Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange

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The interchange between the previously disconnected faunas of North and South America was a massive experiment in biological invasion. A major gap in our understanding of this invasion is why there was a drastic increase in the proportion of mammals of North American origin found in South America. Four nonmutually exclusive mechanisms may explain this asymmetry: 1) Higher dispersal rate of North American mammals toward the south, 2) higher origination of North American immigrants in South America, 3) higher extinction of mammals with South American origin, and 4) similar dispersal rate but a larger pool of native taxa in North versus South America. We test among these mechanisms by analyzing ~20,000 fossil occurrences with Bayesian methods to infer dispersal and diversification rates and taxonomic selectivity of immigrants. We find no differences in the dispersal and origination rates of immigrants. In contrast, native South American mammals show higher extinction. We also find that two clades with North American origin (Carnivora and Artiodactyla) had significantly more immigrants in South America than other clades. Altogether, the asymmetry of the interchange was not due to higher origination of immigrants in South America as previously suggested, but resulted from higher extinction of native taxa in southern South America. These results from one of the greatest biological invasions highlight how biogeographic processes and biotic interactions can shape continental diversity.

America | biogeography | biotic interchange | diversification | mammals

The Great American Biotic Interchange (GABI) occurred between the previously isolated biota of North and South America as facilitated by the formation of the Isthmus of Panama (1). The GABI is a textbook example of a biological invasion in evolutionary time (2, 3). For nonmarine mammals the event took place from the late Miocene (~10 million y ago; Ma) to the late Pleistocene (0.126 to 0.01 Ma), with the peak in the Pleistocene (2.5 to 0.01 Ma) (4, 5). Seminal works propose that mammal interchange was initially symmetrical (6, 7), but that in the Pleistocene an increasing dominance of mammals of North American origin is found in South America (6, 7). This asymmetry puzzle has long-remained an unanswered riddle in the field of biogeography (8). Deciphering the mechanisms underlying such asymmetry would shed light on the dynamics of biological invasions and the legacy of GABI on the current biodiversity patterns across the Americas.

The asymmetry has been associated with biotic interactions, such as competition (3, 6) and predation (9). Habitat change may have also played a role, as savanna-like environments may have developed in Central and South America in response to the Pleistocene glaciations, favoring the dispersal of savanna-adapted mammals (8, 10, 11). In addition, the asymmetry is observed in the

relative diversity of immigrant taxa (defined as taxa that occur in a continent different from the continent of origin of the clade to which they belong) in the fossil record (7, 8), but is not observed through inference of dispersal rates based on molecular phylogenies (12). The reason for this discrepancy remains uncertain, but perhaps dispersal rates from molecular phylogenies and fossil data reflect differences across biomes, as the tropics are underrepresented in the mammal fossil record (12, 13).

Diversity dynamics are determined by dispersal, origination, and extinction. Dispersal (defined here as the range expansion of a genus to a new continent) encompasses several stages and barriers that a successful invader has to overcome including transport, establishment, and population growth (2, 14). During the GABI, certain clades of mammals dispersed to a new continent and became successful invaders, whereas others remained restricted to their continent of origin or may have dispersed but were unsuccessful invaders (8).

The immigrant asymmetry in the Pleistocene could be the result of four nonmutually exclusive mechanisms: Higher dispersal rate (defined as the expected number of dispersal events per genus per million year) from North to South America (Fig. 1A),

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Significance

The biological interchange between North and South America associated with the formation of the Isthmus of Panama is key to defining current gradients of species diversity. A major gap in our understanding of the interchange is its asymmetry, where mammals of North American origin attained higher diversity in South America than vice versa. The prevailing view is that this asymmetry resulted from higher origination of immigrant mammals in South America. In contrast, we find that asymmetry results from high extinction of native mammals in South America, which reduced the diversity of native mammals available to disperse northwards. These results shed light on the legacy of the biotic interchange to understand the current patterns of species diversity across the Americas.

