvia : Arcoida : Arcidae	*Arca imbricata* EP6-8/WA6-10	3.3	12
Bivalvia : Arcoida : Arcidae	*Arca imbricata* EP6/WA7	3.5	12
Bivalvia : Arcoida : Arcidae	*Arca imbricata* EP3/WA4-5	14	12
Bivalvia : Arcoida : Arcidae	*Arca imbricata* EP9/WA11	14	12
Bivalvia : Arcoida : Arcidae	*Barbatia gradata, B. domingensis*	17.4	13
Chondrichthyes : Squatinifromes : Squatinidae	*Squatina californica, S. dumeril*	6.11	14
Crustacea: Decapoda: Alpheidae	*Sesarma rhizophorae vs. S. reticulatum cladec*	2.05	7
Crustacea: Decapoda: Alpheidae	*Alpheus antepenultimus A vs. A. chacei*	2.7	7
Crustacea: Decapoda: Alpheidae	*Sesarma (sulcatum, aequatoriale) vs. S. crassipes*	3.1	7
Crustacea: Decapoda: Alpheidae	*Alpheus rostratus vs. A. paracrinitus spot*	3.2	7
Crustacea: Decapoda: Alpheidae	*Alpheus colombiensis vs. A. estuarensis*	3.4	7
Crustacea: Decapoda: Alpheidae	*Alpheus websteri vs. A. websteri*	3.65	7
Crustacea: Decapoda: Alpheidae	*Alpheus cylindricus vs. A. cylindricus*	4.35	7
Crustacea: Decapoda: Alpheidae	*Synalpheus brevicarpus vs. S. brevicarpus*	4.35	7
Crustacea: Decapoda: Alpheidae	*Alpheus floridanus B' vs. A. floridanus B*	4.7	7
Crustacea: Decapoda:	*Alpheus canalis-sp.B(blue) = millsae vs. A. nuttingi*	4.7	7

Alpheidae			
Crustacea: Decapoda: Alpheidae	*Alpheus paracrinitus no spot vs. A. paracrinitus no spot*	4.75	7
Crustacea: Decapoda: Alpheidae	*Alpheus panamensis vs. A. formosus-sp.A*	4.75	7
Crustacea: Decapoda: Alpheidae	*Synalpheus digueti vs. S. minus*	4.75	7
Crustacea: Decapoda: Alpheidae	*Alpheus bouvieri vs. A. bouvieri*	5.5	7
Crustacea: Decapoda: Alpheidae	*Xiphopenaeus riveti vs. X. sp. 2*	5.55	7
Crustacea: Decapoda: Alpheidae	*Alpheus malleator vs. A. malleator*	5.75	7
Crustacea: Decapoda: Alpheidae	*Synalpheus fritzmuelleri vs.S. fritzmuelleri*	6.05	7
Crustacea: Decapoda: Alpheidae	*Penaeus vannamei vs. P. duorarum cladef*	6.05	7
Crustacea: Decapoda: Alpheidae	*Alpheus umbo vs. A. schmitti*	6.6	7
Crustacea: Decapoda: Alpheidae	*Alpheus saxidomus simus*	6.95	7
Crustacea: Decapoda: Alpheidae	*Alpheus floridanus A' vs. A. floridanus A*	7.55	7
Crustacea: Decapoda: Alpheidae	*Alpheus normanni vs. A. normanni Brazil*	7.75	7
Crustacea: Decapoda: Alpheidae	*Emerita rathbunae vs. E. brasiliensis cladeg*	7.9	7
Crustacea: Decapoda: Alpheidae	*Alpheus (naos, aequus) vs. A. christofferseni*	8.9	7
Crustacea: Decapoda: Alpheidae	*Alpheus cristulifrons vs. A. cristulifrons*	9.45	7
Crustacea: Decapoda: Alpheidae	*Austinixa felipensis vs. A. cristata clade*	9.75	7
Crustacea: Decapoda: Alpheidae	*Synalpheus bannerorum vs. S. dominicensis*	11.3	7
Echinodermata: Temnopleuroida:Toxopneustidae	*Tripneustes depressus-gratilla vs. T. ventricosus*	4.35	7
Echinoidea: Arbacioida:Arbaciidae	*Arbacia spatuligera vs. A. lixula*	6.75	7
Echinoidea: Spatangoida: Brissidae	*Meoma ventricosa grandis vs. M. ventricosa*	2.25	7
Echinoidea:Camarodonta:Echinometridae	*Echinometra vanbrunti vs. E. lucunter*	5.15	7
Echinoidea:Cidaroida:Cidaridae	*Eucidaris thouarsi vs. E. tribuloides*	4.75	7
Echinoidea:Diadematoida : Diadematidae	*Diadema mexicanum vs. D. antillarum*	2.1	7
Echinoidea:Diadematoida: Diadematidae	*Astropyga pulvinata vs. A. magnifica*	4.95	7
Echinoidea:Temnopleuroida: Toxopneustidae	*Lytechinus semituburculatus vs. L. variegatus-williamsi*	6.75	7
Gastropoda : Littorinimorpha : Littorinidae	*Littoraria rosewateri, L. tessellata*	24.2	15
Gastropoda : Littorinimorpha : Littorinidae	*Littoraria nebulosa + (L. varia, L. zebra, L. irrorara, L. variegata)*	25.7	15

