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Mammalian Evolution and the Great American Interchange

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Summary. A reciprocal and apparently symmetrical interchange of land mammals between North and South America began about 3 million years ago, after the appearance of the Panamanian land bridge. The number of families of land mammals in South America rose from 32 before the interchange to 39 after it began, and then back to 35 at present. An equivalent number of families experienced a comparable rise and decline in North America during the same interval. These changes in diversity are predicted by the MacArthur-Wilson species equilibrium theory. The greater number of North American genera (24) initially entering South America than the reverse (12) is predicted by the proportions of reservoir genera on the two continents. However, a later imbalance caused by secondary immigrants (those which evolved from initial immigrants) is not expected from equilibrium theory.

Biogeographers have long recognized the late Cenozoic mingling of the previously separated American continental biotas as a monumental natural experiment, the Great American Interchange. Comparison of the "wonderful extinct fauna . . . discovered in North America, with what was previously known from South America" allowed Wallace to first recognize the existence of this event in 1876 (*1*). However, the direction in which representatives of the various animal groups had dispersed was not well understood by Wallace (*2*). It took another 15 years of intense paleontological exploration and study by Cope and Marsh in North America, and by Carlos and Florentino Ameghino in South America before sufficient data existed to permit clarification of many of the basic issues in this event (*3*). By 1891 a comprehensive and balanced overview of the interchange existed:

> . . . not only did North American taxa cross the newly opened land bridge, greatly expanding their ranges, but also South American autochthons began ranging into North America, and thus toward the end of the Pliocene epoch took place one of the most remarkable faunal exchanges that Geology has known [Karl A. von Zittel (*4*)].

Continued research in the present century has resulted in elaboration of the histories of the participant and nonparticipant taxa. This cumulative knowledge has been periodically summarized by Matthew (*5*), Scott (*6*), Simpson (*7*), Patterson and Pascual (*8*), and others (*9–12*).

Despite the wealth of accumulated knowledge, many finer details of the interchange have remained obscure. Recent improvements in paleontological sampling (especially screen-washing for taxa of small body size); refined taxonomic studies spanning both continents; and availability of an array of radioisotopic age determinations interpolated within the late Cenozoic land-mammal bearing strata on each continent permit clarification of unresolved earlier problems. There now exists sufficient knowledge of these aspects of the interchange to permit quantitative, rather than simply qualitative, examination of patterns of faunal dispersal and evolution. In this article we have compiled such quantitative data, and we use them to examine both empirical patterns of faunal interchange and correspondence to models of equilibrial diversities and biogeography.

Qualitative Aspects of the Interchange

South America was isolated from other continents during most of the Age of Mammals (*8, 13*). This isolation ended about 3 million years ago with the disappearance of the Bolivar Trough Marine Barrier in the area of northwestern Colombia and southern Panama, and the total emergence of the Panamanian land bridge (*8*). Thereafter the fossil record documents a reciprocal intermingling of the long-separated North and South American terrestrial biotas. Since the Bolivar Trough served as the final geographic barrier separating these biotas, the area to the north of it is here referred to as North America and the area south of it as South America. The area of the former Bolivar Trough is thus the "gateway" for the Great American Interchange.

On the basis of the timing and the means of dispersal, the participants in the Great American Interchange can be divided into two groups. The first group includes late Miocene waif immigrants, which are believed to have dispersed along island arcs before the final emergence of the land bridge (*7*). This group includes members of two families of North American origin: (i) procyonids (racoons and allies), which are first recorded in beds of late Miocene (Huayquerian) age in Argentina (*11, 14*), and (ii) cricetid rodents (New World rats and mice) of the tribe Sigmodontini (Hesper-

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omyini), which are first recorded in beds of early Pliocene (Montehermosan) age (*15*) in Argentina. It also includes members of the extinct South American ground sloth families Megalonychidae and Mylodontidae, which are first recorded in North America in beds of late Miocene (Hemphillian) age (*11*).

Included within the second group of participants are those taxa that walked across the bridge after its final emergence. The North American immigrants to South America include members of the families (i) Mustelidae (skunks and allies) and Tayassuidae (peccaries), which first appear in the late Pliocene (Chapadmalalan Age) (*8*); (ii) Canidae (dogs, wolves, foxes), Felidae (cats), Ursidae (bears), Camelidae (camels, llamas), Cervidae (deer), Equidae (horses), Tapiridae (tapirs), and Gomphotheriidae (mastodonts) which appear in the early Pleistocene (Uquian Age) (*8*); and (iii) Heteromyidae (kangaroo rats and allies), Sciuridae (squirrels), Soricidae (shrews), and Leporidae (rabbits) which are known only from Holocene or Recent (or both) (*8, 16, 17*). The South American immigrants to North America include members of the families (i) Dasypodidae (armadillos), Glyptodontidae (glyptodonts), Hydrochoeridae (capybaras), and Erethizontidae (porcupines), which appear in the late Pliocene (late Blancan Age) (*9, 11*); (ii) Didelphidae (opossums) and Megatheriidae (ground sloths), which appear in the early and middle Pleistocene (Irvingtonian Age) (*9, 11*); (iii) Toxodontidae (toxodonts), which are recorded in the late Pleistocene (Rancholabrean Age) (*8*); and (iv) Callitrichidae (marmosets and tamarins), Cebidae (New World monkeys), Choleopodidae (tree sloths), Bradypodidae (tree sloths), Cyclopidae (anteaters), Myrmecophagidae (anteaters), Dasyproctidae (agoutis, pacas), and Echimyidae (spiny rats), which are known only in Recent faunas (*17*).