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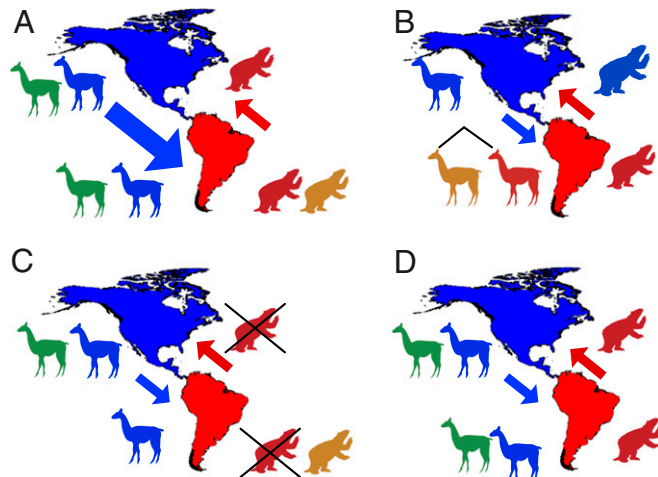
higher origination of mammals of North American origin in South America (Fig. 1B), higher extinction of mammals with South American origin (Fig. 1C), and similar dispersal rate but a larger pool of dispersing taxa from North America to South America than vice versa (Fig. 1D). Here we used a dataset of nearly 20,000 fossil occurrences and apply Bayesian methods to test among these mechanisms. We also test if immigration occurred at random across clades or if there is some selectivity in the dispersing clades. Our results provide insights into the ecological and evolutionary consequences of a biological invasion at a continental level.

Results

We used genera as taxonomic units in our analyses. The diversity of native mammalian genera in South America reached its peak in the late Miocene (11.6 to 5.3 Ma) followed by a 52% decrease in the Pliocene (5.3 to 2.6 Ma). The decreasing trend continued in the early and middle Pleistocene (hereafter Pleistocene; 2.6 to 0.126 Ma) (Fig. 2A). In contrast, the decrease in diversity of native mammal genera in North America from the late Miocene to the Pliocene was only 25% (SI Appendix, Table S2). The estimated diversity of immigrant genera was similar on the two continents during the late Miocene and the Pliocene. However, in the Pleistocene the estimated diversity of immigrant genera in South America had a fourfold increase (SI Appendix, Table S2), whereas it remained relatively low in North America, driving asymmetry (Fig. 2A).

We found no asymmetry in the net diversification of immigrant taxa in the Pleistocene, as the mean net diversification rate (origination rate minus extinction rate) was not significantly higher for immigrant taxa in South America than for their counterparts in North America (Fig. 2B). On both continents, the immigrant taxa showed high origination and low extinction rates through time (Table 1), which yielded an overall positive net diversification (Fig. 2B). Similarly, using a model that explicitly corrects for

Fig. 1. Four potential mechanisms underlying the observed asymmetry across the Americas in the Pleistocene, characterized by higher diversity of mammals with North American origin in South America than vice versa. The arrows show the direction and magnitude (reflected by the arrow's size) of dispersal rate. (A) Higher dispersal rate from North America (blue) to South America (red); (B) similar dispersal rate between the continents but higher diversification of North American migrants in South America than vice versa; (C) similar dispersal rate but mammals with South American origin had a higher extinction; or (D) similar dispersal rate, but there is a larger pool of taxa in North America compared to South America. The four scenarios are not mutually exclusive. Animal silhouettes from Phylopic (phylopic.org). Giant sloth silhouette made by Zimices. Used with permission under license CC BY-NC 3.0 https://creativecommons.org/licenses/by-nc/3.0/.
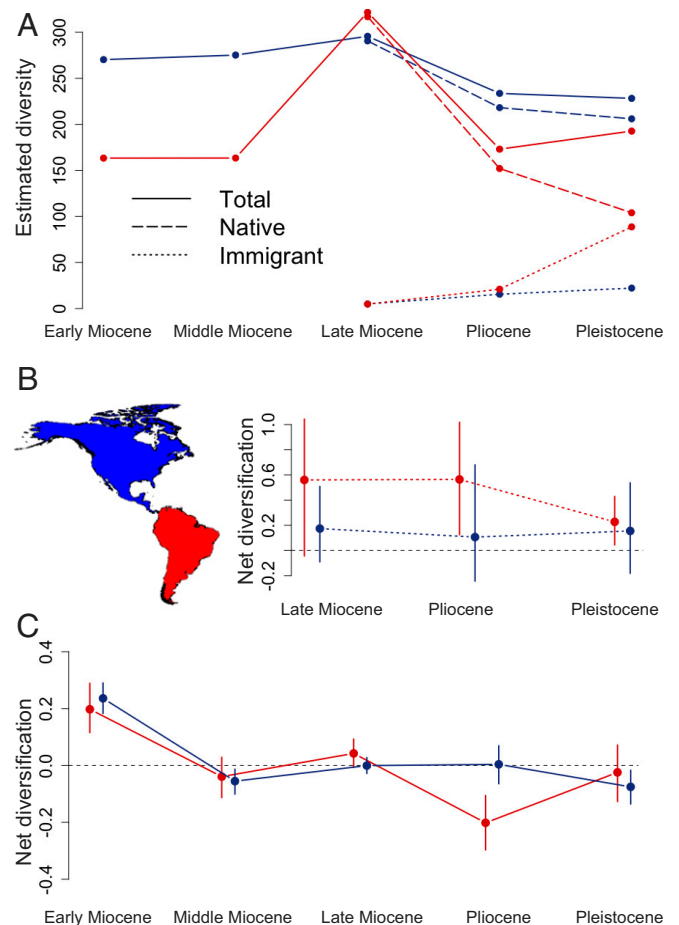
Fig. 2. Diversification dynamics of native and immigrant taxa in North (blue) and South (red) America during the GABI. Bars indicate 95% credible interval. (A) Estimated diversity of native and immigrant genera in North and South America. The increase in diversity of native mammals in South America during the late Miocene was followed by a decrease in the Pliocene, reducing the available pool of taxa to disperse in the Pleistocene. This created the asymmetry in the diversity of immigrant taxa in the Pleistocene. (B) Net diversification rate (origination minus extinction) of immigrant taxa showing no differences in the diversification rate of immigrants in the two continents. (C) Net diversification of native taxa, showing the diversity decline (negative net diversification) of South American natives in the Pliocene.