Taxonomy	Species	Value	Ref
Gastropoda : Littorinimorpha : Littorinidae	*Littoraria irrorara, L. variegata*	8.5	15
Gastropoda : Littorinimorpha : Littorinidae	*Echinolittorina angustor, E. periciliata*	19.2	16
Gastropoda : Littorinimorpha : Littorinidae	*Echinolittorina interrupta + (E. aspera, E. dubiosa, E. tenuistriata)*	19	16
Gastropoda : Littorinimorpha : Littorinidae	*Echinolittorina riser + (E. apicina E. paytensis)*	14.2	16
Gastropoda : Littorinimorpha : Littorinidae	*Echinolittorina conspersa, C. modesta + E. ziczac*	15.5	16
Gastropoda : Littorinimorpha : Littorinidae	*Echinolittorina galapagiensis + (E. vermeiji, E. tuberculata, E. granosa)*	32.5	16
Gastropoda : Neritimorpha : Neritidae	*Nerita scabricosta, N. peloronta / N. versicolor*	19.4	17
Gastropoda : Neritimorpha : Neritidae	*Nerita funiculata, N. tessellata / N. fulgurans / N. senegalensis*	23.3	17
Gastropoda : Unranked : Bullidae	*Bulla gouldiana, B. punctulata + (B. mabillei)*	16.8	18
Gastropoda : Unranked : Conidae	*Conus bartschii, C. brunneus*	14.3	19
Gastropoda : Unranked : Conidae	*Conus regius, C. gladiator + (C. mus)*	6.9	19
Gastropoda : Unranked : Conidae	*Conus ermineus, C. purpurascens*	7.3	19
Gastropoda : Unranked : Muricidae	*Stramonita canaliculata, S. rustica, S. haemastoma*	13	20
Gastropoda : Unranked : Muricidae	*Stramonita brasiliensis, S. floridana, S. biseralis*	7	20
Gastropoda : Unranked : Cerithiidae	*Cerithium stercusmuscarum, C. lutosum*	3.7	21
Gastropoda : Unranked : Cerithiidae	*Cerithium atratum, C. uncinatum*	5.1	21
Gastropoda : Unranked : Potamididae	*Cerithidea montagnaei, c. scalariformis*	6.4	21
Hydrozoa : Anthomedusae : Hydridae	Ophioblennius steindachneri vs. O. atlanticus	12.4	22
Mammalia : Carnivora : Phocidae	*Histriophoca* vs. *Pagophilus*	3.4	23
Terrestrial organisms			
Amphibia : Anura : Brachycephalidae	*Pristimantis ridens*	17	24
Amphibia : Anura : Bufonidae	*Rhinella marina*	2.75	25
Amphibia : Anura : Dendrobatidae	*Phyllobates (P. lugubris, P. vittatus)*	3.17	26
Amphibia : Anura : Dendrobatidae	*Dendrobates granuliferus*	1.39	26
Amphibia : Anura : Dendrobatidae	*Dendrobates* I (*D. arboreus, D. pumilio, D. speciosus, D. vicentei*)	3.01	26
Amphibia : Anura : Dendrobatidae	*Colostethus pratti*	2.94	26
Amphibia : Anura : Dendrobatidae	*Dendrobates* II (*D. claudiae, D. fulguritus, D. minutus*)	9.31	26
Amphibia : Anura : Dendrobatidae	*Silverstoneia nubicola*	4.52	26

Amphibia : Anura : Dendrobatidae	*Silverstoneia flotator*	4.15	26
Amphibia : Anura : Dendrobatidae	*Colostethus panamensis*	3.37	26
Amphibia : Anura : Dendrobatidae	*Allobates talamancae*	3.17	26
Amphibia : Anura : Dendrobatidae	*Dendrobates auratus*	0.58	26
Amphibia : Anura : Eleutherodactylidae	*Craugastor (C. podiciferus, C. longirostris, C. pygmaeus, C. montanus)*	30.51	27
Amphibia : Anura : Eleutherodactylidae	*Eleutherodactylus (E. zeus, E. marnockii)*	19.05	27
Amphibia : Anura : Leptodactylidae	*Physalaemus pustulosus*	5.5	28
Amphibia : Anura : Microhylidae	Origin of clade containing *Elachistocleis, Gastrophryne, Hypopachus* vs	30.3	29
Amphibia : Caudata : Plethodontidae	South American *Bolitoglossa*	18	30
Amphibia : Caudata : Plethodontidae	*Oedipina (O. complex, O. parvipes)*	6	31
Arachnida : Araneae : Sicariidae	*Loxosceles reclusa* group	33	32
Arachnida : Pseudoscorpiones : Chernetidae	*Cordylochernes scorpioides*	10.88	33
Aves : Anseriformes : Anatidae	*Anas acuta & A. georgica*	1.33	34, 35
Aves : Anseriformes : Anatidae	*Anas americana & A. nassibilatrix*	0.08	34, 35
Aves : Anseriformes : Anatidae	*Anas flavirostris & A. carolinensis*	1.44	34, 35
Aves : Apodiformes : Trochilidae	*Eupherusa/Microchera/Elvira*	4.3	34, 36
Aves : Apodiformes : Trochilidae	*Bee Hummingbirds*	4.79	34, 36
Aves : Apodiformes : Trochilidae	*Mt. Gems & Bee Hummingbirds*	12.8	34, 36
Aves : Columbiformes : Columbidae	*Zenaida auriculata vs. Z. macroura/Z. graysoni*	1.48	37
Aves : Columbiformes : Columbidae	*Zenaida asiatica vs. Z. meloda*	1.25	37
Aves : Columbiformes : Columbidae	*Geotrygon chiriquensis vs. G. goldmani*	0.95	37
Aves : Columbiformes : Columbidae	*Leptotila verreauxi*	0.86	37
Aves : Columbiformes : Columbidae	*Leptotila cassini*	0.11	37
Aves : Columbiformes : Columbidae	*Leptotila verreauxi/L. jamaicensis vs. L. cassini/L. plumbeiceps/L. rufaxilla/L. megalura*	3.44	37
Aves : Coraciiformes : Motmotidae	*Baryphthengus ruficapillus/marti & B. martii*	3.24	38
Aves : Cuculiformes : Cuculidae	*Geococcyx velox/californianus & Neomorphus geoffroyi*	7.88	34
Aves : Cuculiformes : Cuculidae	*Piaya cayana*	1.12	39
Aves : Falconiformes :	*Micrastur semitorquatus*	0.4	40