The late Cenozoic record of fossil mammals in North and South America is relatively well documented. The one great deficiency of the South American record is that it is largely restricted to Argentina (*8*) and to a lesser extent Bolivia (*18*). Both the North and South American records are deficient for mammals from tropical latitudes. Nevertheless, inferences gleaned from these records yield generalities that are probably valid for the continents as a whole (*7*). Furthermore, the majority of faunas sampled appear to represent savanna-

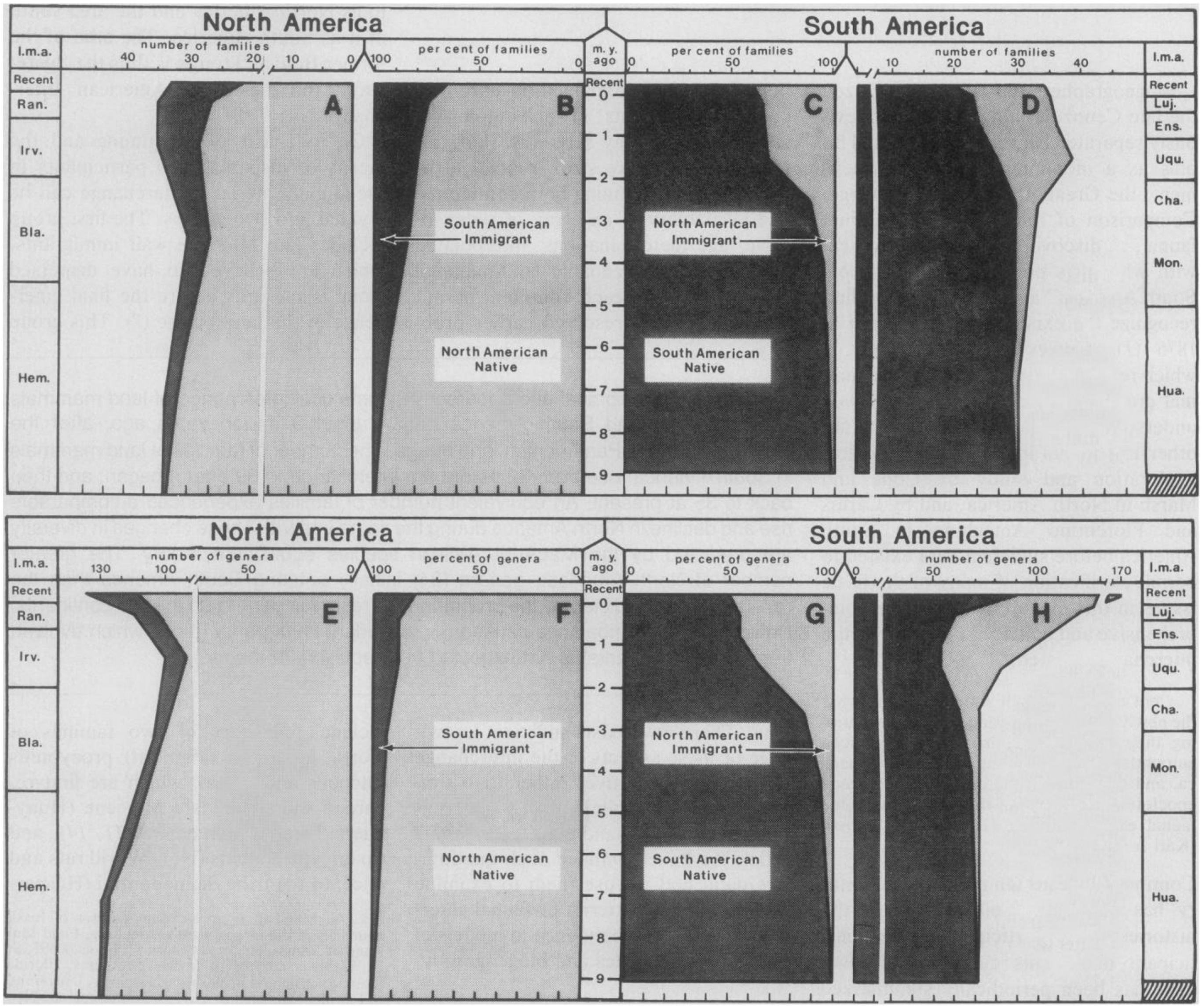

Fig. 1. Numbers (or "diversities") of known families (top) and genera (bottom) in successive late Cenozoic land mammal ages in North (left) and South (right) America. Graphs show total number of native and immigrant taxa and their percentage contribution to each land mammal age fauna. Note that scales are different for cumulative numbers of families and genera. The land mammal ages for North America are *Ran.*, Rancholabrean; *Irv.*, Irvingtonian; *Bla.*, Blancan; and *Hem.*, Hemphillian; for South America they are *Luj.*, Lujanian; *Ens.*, Ensenadan; *Uqu.*, Uquian; *Cha.*, Chapadmalalan; *Mon.*, Montehermosan; and *Hua.*, Huayquerian. Abbreviations: *l.m.a.*, land mammal age; *m.y.*, million years.

grassland habitats. We are thus dealing primarily with the evolutionary history of ecologically similar faunas during the interchange period, and this feature lessens the potential for sampling bias.