area-specific sampling biases (15), we found no difference in the dispersal rates between the two continents (Table 2). Here we define dispersal rates as the estimated number of dispersals per genus per million years (SI Appendix, Fig. S1), and accounting for differences in the total diversity between the continents. These results demonstrate that the asymmetry in the diversity of immigrant taxa in the Pleistocene was not the result of higher dispersal rate from north to south (Fig. 1A), nor higher origination of immigrant taxa in South America (Fig. 1B).

The asymmetry is the result of higher extinction of native mammals in South America (Fig. 1C), which decreased the diversity of native taxa that could disperse to the north (Fig. 1D). In both continents, the native taxa exhibited periods of both positive and negative diversification rates through time (Fig. 2C). The origination rate was similar in the two continents, except in the late Miocene when it was higher in South America (Table 1). During the GABI, we identified two periods during which extinction was significantly higher for native taxa in South America: The late Miocene and the Pliocene (Table 1 and SI Appendix, Fig. S2). As a consequence, there was a decrease in the diversity

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Table 1. Diversification rates of mammals during the GABI

	North America				South America			
	Origination		Extinction		Origination		Extinction	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Natives								
Early Miocene	0.32	0.27–0.37	0.08	0.06–0.11	0.29	0.21–0.38	0.09	0.06–0.14
Middle Miocene	0.12	0.09–0.15	0.17	0.14–0.21	0.13	0.09–0.18	0.17	0.12–0.23
Late Miocene	0.08	0.06–0.10	0.08	0.06–0.11	0.21	0.17–0.25	0.17	0.13–0.21
Pliocene	0.19	0.14–0.23	0.18	0.13–0.23	0.12	0.06–0.17	0.32	0.24–0.40
Pleistocene	0.12	0.08–0.16	0.19	0.15–0.24	0.16	0.09–0.23	0.18	0.12–0.26
Immigrants								
Late Miocene	0.25	0.04–0.50	0.08	0.00–0.23	0.67	0.12–1.41	0.11	0.00–0.36
Pliocene	0.30	0.00–0.72	0.20	0.00–0.52	0.65	0.23–1.12	0.09	0.00–0.22
Pleistocene	0.27	0.03–0.58	0.12	0.00–0.30	0.32	0.14–0.51	0.09	0.03–0.17

Origination and extinction rates are shown for native and immigrant taxa in each continent from the early Miocene to the Pleistocene. CI, credible intervals.

of South American native taxa since the Pliocene (Fig. 2*A* and *SI Appendix*, Table S2), which reduced the available pool of native taxa that could disperse toward the north during the Pleistocene.

In order to determine the evolutionary consequences of the taxa participating in the GABI, we did a permutation to test whether some clades had more immigrants than expected from a random sample from the continent of origin (16). The results identify that two orders of North American origin had more immigrants in South America than expected: even-toed ungulates (Artiodactyla) and Carnivora (Table 3). In contrast, rodents that originated in North America (noncaviomorphs) had fewer immigrants than expected (Table 3). For the clades of South American origin, the number of immigrants did not differ from the null expectation (Table 4). Artiodactyla and Carnivora disproportionally contributed to the diversity of North American immigrants to South America in the Pleistocene and therefore are the primary drivers of the GABI asymmetry.

Discussion

A major gap in our understanding of the GABI is its asymmetry in the diversity of immigrants and specifically to explain a dominance of mammals of North American origin in South America. Here, we tested among four nonmutually exclusive mechanisms responsible for the widely documented asymmetry in the diversity of immigrants after the GABI (Fig. 1). We did not find significant differences in the relative dispersal rate or origination rate of immigrant taxa in either continent. Instead, our results indicate that the asymmetry is the result of a higher extinction of native taxa in South America in the Pliocene that reduced the diversity of taxa that could disperse toward the north.