Falconidae			
Aves : Falconiformes : Falconidae	*Micrastur ruficollis*	0.75	40
Aves : Galliformes : Cracidae	*Crax rubra & Crax SA clade*	2.44	41, 42
Aves : Passeriformes : Cardinalidae	*Cardinalis sinuatus/C. cardinalis & C. phoeniceus*	4.92	38
Aves : Passeriformes : Cardinalidae	*Caryothraustes canadensis & C. poliogaster*	1.3	38
Aves : Passeriformes : Cardinalidae	*Cyanocompsa cyanoides*	0.76	38
Aves : Passeriformes : Cardinalidae	*Granatellus sallaei/ venustus & G. pelzelni*	6.13	38
Aves : Passeriformes : Cardinalidae	*Pheucticus tibialis/chrysopeplus & P. aureoventris/chrysogaster*	1.32	38
Aves : Passeriformes : Cardinalidae	*Piranga flava*	3.34	34, 43
Aves : Passeriformes : Cardinalidae	*Piranga leucoptera*	0.73	34, 43
Aves : Passeriformes : Cardinalidae	*Piranga leucoptera & P. rubriceps*	3.7	34, 43
Aves : Passeriformes : Cardinalidae	*Rhodothraupis celaeno & Periporphyrus erythromelas*	5.2	38
Aves : Passeriformes : Cardinalidae	*Cyanocompsa*	6.06	34
Aves : Passeriformes : Cardinalidae	*Amaurospiza concolor & A. moesta/carrizalensis*	3.1	34
Aves : Passeriformes : Cinclidae	*Cinclus leucocephalus/schulzi & C. mexicanus*	4.66	34
Aves : Passeriformes : Corvidae	*Cyanocorax dickeyi & C. chrysops/cayanus*	2.11	34, 44
Aves : Passeriformes : Corvidae	*Cyanolyca pulchra & C. cucullata*	3.95	34, 44
Aves : Passeriformes : Corvidae	*Cyanolyca viridicyana/turcosa/armillata/pulchra/cucullata*	10.44	34, 44
Aves : Passeriformes : Cotingidae	*Querula purpurata*	0.64	39
Aves : Passeriformes : Emberizidae	*Arremenops tocuyensis & A. conirostris*	5.23	34
Aves : Passeriformes : Emberizidae	*Arremon aurantiirostris*	2.76	34
Aves : Passeriformes : Emberizidae	*Arremonops conirostris*	3.53	34
Aves : Passeriformes : Emberizidae	*Atlapetes*	3.72	34
Aves : Passeriformes : Emberizidae	*Arremon brunneinucha*	1.02	34, 45
Aves : Passeriformes : Emberizidae	*Arremon torquatus & A. torquatus/atricapillus*	3.79	34, 45
Aves : Passeriformes : Emberizidae	*Chlorospingus canigularis*	3.5	34, 45
Aves : Passeriformes : Emberizidae	*Chlorospingus flavigularis*	2.3	34, 46
Aves : Passeriformes : Emberizidae	*Chlorospingus opthalmicus*	3.32	34, 46
Aves : Passeriformes :	*Lysurus castaneiceps & L. crassirostris*	1.28	34, 47

Emberizidae			
Aves : Passeriformes : Emberizidae	*Arremon brunneinucha/virenticeps & A. torquatus/Arremon*	10.5	34, 47
Aves : Passeriformes : Fringillidae	*Carduelis notata & SA Carduelis*	1.55	34, 48
Aves : Passeriformes : Furnariidae	*Xenops minutus*	0.41	34
Aves : Passeriformes : Furnariidae	*Xiphorhynchus erythropygius*	0.79	34, 49
Aves : Passeriformes : Furnariidae	*Xiphorhynchus flavigaster & X. lachrymosus*	2.12	34, 49
Aves : Passeriformes : Furnariidae	*Xiphorhynchus susurrans*	1.05	38
Aves : Passeriformes : Furnariidae	*Automolus ochrolaemus*	3.06	39
Aves : Passeriformes : Furnariidae	*Dendrocincla fuliginosa vs. D. anabatina*	2.6	39
Aves : Passeriformes : Furnariidae	*Dendrocincla fuliginosa*	0.16	39
Aves : Passeriformes : Furnariidae	*Sclerurus mexicanus*	7.41	39
Aves : Passeriformes : Hirundinidae	*Notiochelidon pileata & Neochelidon tibialis*	2.86	34, 50
Aves : Passeriformes : Hirundinidae	*Petrochelidon fulva & P. rufocollaris*	1.62	34, 50
Aves : Passeriformes : Hirundinidae	*Stelgidopteryx serripennis & S. ruficollis*	3.81	34, 50
Aves : Passeriformes : Hirundinidae	*Tachycineta albilinea & T. albiventer*	2.3	34, 50
Aves : Passeriformes : Icteridae	*Icterus graceannae & I. pectoralis*	2.19	38
Aves : Passeriformes : Icteridae	*Icterus gularis & I. nigrogularis*	0.47	38
Aves : Passeriformes : Icteridae	*Icterus mesomelas*	0.31	34, 51
Aves : Passeriformes : Icteridae	*Molothrus ater & M. bonariensis*	1.13	34, 52
Aves : Passeriformes : Icteridae	*Psarocolius decumanus*	1.19	34, 53
Aves : Passeriformes : Icteridae	*Psarocolius montezuma & P. bifasciatus*	0.63	34, 53
Aves : Passeriformes : Icteridae	*Quiscalus lugubris & Q. major/mexicanus/niger*	1.05	38
Aves : Passeriformes : Icteridae	*South American clade of Black Birds*	6.53	34, 52
Aves : Passeriformes : Motacillidae	*Anthus spragueii & A. lutescens*	4.97	34, 54
Aves : Passeriformes : Parulidae	*Basileuterus culicivorus*	2	55
Aves : Passeriformes : Parulidae	*Myioborus South Am. clade (M. albifacies - M. brunniceps)*	3.72	56
Aves : Passeriformes : Parulidae	*Geothlypis aequinoctialis & G. poliocephala*	3.35	38
Aves : Passeriformes : Parulidae	*Geothlypis semiflava*	1.28	34, 57