Aspects of Faunal Dynamics

The late Cenozoic stratigraphic ranges of families and genera of terrestrial mammals can be used to analyze simple aspects of taxonomic evolution [that is, measurements of changes in total numbers of taxa and changes of taxa within clades through time (*19–21*)]. For North America we analyze these data for the last 12 million years (divided into five standard land mammal ages) (*22*), and for South America we analyze these data for the last 9 million years (divided into six land mammal ages) (*18*) (Table 1). The perspective given by this temporal framework permits establishment of a pre–land bridge "basal metabolism" to which post–land bridge faunal dynamics can be compared.

Table 1 lists summations for each land mammal age of (i) familial and generic diversity, (ii) numbers of first and last fossil occurrences (that is, observed originations and extinctions) of genera of native and immigrant taxa, and (iii) aspects of faunal dynamics and taxonomic evolution (*21*) based on data in (*22*) for North America and (*18*) for South America. Numbers of families and genera in each land mammal age on each continent are shown in Fig. 1 (top and bottom, respectively), with shading indicating the continent of origin of the taxa (*23*) (Fig. 1). Below we consider aspects of the taxonomic evolution first of families and then of genera.

Families. The total number of known families remained relatively constant throughout the late Cenozoic on both continents; the average diversity from late Miocene to Recent in both North and South America was about 34. Today, the familial diversities remain similar, with 35 in South America and 33 in North America (*17*).

In South America the peak in familial diversity (39 families) followed the appearance of the land bridge and the arrival of members of eight North American families in the Uquian, raising the number of immigrant families to 12; the total number of families then dropped to 36 before Lujanian time (Table 1). For North America the record likewise indicates a sharp rise in South American immigrant families after emergence of the isthmus: representatives of a total of six new families appeared in the late

Table 1. Faunal dynamics (genera per million years) of late Cenozoic land mammal genera in South America (left) and North America (right). The number of families represented are listed in brackets. The land mammal ages for South America are (from oldest to youngest) H, Huayquerian; M, Montehermosan; C, Chapadmalalan; U, Uquian; E, Ensenadan; and L, Lujanian. For North America they are C, Clarendonian; H, Hemphillian; B, Blancan; I, Irvingtonian, and R, Rancholabrean.

Indices (*21*)	South American land mammal age						North American land mammal age				
	H	M	C	U	E	L	C	H	B	I	R
a. Durations (million years)	4.0	2.0	1.0	1.0	0.7	0.3	2.5	5.0	2.5	1.3	0.7
b. Number of genera											
North American	1[1]	4[2]	10[4]	29[12]	49[12]	61[12]	92[33]	128[33]	99[25]	90[26]	102[26]
South American	72[29]	68[30]	62[29]	55[27]	58[24]	59[24]	0[0]	3[2]	8[6]	11[8]	12[9]
Total	73[30]	72[32]	72[33]	84[39]	107[36]	120[36]	92[33]	131[35]	107[31]	101[34]	114[35]
c. Originations (No.)											
North American	1	3	6	21	26	13	43	75	54	28	22
South American	55	32	14	25	19	8	0	3	7	4	1
Total	56	35	20	46	45	21	43	78	61	32	23
d. Extinctions (No.)											
North American	0	0	2	6	1	20	37	81	40	9	23
South American	36	20	32	16	7	25	0	2	1	0	9
Total	36	20	34	22	8	45	37	83	41	9	32
e. Running means											
North American	0.5	2.5	6.0	15.5	35.5	44.5	52	50.0	65.0	71.5	79.5
South American	26.5	42.0	39.0	34.5	45.0	42.5		0.5	4.0	9.0	7.0
Total	27.0	44.5	45.0	50.0	80.5	87.0	52	50.5	69.0	80.5	86.5
f. Origination rates											
North American	0.3	1.5	6.0	21.0	37.0	43.3	17.2	15.0	21.6	21.5	31.4
South American	13.8	16.0	14.0	25.0	27.0	26.7		0.6	2.8	3.1	1.4
Total	14.1	17.5	20.0	46.0	64.0	70.0	17.2	15.6	24.4	24.6	32.9
g. Extinction rates											
North American	0	0	2.0	6.0	1.5	66.7	14.8	16.2	16.0	6.9	32.9
South American	9.0	10.0	32.0	16.0	10.0	83.3		0.4	0.4	0	12.9
Total	9.0	10.0	34.0	22.0	11.5	150.0	14.8	16.6	16.4	6.9	45.8
h. Turnover rates											
North American	0.1	0.8	4.0	13.5	19.3	55.0	16.0	15.6	18.8	14.2	32.2
South American	11.4	13.0	23.0	20.5	18.5	55.0		0.5	1.6	1.6	7.2
Total	11.5	13.8	27.0	34.0	37.8	110.0	16.0	16.1	20.4	15.8	39.4
i. Per-genus turnover	0.4	0.3	0.6	0.7	0.5	1.3	0.3	0.3	0.3	0.2	0.5
j. Breakdown estimate of immigrants											
Total number											
Primary	1	1	2	10	18	20	0	2	6	8	9
Secondary	0	3	8	19	31	41	0	1	2	3	3
Originations											
Primary	1	0	1	8	9	2	0	2	6	3	1
Secondary	0	3	5	13	17	11	0	1	1	1	0
Extinctions											
Primary	0	0	0	1	0	7	0	2	1	0	7
Secondary	0	0	2	5	1	13	0	0	0	0	2