Diversification Dynamics. The diversity trajectories of native and immigrant taxa in the two continents indicate that, except for the late Miocene, generic diversity was higher in North American

Table 2. Dispersal rates of mammals during the GABI

	Dispersal North to South		Dispersal South to North	
	Mean	95% CI	Mean	95% CI
Late Miocene	0.00	0.00–0.01	0.01	0.00–0.01
Pliocene	0.03	0.00–0.05	0.03	0.00–0.05
Pleistocene	0.65	0.48–0.84	0.60	0.47–0.74

Dispersal rates correspond to the estimated proportion of the total pool of genera that dispersed per million year obtained from the posterior estimates after combining the 100 replicates to account for dating uncertainty in the fossil occurrences. CI, credible intervals.

than in South American mammals. The estimated diversity from fossils mainly reflects the diversity patterns outside the tropics (*SI Appendix*, Table S3). The higher diversity in North America before and during the interchange is consistent with the larger area through time of temperate biomes (e.g., temperate forests and savannas) in North America than in South America (17). The high diversity of North American mammals in the early and middle Miocene (17 to 13 Ma) may be related to tectonic activity in western North America and a global warming event known as the Miocene Climatic Optimum (18, 19).

In South America, there was an increase in the diversity of native mammals during the late Miocene (Fig. 2*A*). This increase is observed in the temperate fossil record, but not in the tropics (*SI Appendix*, Table S3), and most of the fossil occurrences during the late Miocene of South America are recorded from temperate regions (*SI Appendix*, Fig. S3). The increase in diversity in the late Miocene is related with the fossil record of the Ituzaingó Formation in Argentina (20, 21) that harbors ~50% of the sampled diversity of native mammals in South America during this time period. The Ituzaingó Formation crops out along the cliffs of the Paraná river (22) and its high diversity could be related with a heterogeneous landscape of a deltaic system with gallery forests (21). Paleobotanical evidence suggests the presence of a seasonal dry forest and a subtropical climate (23). Finally, the higher diversity could also reflect taphonomy and high fossil sampling from more than a century of paleontological research in the Ituzaingó Formation (21), although our diversity estimates explicitly account for this by applying different estimated sampling rates through time.

The increase in diversity was followed by a high extinction rate in the Pliocene (Table 1 and *SI Appendix*, Fig. S2), which decreased the diversity of South American native mammals again. Most of the fossil occurrences for the Pliocene are recorded in southern South America (*SI Appendix*, Fig. S3), reflecting the rich fossil record of the Pampas in Argentina (24), and the underrepresentation of the tropical fossil record of the continent (13, 25). As result of the high extinction rate in South America during the Pliocene, the diversity of native taxa was 50% less than in North America during the peak of the GABI in the Pleistocene. This difference in diversity of native taxa between the two continents was a major cause of the documented GABI asymmetry.

The temporal resolution used in the analysis allows for the robust estimation of dispersal, origination, and extinction rates, but limits the temporal constraint of the high extinction observed in the Pliocene. However, since most of the fossil occurrences come from high latitudes, the high extinction rate could be associated with

Table 3. Observed and expected diversity of migrant mammal genera in South America during the early and middle Pleistocene (2.6 to 0.126 Ma)

Order	Genera in North America	Immigrants in South America	Difference from expectation
Artiodactyla	34 (31, 37)	****21 (19, 21)**	**10 (−1, 18)**
Carnivora	45 (41, 51)	***21 (18, 21)**	**6 (−5, 17)**
Chiroptera	7 (7, 9)	0	−2 (−8, 0)
Eulipotyphla	12 (9, 13)	1 (0, 1)	−3 (−9, 1)
Lagomorpha	12 (10, 14)	1 (0, 1)	−3 (−9, 1)
Perissodactyla	5 (3, 7)	3	2 (−3, 3)
Proboscidea	8 (7, 8)	3 (2, 3)	1 (−4, 3)
Noncaviomorph rodents	71 (66, 76)	***12 (10, 13)*	*−10 (−24, 3)*

The diversity of native mammals in North America and the diversity of migrant mammals in South America show the median and range of genera per order estimated from 100 replicates to account for the age uncertainty of occurrences. Only clades with a minimum of five genera are shown. The expected number of genera of migrant taxa were selected at random in 10,000 iterations of the permutation test. The difference from the expectation shows the median and range of the difference between the observed and expected number of migrant genera per order. Orders with significantly more migrant genera than expected are shown in bold, whereas orders with significantly fewer migrant genera than expected are shown in italics. $**P > 0.99$; $*P > 0.95$.

the faunal turnover that occurred in the Pampas at ~3.3 Ma (26, 27). It is estimated that 37% of the genera and 53% of the species went extinct in the region at that time (28). The high extinction in the Pampas occurs just above the stratigraphic level where a meteorite impact event is recorded (28, 29). The extinction in the region may have been related with landscape changes caused by the impact itself (29) and climatic changes toward cooler and drier conditions that occurred in the region at the end of the Pliocene (30).