Aves : Passeriformes : Parulidae	*Myioborus miniatus*	0.86	34, 56
Aves : Passeriformes : Parulidae	*Myioborus torquatus & M. melanocephalus/ornatus/albifrons*	2.54	34, 56
Aves : Passeriformes : Parulidae	*Phaeothlypis fulvicauda/rivularis*	2.45	34, 58
Aves : Passeriformes : Pipridae	*Lepidothrix coronata*	0.55	34, 59
Aves : Passeriformes : Polioptilidae	*Microbates cinereiventris*	1.69	38
Aves : Passeriformes : Polioptilidae	*Polioptila plumbea & P. plumbea*	1.66	34
Aves : Passeriformes : Polioptilidae	*Polioptila plumbea & P. plumbea/albiloris*	4.01	38
Aves : Passeriformes : Polioptilidae	*Ramphocaenus melanurus*	4.18	38
Aves : Passeriformes : Polioptilidae	*Polioptila dumicola/plumbea/lactea & P. albiloris/melanura/californica/nigriceps/plumbea/caerulea**	6.13	34
Aves : Passeriformes : Thamnophilidae	*Thamnophilus nigriceps vs. T. praecox*	1.1	60
Aves : Passeriformes : Thamnophilidae	*Thamnophilus atrinucha/bridgesi & T. bernardi*	4.2	34, 60
Aves : Passeriformes : Thamnophilidae	*Cymbilaimus lineatus*	0.24	39
Aves : Passeriformes : Thamnophilidae	*Myrmotherula axillaris*	0.25	39
Aves : Passeriformes : Thraupidae	*Diglosssa plumbea vs. D. baritula*	0.8	61
Aves : Passeriformes : Thraupidae	*Ramphocelus dimidiatus*	0.9	62
Aves : Passeriformes : Thraupidae	*Tachyphonus delatrii*	8.8	62
Aves : Passeriformes : Thraupidae	*Tachyphonus luctuosus*	5.6	62
Aves : Passeriformes : Thraupidae	*Lanio fulvus vs. L. leucothorax/L. aurantius*	4.6	62
Aves : Passeriformes : Thraupidae	*Eucometis penicillata*	4.2	62
Aves : Passeriformes : Thraupidae	*Tachyphonus rufus*	3.7	62
Aves : Passeriformes : Thraupidae	*Heterospingus rubrifrons & H. xanthopygius*	1	34, 62, 63
Aves : Passeriformes : Thraupidae	*Saltator atripennis & S. atriceps*	3.08	38
Aves : Passeriformes : Thraupidae	*Saltator grandis/coerulescens & S. coerulescens/striatipectus*	3.85	34
Aves : Passeriformes : Thraupidae	*Saltator grossus*	0.51	34
Aves : Passeriformes : Thraupidae	*Saltator maximus*	0.56	38
Aves : Passeriformes : Thraupidae	*Tangara fucosa & T. dowii*	3.14	34, 64
Aves : Passeriformes : Thraupidae	*Tangara inornata & T. mexicana*	2.42	34, 64
Aves : Passeriformes :	*Ramphocelus passerinii/costaricensis & R.*	2.98	34, 65

Thraupidae	*icteronotus*		
Aves : Passeriformes : Thraupidae	*Chlorophanes spiza*	0.43	39
Aves : Passeriformes : Thraupidae	*Tangara gyrola*	0.49	39
Aves : Passeriformes : Tityridae	*Schiffornis turdina*	0.62	34, 66
Aves : Passeriformes : Tityridae	*Tityra semifasciata*	0.71	39
Aves : Passeriformes : Troglodytidae	*Campylorhynchus chiapensis & C. griseus*	1.11	38
Aves : Passeriformes : Troglodytidae	*Cantorchilus nigricapillus*	0.87	38
Aves : Passeriformes : Troglodytidae	*Henicorhina leucophrys*	2.67	34
Aves : Passeriformes : Troglodytidae	*Henicorhina leucophrys & H. leucosticta*	5.07	34
Aves : Passeriformes : Troglodytidae	*Henicorhina leucosticta*	4.03	38
Aves : Passeriformes : Troglodytidae	*Pheugopedius sclateri & P. felix*	1.15	38
Aves : Passeriformes : Troglodytidae	*Thryothorus thoracicus & T. leucopogon*	2.15	34, 67
Aves : Passeriformes : Troglodytidae	*Troglodytes aedon*	2.14	38
Aves : Passeriformes : Trolodytidae	*Campylorhynchus (Basal NA and SA split)*	7.07	34
Aves : Passeriformes : Trolodytidae	*Troglodytes rufociliatus & T. ochraceus/rufulus/solstitialis*	4.35	34
Aves : Passeriformes : Trolodytidae	*Micorcerculus marginatus*	4.25	39
Aves : Passeriformes : Turdidae	*Myadestes melanops & M. coloratus*	0.85	34, 68
Aves : Passeriformes : Turdidae	*Turdus albicollis & T. assimilus*	3.97	34, 69
Aves : Passeriformes : Turdidae	*Cichlopsis/Entomodestes & Catharus clade*	6.51	34, 70
Aves : Passeriformes : Tyrannidae	*Mionectes oleagineus (node C)*	0.2	71
Aves : Passeriformes : Tyrannidae	*Mionectes oleagineus (SW + Central Panama clade)*	0.5	71
Aves : Passeriformes : Tyrannidae	*Mionectes oleagineus (NW Panama + SE Mexico)*	0.1	71
Aves : Passeriformes : Tyrannidae	*Elaenia flavogaster*	0.66	34, 72
Aves : Passeriformes : Tyrannidae	*Elaenia frantzii & E. pallatangae*	1.96	34, 72
Aves : Passeriformes : Tyrannidae	*Myiarchus tuberculifer*	0.48	34, 73
Aves : Passeriformes : Tyrannidae	*Myiarchus tyrannulus*	0.52	34, 73
Aves : Passeriformes : Tyrannidae	*Attila spadiceus*	1.83	39
Aves : Passeriformes : Tyrannidae	*Colonia colonus*	0.44	39