Blancan (four families) and early Irvingtonian (two families). Both continents experienced a notable decline in familial diversity at the end of the Pleistocene (*24*).

A sharp rise in the number of known immigrant families between the late Pleistocene and Recent occurs on both continents. This rise is due to our ignorance of late Cenozoic tropical faunas (*17*). Today, members of 14 North American families occur in South America and contribute 40 percent to the familial diversity of that continent, whereas members of 12 South American families occur in North America and account for a nearly equivalent 36 percent of that continent's familial diversity.

In summary, the data show that at the family level the interchange was balanced (*12*). The fact that total familial diversity on both continents is virtually the same today as it was in pre–land bridge times might be construed as indicative of symmetrical replacement of native by immigrant taxa at high taxonomic levels (Fig. 1).

Genera. The known late Cenozoic diversity of fossil genera is, on the average, greater in North America than in South America (Table 1, row b); this is in contrast to the Recent fauna which is slightly more diverse in South America (170 genera) than in North America (141 genera) (*17*). In South America known diversity remained near 72 genera for at least 6 million years prior to the land bridge (Fig. 1, column H), suggesting that an equilibrium was established at about that level, at least in the environments sampled. After the appearance of the land bridge, generic diversity rose rapidly to 84 in the Uquian, 107 in the Ensenadan, and 120 in the Lujanian (Table 1, row b). During this time the North American immigrants increased sharply but steadily in number and progressively contributed a larger part of the South American land mammal fauna. Today, 85, or 50 percent, of the mammal genera in South America are derived from members of immigrant North American families (*17*).

In North America, observed numbers of genera drop from 131 in the Hemphillian to 101 in the Irvingtonian and then rise to 114 in the Rancholabrean (Table 1). The known South American immigrants rose from 3 to 12 during this period and came to contribute only 11 percent to the total North American land mammal fauna in the Rancholabrean. Today, 29 (21 percent) of the land mammal genera in North America are derived from immigrant South American families (*17, 25, 26*). Most of the genera not sampled as fossils in North America live in subtropical to tropical latitudes in the Neotropical Realm (*8*).

The generic diversities of Recent and pre–land bridge faunas in North America are similar. However, in South America a major increase in generic diversity followed the appearance of the land bridge, the result of adding immigrant taxa. At the same time, the number of native South American genera declined by 13 percent between pre–land bridge and Lujanian faunas, a percentage reduction comparable to the 11 percent decline among native genera in North America. Thus, as in the case of families, the percentage decline of native genera was virtually identical on both continents, and in this regard the interchange was balanced. But the increase in both numbers and percentages of immigrant taxa was much greater in South America, as is discussed further below.