Another possible factor for the high extinction of native mammals in South America is competitive displacement by immigrants from the north (3, 6). Before the GABI, the mammal carnivore guild in South America was represented by Sparassodonta (a group of methatherians closely related to living marsupials). Sparassodonts went extinct in the early Pliocene (4.5 to 3.3 Ma) (31) and it has been proposed that they were outcompeted by placental carnivores that arrived from North America (3, 32). However, analyses based on the diversity trends, temporal and ecological overlap between sparassodonts and placental carnivores do not support the competition hypothesis (33, 34). The extinction of sparassodonts left an empty ecological space which was occupied by placental carnivores (34).

After the extinction of sparassodonts, placental carnivores diversified in South America (25, 31). We found a higher diversity than expected of placental carnivores in South America in the Pleistocene as part of the GABI (Table 3). Placental carnivores attainted higher diversity in South America than sparassodonts did in the past (31). This may be related to a higher morphological variation (disparity) and ecological diversity of placental carnivores that allowed them to occupy diverse niches across South America (35). Sparassodonts had lower diversity (36) and dental disparity (37) than placental carnivores, a pattern that is general to placental vs. nonplacental mammals (38). Differences in patterns of tooth replacement could explain the

higher dental disparity in placental carnivores and the reduced morphological dental specialization in marsupials (39).

Competition has also been suggested to explain the decline in diversity of native South American ungulates and the success of ungulates that arrived to South America during the GABI (6). However, differential susceptibility to predation may be a more plausible explanation. Native South American mammals did not coevolve with placental carnivores and were therefore potentially more susceptive to predation by them, which could also have led to a higher extinction (9, 32). We found that Artiodactyla had a higher diversity in South America in the Pleistocene than expected by chance (Table 3). We hypothesize that as artiodactyls coevolved with placental carnivores outside South America, they were less likely to be susceptible to predation than the native South American ungulates (9), favoring their diversification in South America. An alternative, but not mutually exclusive explanation is the enemy-release hypothesis (40) that argues that invaders escape their enemies (e.g., pathogens) when leaving their native ranges and move into new areas.

Rodent groups of North American origin (noncaviomorphs) had a lower diversity of immigrants in South America than expected (Table 3). Although their diversity in South America was high in the early and middle Pleistocene (12 genera), it is less than expected given the 71 genera recorded in North America for the same time interval (Table 3). Noncaviomorph rodents are highly diverse and widely distributed in South America today (41), and its diversification is an example of an evolutionary radiation at the continental level (42). Evidence from molecular phylogenies indicate that this radiation occurred before the Pleistocene (42, 43). However, the fossil record of noncaviomorph rodents prior to the late Pleistocene is still fragmentary (44). It is possible that their diversity in the early and middle Pleistocene has been underestimated because there are relatively few well-sampled

Table 4. Observed and expected diversity of migrant mammal genera in North America during the early and middle Pleistocene (2.6 to 0.126 Ma)

Order	Genera in South America	Immigrants in North America	Difference from expectation
Cingulata	17 (16, 18)	5 (5, 6)	−3 (−11, 8)
Litopterna	5 (4, 6)	0	1 (−5, 9)
Notoungulata	8 (6, 8)	1	0 (−7, 9)
Caviomorpha	19 (16, 21)	4 (3, 4)	−3 (−12, 9)
Pilosa	16 (13, 18)	9 (8, 10)	−2 (−11, 9)

The diversity of native mammals in South America and the diversiy of migrant mammals in North America show the median and range of genera per order estimated from 100 replicates to account for the age uncertainty of occurrences. Only clades with a minimum of five genera are shown. The expected number of genera of migrant taxa were selected at random in 10,000 iterations of the permutation test. The difference from the expectation shows the median and range of the difference between the observed and expected number of migrant genera per order.

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localities from the Andes. Andean uplift promoted diversification and morphological evolution (45, 46), and today the Andes is the region with the highest diversity of noncaviomorph rodents (41).