Aves : Passeriformes : Vireonidae	*Cyclarhis gujanensis*	2.94	38
Aves : Passeriformes : Vireonidae	*Hylophilus decurtatus*	2.72	34
Aves : Passeriformes : Vireonidae	*Hylophilus ochraceiceps*	2.23	38
Aves : Passeriformes : Vireonidae	*Vireo leucophrys & V. chiriquensis*	1.24	34
Aves : Passeriformes : Vireonidae	*Vireo olivaceus & V. flavoviridis*	2.63	34
Aves : Picidae : Picinae	*Veniliornis South Am, clade (V. affinis - P. mixtus)*	5.1	74
Aves : Picidae : Picinae	Colaptes South Am. clade	3.6	75
Aves : Piciformes : Bucconidae	*Notharchus tectus*	3.09	38
Aves : Piciformes : Ramphastidae	*Aulacorhynchus prasinus*	4.17	34, 76
Aves : Piciformes : Ramphastidae	*Ramphastos swaninsonii & R. ambiguus*	0.38	34, 77
Aves : Piciformes : Ramphastidae	Pteroglossus frantzii & P. sanguineus/erythropygius	0.4	34, 78
Aves : Piciformes : Ramphastidae	*Pteroglossus frantzii/sanguineus/erythropygius/torquatus*	1	81
Aves : Piciformes : Semnornithidae	*Semnornis frantzii & S. ramphastinus*	5.05	34, 39
Aves : Psittaciformes : Psittacidae	*Brotogeris jugularis vs. Brotogeris pyrrhopterus*	2.01	81
Aves : Psittaciformes : Psittacidae	*Amazona autumnalis*	1.23	34, 82
Aves : Psittaciformes : Psittacidae	*Amazona farinosa*	2.71	34, 82
Aves : Psittaciformes : Psittacidae	*Amazona ochrocephala*	1	34, 82, 83
Aves : Psittaciformes : Psittacidae	*Forpus cyanopygius & F. passeririnus/xanthops/xanthoptergyius/conspicillatus/ coelestis*	3.22	38
Aves : Psittaciformes : Psittacidae	*Pionus senilis & P. chalcopterus*	0.31	38
Aves : Psittaciformes : Psittacidae	*Pyrilia haematotis & P. coccinicollaris*	2.62	34, 84
Aves : Psittaciformes : Psittacidae	*Pyrrhura eisenmanni & Pyrrhura picta/emma*	0.64	34, 84
Aves : Psittaciformes : Psittacidae	*Pyrrhura hoffmanni & P. rhodocephala*	1.14	34, 84
Aves : Strigiformes : Strigidae	*Aegolius harrisii & A. ridgwayi/acadicus*	7.37	34
Aves : Trogoniformes : Trogonidae	*T. violaceus/T. curucui/T. surrucura*	3.1	85
Aves : Trogoniformes : Trogonidae	*Trogon viridis*	2.4	85
Aves : Trogoniformes : Trogonidae	*Trogon clathratus*	4.8	85
Aves : Trogoniformes : Trogonidae	*Trogon personatus*	8.9	85
Aves : Trogoniformes : Trogonidae	*Trogon collaris*	1.8	85

Aves : Trogoniformes : Trogonidae	*Pharomachrus antisianus/auriceps/fulgidus/pavoninus*	4.76	34, 85
Aves : Trogoniformes : Trogonidae	*Trogon rufus*	3.93	38
Aves: Piciformes : Capitonidae	*Capito squamatus & C. maculicoronatus*	0.77	34, 39
Aves: Piciformes : Capitonidae	*Eubucco bourcierii*	0.04	34, 39
Dicot : Asterales : Boranginaceae	*Lithospermum*	3.75	86
Dicot : Asterales : Boranginaceae	*Heliotropium curassavicum*	23	87
Dicot : Asterales : Boranginaceae	*Heliotropium molle*	8	87
Dicot : Asterales : Lobelioideae	*Lobelia laxiflora*	7	88
Dicot : Brassicales : Caricaceae	South American clade	23	89
Dicot : Caryophyllales : Cactaceae	North American *Opunitia* clade	5.12	90
Dicot : Caryophyllales : Polygonaceae	*Ruprechtia* South Am. clade	1.2	91
Dicot : Chloranthales : Chloranthaceae	*Hedyosmum (H. costaricense - H. racemosum)*	19.4	92
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos warmingii* to *Sicyos baderoa*	4.5	93
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos polyacanthus*	3	93
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos acarieanthus - S. quinquelobatus*	1.7	93
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos malvifolius*	2.8	93
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos longisetosus*	3.9	93
Dicot : Cucurbitales : Cucurbitaceae	*Sicyos andreanus*	12.3	93
Dicot : Cucurbitales : Cucurbitaceae	*Cyclanthera carthagenensis - C. australis*	9.4	93
Dicot : Dipsacales : Valerianaceae	*Valeriana*	23.75	94
Dicot : Fabales : Fabaceae : Faboideae	*Vicia montevidensis + V. stenophylla*	2.6	95
Dicot : Fabales : Fabaceae : Faboideae	*Vicia humilis + V. vicina*	2.65	95
Dicot : Fabales : Fabaceae : Faboideae	*Vicia gigantea*	0.75	95
Dicot : Fabales : Fabaceae : Faboideae	*Lathyrus pusillus*	2.5	95
Dicot : Fabales : Fabaceae : Faboideae	*Chaetocalyx* (South Am. clade)	5.9	96
Dicot : Fabales : Fabaceae : Faboideae	*Ateleia* ("RESI" clade)	4.24	97
Dicot : Fabales : Fabaceae : Faboideae	*Ateleia* ("GUAR" clade)	0.52	97
Dicot : Fabales : Fabaceae : Faboideae	*Lupinus* (Andean polytomy)	1.47	98

Dicot : Fabales : Fabaceae : Faboideae	*Phaseolus lunatus* Andean	1.04	99
Dicot : Fabales : Fabaceae : Faboideae	*Platymiscium pinnatum ssp. polystachyum*	3.9	100
Dicot : Fabales : Fabaceae : Faboideae	*Platymiscium yucatanum - P. trifoliatum*	5.9	100
Dicot : Gentianales : Apocynaceae	*Cynanchum*	18.6	101
Dicot : Gentianales : Rubiaceae	*Cinchona pubescens*	3	102
Dicot : Gentianales : Rubiaceae	*Isertia (I. hypoleuca, I. haenkeana, I. laevis)*	14.8	102
Dicot : Lamiales : Gesneriaceae	Gloxineae widely distributed clade	6.5	103
Dicot : Lamiales : Gesneriaceae	Gloxineae Central American clade	17.5	103
Dicot : Lamiales : Gesneriaceae	Episcieae clade	11	103
Dicot : Lamiales : Lamiaceae	Clades B and C	12.65	104
Dicot : Lamiales : Lamiaceae	*Salvia polystachia* (node IV)	9.5	105
Dicot : Lamiales : Lamiaceae	Node III	11	105
Dicot : Lamiales : Lamiaceae	Node II	2.5	105
Dicot : Lamiales : Lamiaceae	Node III	6	105
Dicot : Laurales : Lauraceae	*Ocotea* complex (*Endlicheria chalisea - Pleurothyrium insigne*)	18.5	106
Dicot : Magnoliales : Annonaceae	*Anaxagorea*	40	107
Dicot : Magnoliales : Annonaceae	*Cremastosperma*	7.17	108
Dicot : Magnoliales : Annonaceae	*Guatteria* SAC clade (*G. hyposericea - G. megalophylla*)	6.75	109
Dicot : Magnoliales : Annonaceae	*Klarobelia*	7.69	109
Dicot : Magnoliales : Annonaceae	*Malmea*	9.54	109
Dicot : Magnoliales : Annonaceae	*Mosannona costaricensis*	17.5	110
Dicot : Malpigiales : Chrysobalanaceae	*Chrysobalanaceae*	47	111
Dicot : Malpigiales : Clusiaceae	*Symphonia* (trans-Andes clade)	5.03	112
Dicot : Mrytales : Melastomataceae	*Rhexia / Arthrostemma* divergence	23	113
Dicot : Piperales : Piperaceae	*Tildenia* (Central Am. clade)	20.6	114
Dicot : Ranunculales : Ranunculaceae	*Callianthemoides - Peltocalathos* (node 14)	8.67	115
Dicot : Rhamnales : Vitaceae	*Cissus gongylodes*	12	116
Dicot : Rhamnales : Vitaceae	*Cissus erosa, C. ulmifolia, C. obliqua*	19	116
Dicot : Rhamnales : Vitaceae	*Cissus amazonica + C. pseudoverticillata*	9.75	116
Dicot : Sapindales : Bursuraceae	*Protieae*	37	117
Dicot : Sapindales : Meliaceae	*Cedrela I (C. fissilis, C. balansae, C. sp5, C. weberbaueri, C. sp2)*	15.7	118