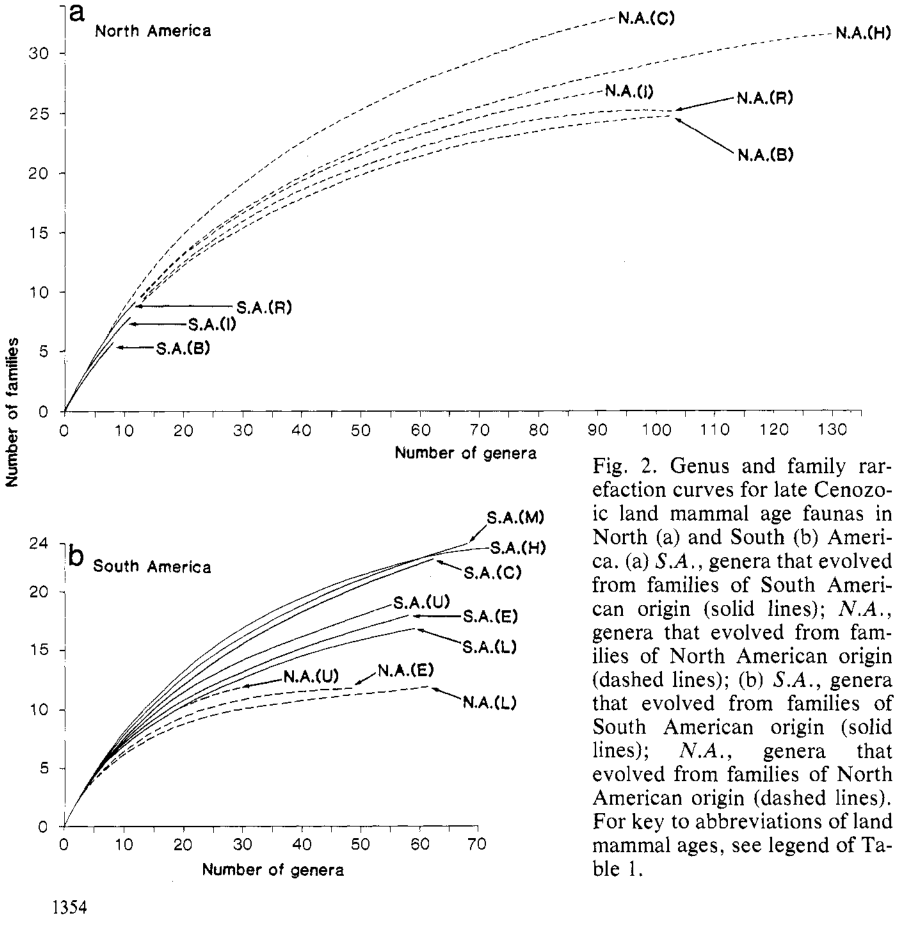

Fig. 2. Genus and family rarefaction curves for late Cenozoic land mammal age faunas in North (a) and South (b) America. (a) *S.A.*, genera that evolved from families of South American origin (solid lines); *N.A.*, genera that evolved from families of North American origin (dashed lines); (b) *S.A.*, genera that evolved from families of South American origin (solid lines); *N.A.*, genera that evolved from families of North American origin (dashed lines). For key to abbreviations of land mammal ages, see legend of Table 1.

Rarefaction Analysis

Before considering the dynamics of the Great American Interchange further, some aspects of the quality and robustness of the taxonomic data must be analyzed in more detail. The diversity values for land mammal age faunas shown in Table 1 and Fig. 1 are somewhat higher than the numbers of taxa actually recorded. Some taxa occur in preceeding and succeeding land mammal age faunas, and their presence in the intervening fauna or faunas is inferred. This usage of inferred ranges is conventional and legitimate for general analysis of diversity patterns, although an alternative analysis by rarefaction methods incorporates only the genera and families actually recorded in a particular land mammal age (*27*).

A taxonomic rarefaction curve is computed on the basis of the frequency distribution of genera within families in each land mammal age (Fig. 2). The distal end of each curve represents the number of genera and families actually recorded, and the curves provide estimates of the number of families that would have been recorded had fewer genera been found. Thus, rarefaction analysis provides answers to two basic questions: (i) Is the nature of sampling and taxonomic treatment consistent throughout the data set? and (ii) Did familial diversity differ significantly among the time intervals (land mammal ages) sampled?

All of the rarefaction curves in Fig. 2 have approximately the same shape, and crossing of curves is minimal, suggesting minimal overall differences in sampling both among land mammal ages and between continents. A sharp drop in North American native families (statistically significant, $P < .05$) occurs between the Clarendonian and Hemphillian (Fig. 2a), although no drop is seen in the number of actual or inferred families shown in Table 1. This drop could represent either a true decrease in diversity or a generic radiation among existing families. The diversity of native North American families within North America continues to drop after initiation of the interchange, but the changes are not statistically significant.

Diversity histories for South American natives in South America (Fig. 2b) reflect effects of the interchange. The post-interchange faunas (Uquian, Ensenadan, Lujanian) show significantly lower familial diversities than the pre–land bridge faunas, and the post-interchange curves for South American natives show decreasing diversity in chronostratigraphic order, the youngest being the lowest.

Thus, analysis of the data by rarefaction confirms the analysis of the raw family data presented above. The rarefaction work also lessens the possibility that the patterns observed in Fig. 1 are artifacts of sampling.

Patterns and Rates of Generic Evolution

The Great American Interchange has played a primary role in the development of basic biogeographic principles regarding tempo and mode of large-scale dispersal. Although these principles were formulated under a model of stationary continents, most can be applied to the dynamic paradigm with logical modifications and extensions (*28*). With the documentation and acceptance of plate tectonic theory, the Great American Interchange has become a classic example for studying the biological consequences of continental suturing.

Equilibrial biogeographic models have been suggested as applicable to the Great American Interchange (*9, 19, 29*) and have been used to test the extension of the island biogeographic theory of MacArthur and Wilson (*30*) to continental scales. This theory was first developed to explain biogeographic patterns on oceanic islands (*30, 31*) and only later was applied to continental and global systems (*19, 32–36*). The fundamental prediction of equilibrium models is that species diversity in any restricted area (that is, island, continent) will, under constant conditions, eventually attain a dynamic equilibrium maintained by balanced rates of origination (or immigration, or both) and extinction (Fig. 3). The resultant diversity and the time span required to attain equilibrium are largely dependent on the size of the area; thus continents will have a higher species diversity and lower per-species turnover rate and will require a longer time span to attain equilibrium, as compared to oceanic islands (*37*). Monte Carlo simulations and empirical studies of fossil data indicate that genera and families show patterns of diversification commensurate with diversification of their constituent species so long as large numbers of higher taxa are involved (*29, 34, 36*). This relationship permits study of patterns of diversification at higher taxonomic levels even though species are the real units of evolution.