Dispersal and Diversification of Immigrants. We estimated dispersal and diversification of immigrants during the GABI (Fig. 2 and Tables 1 and 2). Origination rates quantified the expected number of new genera per million year that originated in the new continent from an immigrant ancestor, whereas dispersal rates quantified the frequency of range expansion of immigrant genera. Overall, origination rates were high and the dispersal rates low in the late Miocene and Pliocene (Fig. 2). The origination rates of immigrant taxa decreased in the Pleistocene (Table 1). Nevertheless, immigrants had higher origination than the natives on both continents, characterizing the Pleistocene as the peak of the GABI for mammals with high origination and high dispersal of immigrant taxa.

Bacon et al. (12) estimated dispersal rates of terrestrial fauna during the GABI based on phylogenetic data and showed that dispersal rates in both directions were similar until ~6 Ma when the dispersal rate from South to North America was found to be 30% higher. Phylogenetic data in birds also indicate a predominant dispersal from South to North America (47). Based on mammal fossil data, here we found no differences in the dispersal rates (Table 2). The reason for this discrepancy is likely that molecular phylogenies reflect mainly dispersals in tropical biomes, whereas fossil occurrences reflect mainly dispersals in temperate biomes (12, 47). There are few fossil occurrences in the tropics of North America from the late Miocene to Pleistocene (*SI Appendix*, Fig. S3). Therefore, the higher dispersal from tropical South America to North America observed from molecular phylogenies is unlikely to be seen in the fossil record. Today, 45% of the living South American mammal genera are descendants of North American immigrants, whereas in North America (including Central America) 37% of the genera are derived from South American immigrants. If Central America is excluded, only 10% of the genera are derived from South American immigrants (48). This is further illustrated with a comparison of the fossil and extant fauna of Panama (the southernmost part of North America). The early Miocene fossil fauna in Panama records only 5% of mammals with South American origin, whereas in the extant fauna is 57% (1), suggesting a high dispersal from the tropics of South America into Panama during the GABI.

Conclusion

Our study identifies higher extinction of native taxa in South America, which in turn reduced the diversity of native taxa that dispersed northwards. This extinction of South American natives is the main driver of the asymmetrical pattern of mammal diversity between North and South America after the GABI. Our results reject previous suggestions that the asymmetry was driven by higher origination of immigrant taxa in South America. In addition, we found that two orders of mammals of North American origin (Carnivora and Artiodactyla) had a higher diversity of immigrants than expected, leading to a strong pattern of asymmetry. Our results shed light on one of the most compelling events of biotic interchange in Earth history and highlights how biogeographic processes and biotic interactions can shape continental diversity. These insights provide clues to the long-term evolutionary and ecological consequences of on-going biological invasions and may provide information on the consequences of the current movement of species on geological time scales.

Materials and Methods

Methods Summary. Challenges to evaluate the mechanisms of the asymmetry in the GABI include sampling and preservation biases of the fossil record of mammals in the Americas (13). However, new Bayesian methods have been developed to estimate dispersal (15) and diversification rates (49) from fossil occurrences, which explicitly account for sampling and preservation differences. As expected, these models estimated a higher sampling rate (number

of occurrences per genus per million year) in North America than South America through the time periods analyzed (*SI Appendix*, Fig. S4). For example, for the Pleistocene (the peak of the GABI) the sampling rate in North America was 3.75 times higher than in South America (*SI Appendix*, Fig. S4). We accounted for sampling differences when analyzing the diversity and dispersal dynamics during the interchange.

We obtained fossil occurrences of mammals in North and South America from the PaleoBiology Database (PBDB; paleobiodb.org/), to which we contributed ~500 references for occurrences and taxonomic opinions of fossil mammals in the Americas. We used genera as taxonomic units because few fossil occurrences are identified to the species level and the alpha taxonomy of several extinct mammal clades is poorly resolved at the species level. Reliance on precompiled databases is a requirement for analyses like this one. Although our dataset might not include all of the fossil mammal genera that have been described in the Americas, our reliance on precompiled data are more likely to introduce uncertainty rather than biased conclusions. We classified each genus as having North or South American origin based on the oldest record of the order to which the genus belongs, except for rodents and bats where it was based on the oldest record of the family. The upper Pleistocene megafauna extinction, reviewed in Sandom et al. (50), would bias the diversification and dispersal rates estimates since the upper Pleistocene extinction disproportionally affected South American immigrants to North America (9). The diversity of large-size taxa was considerably higher in mammals of South American origin (51) and large-size correlates with the probability of extinction at this time interval (52). Therefore, we excluded the upper Pleistocene from the dispersal and diversification analyses. We estimated the generic richness (hereafter diversity) of native and immigrant mammals on the two continents for five time bins: Early Miocene (23 to 15.9 Ma), middle Miocene (15.9 to 11.6 Ma), late Miocene (11.6 to 5.3 Ma), Pliocene (5.3 to 2.6 Ma), and Pleistocene (excluding the upper Pleistocene; 2.6 to 0.126 Ma).