Dicot : Sapindales : Meliaceae	*Cedrela II (C. angustifolia, C. montana)*	6.9	118
Dicot : Sapindales : Simaroubaceae	*Simarouba amara, S. versicolor*	9.3	119
Dicot : Sapindales : Simaroubaceae	*Castela erecta, C. refusa*	5	119
Dicot : Scrophulariales : Bignoniaceae	*Tanaecium crucigerum*	23	120
Dicot : Vitales : Vitaceae	Node 3	30.5	121
Fungi : Lecanorales : Parmeliaceae	*Xanthoparmelia* SA clade	3.44	122
Insecta : Coleoptera : Chrysomelidae	*Stator limbatus*	2.4	123
Insecta : Diptera: Culicidae	*Anopheles albimanus*	0.85	124
Insecta : Hymenoptera : Apidae	*Coccineobombus - Rubicundobombus*	7.2	125
Insecta : Hymenoptera : Apidae	*Funebribombus funebris*	7	125
Insecta : Hymenoptera : Apidae	*Robustobombus*	3.1	125
Insecta : Hymenoptera : Apidae	*Robustobombus volucelloides*	0.6	125
Insecta : Hymenoptera : Apidae	*Fervidobombus opifex, F. bellicosus*	1.5	125
Insecta : Hymenoptera : Apidae	*Fervidobombus atratus, F. transversalis, F. brasilensis*	2	125
Insecta : Hymenoptera : Apidae	*Euglossa heterosticta - E. dissimula*	5	126
Insecta : Hymenoptera : Apidae	*Eulaema*	13	126
Insecta : Hymenoptera : Apidae	*Melikerria beecheii*	3.5	127
Insecta : Hymenoptera : Apidae	*Michmelia fasciata*	5.5	127
Insecta : Hymenoptera : Apidae	*Nannotrigona perilampoides*	4	127
Insecta : Hymenoptera : Apidae	*Noguierapis mirandula*	20.5	127
Insecta : Hymenoptera : Apidae	*Oxytrigona mediorufa + O. mellicolor*	4.5	127
Insecta : Hymenoptera : Apidae	*Partamona musarum + P. orizabaensis polytomy*	4	127
Insecta : Hymenoptera : Apidae	*Plebeia frontalis*	13	127
Insecta : Hymenoptera : Apidae	*Scaptotrigona meciana + S. pectoralis*	2	127
Insecta : Hymenoptera : Apidae	*Tetragona perangulata + T. ziegleri*	16	127
Insecta : Hymenoptera : Apidae	*Trigona fulviventris*	5	127
Insecta : Hymenoptera : Apidae	*Trigona fuscipennis*	3	127
Insecta : Hymenoptera : Apidae	*Trigona nigerrima, T. corvina*	8	127
Insecta : Hymenoptera :	*Trigonisca buyssoni*	9	127

Apidae			
Insecta : Hymenoptera : Apidae	*Battus*	21.66	128
Insecta : Hymenoptera : Apidae	*Euryades & Parides*	27.45	128
Insecta : Lepidoptera : Nymphaelidae	Limenitis (Neartic/Palaearctic)	9.95	127
Insecta : Lepidoptera : Nymphaelidae	clade of *Ithomia patilla - I.heraldica*	5.29	129
Insecta : Lepidoptera : Nymphaelidae	*Ithomia xenos*	5.48	130
Insecta : Lepidoptera : Nymphaelidae	*Ithomia terra*	4.48	130
Insecta : Lepidoptera : Nymphaelidae	*Napeogenes peridia*	5.65	130
Insecta : Lepidoptera : Nymphaelidae	*Napeogenes tolosa*	6.95	130
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Insecta: Orthoptera: Acrididae	*Trimerotropis pallidipennis* NA/*T. saxatilis* vs *T. ochraceipennis*/*T. pallidipennis* SA	0.7	129
Mammalia : Artiodactyla : Cervidae	Cervidae (South American clade)	4.15	130
Mammalia : Carnivora : Canidae	*South American endemic clade*	4.25	131
Mammalia : Carnivora : Felidae	*Leopardus tigrinus*	3.7	132
Mammalia : Carnivora : Mustelidae	*Lontra longicaudis, L. felina*	1.5	133
Mammalia : Carnivora : Mustelidae	*Pteronura brasiliensis vs.Clade at Node 8*	7.7	133
Mammalia : Carnivora : Procyonidae	*Nasua narica vs. N. nasua*	7.5	134
Mammalia : Carnivora : Procyonidae	*Procyon cancrivorus vs. P. lotor*	5.35	134
Mammalia : Carnivora: Ursidae	*Tremarctos ornatus vs. Arctodus simus*	5.66	135
Mammalia : Chiroptera : Phyllostomidae	*Desmodus rotundus*	1	136
Mammalia : Chiroptera : Emballonuroidea	*Centronycteris centralis*	5.5	137
Mammalia : Chiroptera : Emballonuroidea	*Cormura brevirostris*	19.4	137
Mammalia : Chiroptera : Emballonuroidea	*Cyttarops alecto*	14.6	137
Mammalia : Chiroptera : Emballonuroidea	*Diclidurus albus*	2	137
Mammalia : Chiroptera : Emballonuroidea	*Peropteryx kappleri*	1	137
Mammalia : Chiroptera : Emballonuroidea	*Rhynchonycteris naso*	19	137
Mammalia : Chiroptera : Emballonuroidea	*Saccopteryx bilineata, S. leptura*	5.1	137
Mammalia : Chiroptera : Vespertilionidae	*Myotis ruber, M. riparius + (M. keaysi)*	2.8	138