As discussed above, North and South American land mammal faunas each appear to have attained equilibrial diversity prior to the Great American Interchange. These equilibria were dynamic, with diversity remaining steady despite continuous origination and extinction of taxa (Table 1). In South America, per-genus turnover rate averaged 0.4 genera per genus per million years from 9 to 2 million years ago, while in North America the per-genus turnover rate averaged only 0.3 genera per genus per million years over the same period. The greater generic diversity and lower overall turnover rates of mammals in North America prior to the interchange are consistent with its greater total area (24×10^6 square kilometers compared to 18×10^6 square kilometers for South America), as predicted by equilibrium models (*38*).

The emergence of the Panamanian land bridge ended the phase of simple equilibrium for both continents and made each a potential source of immi-

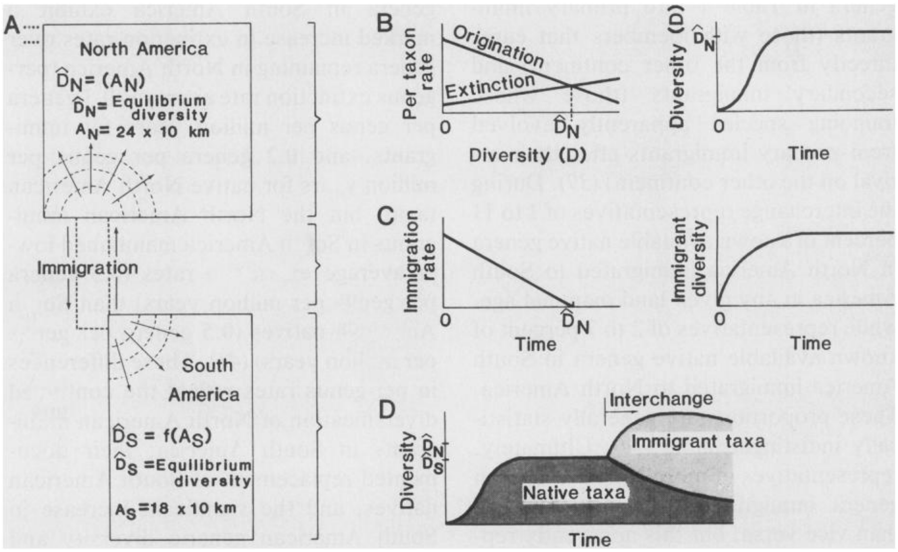

Fig. 3. Components of a hypothetical equilibrium model for the Great American Interchange. (A) Geographic constraints. North and especially South America were isolated continents through much of the Tertiary Period. As such, each should have supported a unique equilibrium diversity ($\hat{D}$), which may have been proportional, to a first approximation, to the area (A) of the continent (*29, 30*). Interconnection of the continents across the Panamanian land bridge terminated the equilibrium phase and permitted immigration of taxa between the two continents. (B) Closed-system diversification. Prior to interconnection, per taxon rates of origination (speciation) may have been high and rates of extinction low when diversity was low; with increasing diversity (and hence crowding of ecosystems), origination rates may have decreased, and extinction rates increased until becoming approximately equal at the equilibrium diversity $\hat{D}$ (*33–35*). This "diversity dependence" of evolutionary rates would result, in a simple deterministic system, in diversity increasing sigmoidally from some initial low to the equilibrium and then maintaining that equilibrium so long as the system remained closed (*43*). (C) Open-system immigration. Complete or partial interconnection of a large fauna at equilibrium with an area lacking fauna will initiate a flow of immigrants to the new area. The rate of immigration will be high at first and decline as the fauna in the newly colonized area becomes a larger and larger subset of the source fauna (*30, 37*). As a result, diversity in the new area should increase rapidly at first but later asymptotically approach an equilibrium determined by the equilibrium of the source area and by the local immigration and extinction rates. (D) Combined models. If taxa immigrate into a large area containing a native fauna, such as occurred in South America, the addition of immigrant taxa will, in essence, supersaturate the fauna of the new area. Extinction rates of both native and immigrant taxa will increase as diversity exceeds the equilibria of both faunal components. This will slow the increase in immigrant diversity and cause an exponential decline in native diversity. If the diversity of the source fauna is greater than the equilibrium of the native fauna, native diversity will eventually dwindle to zero in this simple model. More realistic constraints in the model (which could slow or prevent extinction of native taxa) would include backflow of immigrants north into North America and autochthonous evolution of taxa of immigrant ancestry, such as seen in the actual fossil records of North and South America.

grant taxa for the other. However, the tropical areas of North and South America seem to have acted as a barrier to dispersal of some representatives of genera and families. Only families with at least some constituent species distributed in tropical or subtropical areas took part in the interchange, whereas families with only temperate species did not disperse. Of all the families with part or all of their distribution in tropical areas, 17 South American families and 16 North American families dispersed; six South American and seven North American families did not. Thus, with regard to the potential family participants, the interchange was balanced (*10*, *12*, *17*).