We used a Bayesian approach to estimate origination and extinction rates of native and immigrant taxa and dispersal rates of immigrants on the two continents, taking into account differences in sampling and preservation (49). We used the same time bins as in the estimation of diversity. Finally, we used the permutation approach described in Blackburn et al. (16) to test if there are differences between the number of migrant genera per order (or families in the case or rodents and bats) in each continent and the number that would be expected if immigrant genera were selected at random. Previous work that quantified origination and extinction rates of fossil mammals during the interchange used taxonomic lists and the age ranges of the taxa in each continent (7). In our approach, we used not only the age range, but all of the available occurrences reported for each taxon. This allowed us to explicitly account for the differences in fossil sampling between the two continents and among the time periods used in the analyses. In addition, we accounted for the uncertainty in the dating associated with each fossil occurrence. Our estimates of diversity, origination, extinction, and dispersal are particularly robust as they account for the differences in fossil sampling and provide the mean and 95% credible interval (CI) for each parameter estimated.

There are challenges to inferring diversity dynamics from the fossil record, in particular related to the limitations of the data across temporal and spatial scales (53). North America has a more robust and complete fossil record of mammals from the Cenozoic (54) than South America (55). An additional limitation is the underrepresentation of tropical and high elevation localities in the fossil occurrences of American mammals. The sampling bias toward the tropics is a pattern seen in both continents (8). The Neotropics are home to a great diversity of living mammals (56), but despite important advances in Neotropical paleontology (57, 58), they remain underrepresented in the fossil record (13). Similarly, mountains are currently associated with high biodiversity (59, 60), but the mammal fossil record in mountain ranges (e.g., the Andes) is limited because high-elevation environments are erosional and rarely represented in long-term stratigraphic records with relative complete fossil sampling (18). For example, small mammals are underrepresented in fossil localities that are not well-sampled (61). This sampling bias may have also contributed to the underestimation of noncaviomorph rodent diversity in South America in the Pleistocene. Our Bayesian model explicitly incorporates sampling and preservation differences between the two continents to estimate dispersal (15) and diversification rates (49) during the GABI. Nevertheless, incompleteness with the available fossil data may have led our results to reflect predominantly the dynamics of lowland temperate habitats.

Compilation of Fossil Occurrence Data. We used the paleobioDB R package (62) to download Neogene and Pleistocene occurrences of nonmarine mammals from the PBDB on August 15, 2018. We excluded the occurrences identified above the genus level and the records of the dromomerycine artiodactyl, peccaries, tapirs, and gomphotheres reported from the late

EVOLUTION

Miocene (~9 Ma) of Amazonia (63, 64), since the age of the records is controversial (65). We cleaned fossil occurrence data using the "clean_fossils" function implemented in CoordinateCleaner (66). This function runs multiple empirical tests to identify occurrences with potentially erroneous coordinates and time-spans (66). The flagged records represented 5.1% of the occurrences in North America and 2.3% of the occurrences in South America. After careful inspection of the dataset and flagged occurrences, we excluded occurrences with age ranges larger than 10 Ma. For occurrences with ranges smaller than 10 Ma, we excluded temporal range outliers (i.e., records with unexpectedly large temporal ranges based on an interquartile outlier test) at the genus level (66). The final dataset includes 19,878 fossil occurrences, with 16,859 from North America (north of Uramite suture in western Colombia, the tectonic boundary between South America and Central America, and we also excluded the Caribbean islands) and 3,019 from South America. All analyses were performed in R v3.5.1 (67). All scripts and input data used for this study are available in Zenodo (https://doi.org/10.5281/zenodo.3770347).

Upper Pleistocene Records. In order to obtain the unbiased geographic distribution of the upper Pleistocene mammals in the Americas we used the Phylacine v1.2 database (68), which is based on range data from the International Union for Conservation of Nature 2016 -3 and Faurby and Svenning (69). When necessary, we matched the PBDB taxonomy of the upper Pleistocene genera with the Phylacine taxonomy. The taxonomic synonyms between PBDB and Phylacine are: *Alopex* (=*Vulpes*), *Liomys* (=*Heteromys*), *Hesperomys* (=*Calomys*), *Mictomys* (=*Synaptomys*), *Pekania* (=*Martes*), *Uncia* (=*Panthera*).