Mammalia : Primates: Atelidae	*Alouatta pigra, A. palliata*	3	139
Mammalia : Primates: Atelidae	*Ateles geoffroyi (- subsp. robsutus)*	1.29	140
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Mammalia : Rodentia : Cricetidae	*Sigmodontinae*	12	143
Mammalia : Rodentia : Sciuridae	*Sciurus South American Clade*	2.8	144
Monocot : Alismatales : Hydrocharitaceae	*Elodea*	2.5	145
Monocot : Arecales : Arecaceae	*Astrocaryum (A. murumuru - A.paramaca)*	22	146
Monocot : Arecales : Arecaceae	*Astrocaryum standleyanum*	6	147
Monocot : Arecales : Arecaceae	*Chamaedorea (C. linearis, C. fragrans)*	9	148
Monocot : Arecales : Arecaceae	*Copernicia* crown clade	16.34	149
Monocot : Arecales : Arecaceae	*Geonoma (G. hugonis, G. epetiolata, G. monospatha, G. longevaginata, G. scoparia, G. poeppigiana, G. undata, G. jussieuana, G. orbignyana, G. weberbaueri)*	8.8	150
Monocot : Arecales : Arecaceae	*Phytelepheae (Phytelephus schottii, P. seemanii, P. macrocarpa, P. tenuicaulis, P. aequatorialis, P. turnacana, Amandra decasperma, Aphandra natalia)*	17	151
Monocot : Poales : Bromeliaceae	*Fosterella micrantha*	0.6	152
Monocot : Poales : Bromeliaceae	*Pitcairnia wendlandii + P. orchidifolia*	4.5	153
Monocot : Poales : Bromeliaceae	*Tillsandia utriculata - T. viridiflora* polytomy	6	153
Monocot : Poales : Cyperaceae	*Oreobolus* South American clade	3.7	154
Monocot : Poales : Poaceae	*Festuca calligera + (F. anicola - H. fragilis)*	3.1	155
Monocot : Poales : Poaceae	*Festuca purpurascens + F. subantartica*	2	155
Pteridophytes : Polypodiales : Dryopteridaceae	SA members of clade IV	9	156
Reptilia : Squamata : Boidae	*Corallus annulatus*	10.1	157
Reptilia : Squamata : Boidae	*Corallus ruschenbergerii*	1.5	157
Reptilia : Squamata : Colubridae	*Leptodeira*	3.91	158
Reptilia : Squamata : Viperidae	*Atropoides + Cerrophidion*	10	159
Reptilia : Squamata : Viperidae	*Crotalus durissus*	1.54	160
Reptilia : Squamata : Viperidae	*Bothrops diporus - B. taeniatus*	12.5	161
Reptilia : Squamata : Viperidae	*Porthidium (node 1)*	2.5	161
Reptilia : Squamata : Viperidae	*Lachesis muta*	7.25	161

Reptilia : Squamata : Viperidae	*Lachesis stenophrys*	7.5	162
Reptilia : Testudines : Emydidae	*Trachemys callirostris*	0.98	163
Reptilia : Testudines : Emydidae	*Trachemys adiutrix vs. T. dorbigni*	2.28	163
Reptilia : Testudines : Geoemydidae	*Rhinoclemmys nasuta vs R. areolata/R. diademata/R. punctularia/R. funerea/R. melanosterna/R. annulata*	20.1	164
Reptilia : Testudines : Geoemydidae	*Rhinoclemmys diademata, R. punctularia, R. funerea, P. melanosterna (node 6)*	5.3	164
Reptilia : Testudines : Geoemydidae	*Rhinoclemmys annulata vs. R. pulcherrima*	15.3	164
Reptilia: Crocodylia: Alligatoridae	Caiman crocodilus (Central American Crown Age)	2.7	165
Reptilia:Squamata: Phyllodactylidae	*Phyllodactylus reissii vs North American Phyllodactylus clade*	23	166
Reptilia:Squamata: Sphaerodactylidae	*Gonatodes albogularis vs. Gonatodes vittatus*	13	167

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Table S9. List of journals used for the present study.

Name of scientific journal
American Journal of Botany
Biological Journal of the Linnean Society
BMC Biology
BMC Evolution Biology
Botanical Journal of the Linnean Society
Cladistics
Evolution
International Journal of Primatology
Journal of Biogeography
Journal of Evolutionary Biology
Journal of Mammalian Evolution
Journal of Zoological Systematics and Evolutionary Research
Molecular Biology and Evolution
Molecular Ecology
Molecular Phylogenetics and Evolution
Nature
Organisms Diversity and Evolution
Philosophical Transactions of the Royal Society B
Proceedings of the National Academy of Sciences, USA
Proceedings of the Royal Society B
Science
Systematic Biology
Systematic Botany
Taxon
The American Naturalist
The Auk
Zoological Journal of the Linnean Society

Table S10. Migration models estimated from analysis of phylogenetic data.