Island biogeographic theory predicts that the effect of a source fauna on another fauna receiving immigrants should be proportional to the size (or diversity) of the source fauna (Fig. 3). In an attempt to apply this prediction to the interchange we divided the immigrant genera in Table 1 into primary immigrants (those with members that came directly from the other continent) and secondary immigrants (those whose founding species apparently evolved from primary immigrants after their arrival on the other continent) (*39*). During the interchange representatives of 1 to 11 percent of known available native genera in North America immigrated to South America in any given land mammal age, while representatives of 2 to 7 percent of known available native genera in South America immigrated to North America. These proportions are generally statistically indistinguishable (*40*). Ultimately, representatives of more North American genera immigrated to South America than vice versa, but this apparently represents a simple consequence of North America having a 60 percent greater average generic diversity than South America during the late Cenozoic. Thus, as predicted, the number of primary immigrants appears proportional to the size of the respective source faunas.

However, the subsequent evolutionary histories of the primary immigrants are significantly different. Various members of the 12 South American primary immigrants in North America gave rise to three secondary genera, whereas the 21 North American primary immigrants in South America gave rise to 49 secondary genera, derived subequally from members of five immigrant groups: cricetine rodents, carnivorans, proboscideans, perissodactyls, and artiodactyls (Table 1, row j). This difference in evolutionary histories represents nearly an order of magnitude difference in per-genus rates of origination between the respective primary immigrants (*26*). The Recent record further emphasizes this trend as demonstrated by the remarkable secondary diversity (more than 40 genera) of cricetine rodents.

The resulting faunal dynamics of native taxa on the two continents are predictable. North America, with a proportionately small "input" of primary immigrants, exhibits no detectable change in per-genus turnover rate; on the other hand, South America, where generic diversity eventually exceeded previous equilibrium levels by more than 50 percent, exhibits an increase of nearly 70 percent in per-genus extinction rates among native taxa (Table 1). The observed gradual decline in diversity of native South American genera subsequent to the land bridge (Fig. 1, column H and Table 1, row b) is consistent with patterns expected for a supersaturated biogeographic system (Fig. 3) [figure 6 in (*35*)]. North American immigrant genera in South America exhibit a marked increase in extinction rates over genera remaining in North America (per-genus extinction rate averages 0.3 genera per genus per million years for immigrants, and 0.2 genera per genus per million years for native North American taxa), but the North American immigrants in South America maintained lower average extinction rates (0.3 genera per genus per million years) than South American natives (0.5 genera per genus per million years) (*41*). These differences in per-genus rates reflect the continued diversification of North American immigrants in South America, their documented replacement of South American natives, and the significant increase in South American generic diversity and faunal enrichment on a continent-wide basis.

Conclusions

Some aspects of faunal dynamics of the Great American Interchange (that is, prior equilibrium, difference in turnover rates, importance of source faunas, and increased extinction with supersaturation) are predicted from elementary considerations of equilibrium theory. However, the significant and apparently rapid diversification of North American secondary immigrants within South America is not predicted by simple extrapolation of equilibrium models into evolutionary time frames. This radiation is thus the unique aspect of the interchange story; it alone seems to account for the long-observed asymmetry in interchange dynamics between the two continents and for the great change in taxonomic composition of the post–land bridge mammal fauna in South America (Fig. 1).

A possible but speculative explanation for the post–land bridge history of the South American fauna exists. During the late Cenozoic, a phase of orogeny beginning about 12 million years ago resulted in a significant elevation of the Andes Mountain range (*8*). A major phase of these orogenic movements occurred between 4.5 and 2.5 million years ago with a rise of from 2000 to 4000 meters (*42*). The newly elevated Andes served as a barrier to moisture-laden Pacific winds (*8*), and a rain shadow was created on the eastern (leeward) side. The southern South American habitats changed from primarily savanna-woodland to drier forests and pampas, and precocious pampas environments and desert and semidesert systems came into prominence at about that time. Many subtropical savanna-woodland animals retreated northward (*8*), and new opportunities favoring higher generic diversity arose for those animals able to adapt to these new ecologies.

The greater diversification of North American genera after they had reached South America is evident in such different groups as cricetid rodents, canid carnivores, gomphotheres, horses, llamas, and peccaries. If the relative success of northern groups is attributed to competitive displacement of equivalent southern groups, it becomes necessary to develop a number of complex scenarios with a great deal of uncertainty concerning which groups of species compete and on which adaptive bases (*10*). Perhaps it is more reasonable to attribute the success of the North American groups to some general ability inherent in their previous history to insinuate themselves into narrower niches (*8*). In any event, their success in South America is a clear pattern not predicted by simple equilibrium theory.

References and Notes

1. A. R. Wallace, *The Geographical Distribution of Animals* (Macmillan, London, 1876).
2. For example, Wallace (*1*) regarded *Galera* (a skunk), *Tapirus*, and *Lama* as moving from South America to North America, but the reverse is now known to be true.
3. It is somewhat ironic that these workers neither discussed, nor even believed in, the Great American Interchange as such (G. G. Simpson, personal communication, 11 June 1981); see also (*6*).
4. Translated from K. A. von Zittel, in *Handbuch der Palaeontologie*, vol. 4, *Band Vertebrata (Mammalia)* (Ouldenberg, Munich, 1891–1893), pp. 754–755. "Aber nicht nur nordamerikanische Typen benützen die neuröffnete Bahn, um ihr Verbreitungsgebiet zu vergrössen, sondern auch die südlichen Autochthonen begannen nach Norden zu wandern, und so vollzog sich am Schluss der Pliocaenzeit eine der merkwürdigsten Faunenüberschliebungen, welche die Geologie zu verzeichnen hat."