Classification of Immigrant Taxa. We classified each genus as having North or South American origin if the clade to which it belongs (i.e., family or order) had known records in either continent before 10 Ma, predating the record of the earliest immigrant taxa (4). Platyrrhine monkeys are recorded in South America since the late Eocene (70), therefore we assigned a South American origin to the clade, even though there is one record in Panama at 20.9 Ma (71). The fossil record of bats is poor in comparison with other mammals and in order to assign the origin of the different clades of New World bats, we complemented the information from its fossil record with biogeographic analyses based on molecular phylogenies (*SI Appendix*, Table S1). Bats, however, constitute only 1.2% of all of the fossil occurrences. While using ancestral area reconstructions to assign the continent of origin of bat clades could increase uncertainty, bats are therefore too rare in the fossil record to likely influence the overall conclusions. In order to account for the uncertainty in the age range of fossil occurrences, we generated 100 replicates with a random age for each occurrence derived from a uniform distribution, with the lower and upper limits being the maximum and minimum age estimate, respectively.

Estimation of Diversity through Time. We used the "divDyn" function implemented in divDyn (72) to obtain the sample in bin diversity for each time bin in the 100 replicates. Then, we calculated the mean diversity of the 100 replicates for each time bin. Finally, we calculated the diversity corrected by the probability of sampling obtained in the dispersal extinction sampling (DES) (15) analysis following the equation: $D_t = S_t + S_t \times (1 - p_t)$, where D_t is the estimated diversity in the time bin t, S_t is the sampled in bin diversity, and p_t is the probability of sampling. The latter is obtained from the sampling rate (q_t) with the equation: $p_t = 1 - \exp(-q_t)$ (15). The sampling rate (q) quantifies the expected number of fossil occurrences per genus per million year and it is jointly estimated with dispersal and extinction rates from the fossil occurrence data within the DES framework.

Estimation of Diversification and Dispersal Rates. Following Marshall et al. (7), we differentiated the immigrant taxa into primary or secondary immigrants. Primary immigrants are taxa that dispersed and are recorded in both continents at a given time bin. For example, the Pleistocene notoungulate *Mixotoxodon* is native from South America and is also recorded in North America, therefore is considered a primary immigrant in North America. Secondary immigrants are taxa that evolved from a primary immigrant after

their arrival to the new continent. For example, *Cyonasua* is an immigrant recorded in the late Miocene of South America, as it belongs to Procyonidae, which originated in North America. *Cyonasua* evolved from a procyonid ancestor that dispersed from North America, but *Cyonasua* is only recorded in South America and therefore is considered a secondary immigrant.

We estimated origination and extinction rates of native and secondary immigrant taxa using the program PyRate (49). We used a time-variable Poisson Process model of preservation, coupled with a Gamma model of rate heterogeneity through time and across taxa (49). The analysis was run for 10,000,000 Markov Chain Monte Carlo (MCMC) generations for each of the 100 replicates. We estimated the dispersal rates of primary immigrants using the DES model (15). We defined dispersal as the range expansion of a genus to a new continent. We specified time-dependent dispersal and extinction. The DES analysis was run for 600,000 MCMC generations for each of the 100 replicates generated to account for the age uncertainty of the occurrences. For all of the estimations described above, we used the same time bins as in the estimation of diversity. We used Tracer (73) for the visualization and convergence diagnostic of the MCMC. Output from the DES and origination and extinction analyses were combined across replicates after discarding burn-in. We summarized the posterior parameter samples as mean and 95% CI.

Permutation Test of Asymmetry. As the asymmetry is recorded in the Pleistocene, we included only the records from the early and middle Pleistocene (2.6 to 0.126 Ma). For each order, we obtained the diversity of genera in the continent of origin and the diversity of immigrants in the receiving continent. Because some orders are poorly represented in the fossil record, we performed the analysis for the orders with at least five genera in the continent of origin. For each continent, we used the "sample" base function in R to pick n genera at random and without replacement from the native mammal fauna, and we summed the randomly chosen genera in each order. n is the number of immigrant genera from the continent in each of the 100 replicates generated to account for the age uncertainty of the fossil occurrences. n had a median of 62 (range from 58 to 62) for North America and a median of 23 (range 21 to 25) for South America. In each continent, we repeated the process 100 times for each of the 100 replicates for a total of 10,000 lists of randomly chosen genera. Finally, for each of the 10,000 permutations, we calculated the difference between the observed and expected number of immigrants per order and we estimated the probability that it was different from 0. The observed number of immigrant genera in each order was judged significantly greater than expected by chance if the difference from expectation was greater than 0 with a probability higher than 0.975. Similarly, the number of immigrant genera for each order was considered less than expected by chance if the difference from expectation was smaller than 0 with a probability higher than 0.975.

Data Availability. Datasets and code have been deposited in Zenodo (https://doi.org/10.5281/zenodo.3770347) (74).

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