Data set	Sample size	Families	Model	d.f.	log likelihood	AICc	stepwise deltaAICc	delta AICc*	AICc threshold
All taxa	426	138	constant rate	1	453.175	-904.34		965.14	6.081
			2 rates	3	865.231	-1724.405	820.065	145.075	
			3 rates	5	921.034	-1831.924	107.519	37.556	
			4 rates	7	937.353	-1860.438	28.514	9.042	
			5 rates	**9**	**943.957**	**-1869.48**	**9.042**	**0**	
			6 rates	11	946.148	-1869.658	0.178	-0.178	
			exponential	2	458.689	-913.35		956.13	
			shift at 3.5	2	670.723	-1337.417		532.063	
NA -> SA	144	60	constant rate	1	17.232	-32.436		248.492	5.984
			2 rates	3	127.556	-248.941	216.505	31.987	
			3 rates	**5**	**145.682**	**-280.928**	**31.987**	**0**	
			4 rates	7	149.98	-285.136	4.208	-4.208	
			exponential	2	20.925	-37.765		243.163	
			shift at 3.5	2	78.938	-153.792		127.136	
SA -> NA	154	62	constant rate	1	7.131	-12.235		377.276	5.995
			2 rates	3	179.948	-353.737	341.502	35.774	
			3 rates	**5**	**199.958**	**-389.511**	**35.774**	**0**	
			4 rates	7	205.088	-395.408	5.897	-5.897	
			exponential	2	14.706	-25.333		364.178	
			shift at 3.5	2	102.847	-201.615		187.896	
Marine (Atlantic - Pacific)	86	13	constant rate	1	-2.313	6.673		94.847	5.853
			2 rates	3	38.810	-71.327	78.000	16.847	
			3 rates	5	44.363	-77.977	6.650	10.197	
			4 rates	**7**	**51.805**	**-88.174**	**10.197**	**0**	
			5 rates	9	53.35	-86.331	-1.843	1.843	
			exponential	2	-0.902	5.949		94.123	
			shift at 3.5	2	5.413	-6.681		81.493	
Terrestrial tetrapods	59	29	constant rate	1	-23.673	49.416		63.754	5.675
			2 rates	3	7.02	-7.604	57.02	6.734	

			3 rates	**5**	**12.735**	**-14.338**	**6.734**	**0**	
			4 rates	7	14.22	-12.244	-2.094	2.094	
			exponential	2	-21.867	47.948		62.286	
			shift at 3.5	2	-9.674	23.563		37.901	
Reptiles and amphibians	35	15	constant rate	1	-32.32	66.761		22.364	5.210
			2 rates	**3**	**-18.811**	**44.397**	**22.364**	**0**	
			3 rates	5	-15.594	43.258	1.139	-1.139	
			exponential	2	-30.999	66.372		21.975	
			shift at 3.5	2	-26.671	57.718		13.321	
Fresh water fish	14	4	constant rate	1	-31.534	65.402		3.937	2.872
			2 rates	**3**	**-26.533**	**61.465**	**3.936**	**0**	
			3 rates	5	-24.241	65.983	**-4.518**	4.518	
			exponential	2	-31.700	68.492		7.027	
			shift at 3.5	2	-30.904	66.898		5.433	
Arthropods	35	7	constant rate	1	-37.26	76.642		37.571	5.210
			2 rates	**3**	**-16.148**	**39.071**	**37.571**	**0**	
			3 rates	5	-12.573	37.215	1.856	-1.856	
			exponential	2	-35.519	75.414		36.343	
			shift at 3.5	2	-33.065	70.506		31.435	
Plants	74	31	constant rate	1	-40.41	82.876		85.756	5.793
			2 rates	3	-3.479	13.301	69.575	16.181	
			3 rates	**5**	**6.881**	**-2.88**	**16.181**	**0**	
			4 rates	7	9.342	-2.987	0.107	-0.107	
			exponential	2	-38.638	81.446		84.326	
			shift at 3.5	2	-31.987	68.144		71.024	
Birds	158	36	constant rate	1	236.021	-470.017		188.115	5.999
			2 rates	3	319.657	-633.158	163.141	24.974	
			3 rates	5	330.176	-649.958	16.8	8.174	
			4 rates	**7**	**336.439**	**-658.132**	**8.174**	**0**	
			5 rates	9	338.829	-658.443	0.311	-0.311	
			exponential	2	238.056	-472.035		186.097	

			shift at 3.5	2	293.5	-582.923		75.209	
Mammals	24	14	constant rate	1	-18.893	39.968		17.532	4.585
			2 rates	**3**	**-7.618**	**22.436**	**17.532**	**0**	
			3 rates	5	-6.225	25.783	-3.347	3.347	
			exponential	2	-17.809	40.19		17.754	
			shift at 3.5	2	-13.78	32.132		9.696	
Mollusc + Urchin	32	13	constant rate	1	-32.496	67.126		12.252	5.090
			2 rates	3	-25.188	57.232	9.894	2.358	
			3 rates	**5**	**-21.283**	**54.874**	**2.358**	0	
			4 rates	7	-16.522	51.71	3.164	-3.164	
			exponential	2	-32.112	68.638		13.764	
			shift at 3.5	2	-32.445	69.304		14.43	
Low dispersal ability	61	30	constant rate	1	-53.666	109.4		72.213	5.695
			2 rates	3	-23.431	53.283	56.117	16.096	
			3 rates	**5**	**-13.048**	**37.187**	**16.096**	**0**	
			4 rates	7	-9.672	35.457	1.73	-1.73	
			exponential	2	-51.337	106.88		69.693	
			shift at 3.5	2	-43.44	91.087		53.9	
Medium dispersal ability	78	36	constant rate	1	-38.488	79.029		92.131	5.815
			2 rates	3	0.479	5.365	73.664	18.467	
			3 rates	**5**	**11.968**	**-13.102**	**18.467**	**0**	
			4 rates	7	14.598	-13.595	0.493	-0.493	
			exponential	2	-36.483	77.126		90.228	
			shift at 3.5	2	-28.173	60.505		73.607	
High dispersal ability	287	77	constant rate	1	298.351	-594.688		634.561	6.061
			2 rates	3	572.303	-1138.522	543.834	90.727	
			3 rates	5	603.258	-1196.303	57.781	32.946	
			4 rates	**7**	**621.825**	**-1229.249**	**32.946**	0	
			5 rates	9	626.939	-1235.229	5.98	-5.98	
			exponential	2	303.134	-602.226		627.023	
			shift at 3.5	2	457.524	-911.005		318.244	

The results of migration rate analyses are shown for the full dataset, and several subsets defined by direction of migration, habitat, taxonomic group. Different migration models were compared by AICc values. To determine the number of rate shifts supported by the data we optimized models with increasing number of rate shifts using a stepwise AICc approach, i.e. new rate shifts were added to the model until the improvement in AICc score was lower than a threshold estimated from simulations (see text for more details). The 'stepwise deltaAICc' column shows the difference in AICc scores between the current migration model and the previous, i.e. with one fewer rate shift. Additionally, we optimized a migration model with exponentially increasing rates and a "Standard" model (assuming one rate shift fixed at time 3.5 Ma). These models were rejected by AICc in favor of models with one or more rate shifts. The overall preferred model, used for parameter estimation, is highlighted in bold and delta-AICc scores are calculated with respect to the preferred model.