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18. The range distributions of South American taxa are drawn from L. G. Marshall, R. Hoffstetter, R. Pascual, *Fieldiana Geol.*, in press; and L. G. Marshall *et al.*, *ibid.*, in press.
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21. Indices used for measuring aspects of mammalian faunal dynamics in Table 1 are defined and computed as follows: (i) Durations of each land mammal age are given in millions of years (to the nearest tenth) and are based on all available radioisotopic, paleomagnetic, and biostratigraphic data, much of which is summarized in (*11*). (ii) The number of genera is the total number (or "diversity") of terrestrial mammal genera known for each land mammal age in each continent. We exclude *Homo*, and aquatic and volant mammals such as sea cows and bats. (iii) Originations are number of first appearances of a particular taxon (genus) in a given time interval (land mammal age) on each continent. This category combines three different kinds of originations: (a) New native autochthons (taxa whose members evolved in situ); (b) new immigrant allochthons (taxa with members that immigrated from outside the continent, or at least outside the area previously sampled); and (c) pseudo-originations produced by taxonomists when an evolving lineage changes enough to warrant a new name. Sufficient data are not available to consistently make distinctions among these alternatives. (iv) Extinctions are last appearances of a taxon on a given continent. These may not be "true extinctions" since the same taxon may continue to live on another continent, as with the Rancholabrean "extinctions" of *Tapirus* and *Equus* in North America, or the same population evolves to the point where it receives a new name, thus producing a taxonomic or pseudoextinction. As in the case of originations, the data do not consistently permit discrimination between these alternatives; however, pseudoextinctions appear to be of minor importance in this data set. (v) Running means (R_m) are expressions of the standing crop of a taxon (*19*, *20*). This statistic compensates for time intervals of unequal duration by subtracting the average of originations (O_i) and extinctions (E_i) for a given age from the number of genera (S_i) for that age; thus, $R_m = S_i - (O_i + E_i)/2$. (vi and vii) Origination rates (O_r) are indices adjusted for time intervals of unequal length by dividing the total number of originations (O_i) of taxa occurring during a given time interval by the duration (d) of that interval; thus, $O_r = O_i/d$. By similar reasoning, the extinction rate, $E_r = E_i/d$. (viii) Turnover rates (T) are the average number of taxa of a given rank that either originate or go extinct during a given time interval (that is, rates of first and last appearances). Turnover rates represent the average of origination rates and extinction rates for a given time interval; thus, $T = (O_r + E_r)/2$. (ix) The per-genus turnover rate is the turnover rate adjusted for average diversity calculated by dividing the total turnover rate (T) by the total running mean (R_m).
22. The range distributions of North American genera are drawn from S. D. Webb, in *Pleistocene Extinctions, the Search for a Cause*, P. Martin and R. Klein, Eds. (Univ. of Arizona Press, Tucson, ed. 2, in press).
23. We have counted the trans-Beringian immigrants with the native North American genera, while freely recognizing the fact that North America was not a "closed system" as was South America. Three trans-Beringian genera (*Pseudocyon, Pseudoceras, Torynobelodon*) appear in the North American Clarendonian. After the Clarendonian, incursions into North America from the Old World grew steadily; trans-Beringian origins account for 18 genera in the Hemphillian, 20 genera in the Blancan and Irvingtonian, and 27 genera in the Rancholabrean. Most Hemphillian and Blancan immigrants were cricetid rodents and diverse Carnivora; by Irvingtonian and Rancholabrean time the principal taxa were arvicoline rodents and bovid and cervid ruminants. In fact, the balance of generic exchange between North America and Eurasia shifted strongly in favor of the latter during the late Cenozoic [C. A. Repenning, in *The Bering Land Bridge*, D. M. Hopkins, Ed. (Stanford Univ. Press, Stanford, Calif., 1967)], p. 288. Nonetheless, virtually all Irvingtonian and Rancholabrean immigrants from trans-Beringea were steppe-tundra grazers. Their ecological impact was surely concentrated in north temperate latitudes and considerably removed from major impact on the Great American Interchange in tropical North America.
24. Of the 36 families of mammals recorded in beds of Lujanian age in South America, 8 (22 percent) are now extinct. These include 6 of 24 (25 percent) native and 2 of 12 (17 percent) immigrant groups. All eight families were present in North America at about that time, and became extinct there as well. Of the 35 families of mammals recorded in beds of Rancholabrean age in North America, 11 (31 percent) are now extinct. These include 6 of 26 (23 percent) native families and 5 of 9 (56 percent) immigrant families.
25. Of the 120 genera known from the Lujanian of South America, 45 (40 percent) became extinct. Included were 25 of 59 (42 percent) native South American genera and 20 of 61 (33 percent) immigrant genera. These differences are not statistically significant (*26*). Of the 114 genera known from the Rancholabrean of North America, 32 (28 percent) became extinct. Included are 23 of 102 (23 percent) native North American genera, and 9 of 12 (75 percent) immigrant genera.
26. Tests for differences in proportions: $z = 1.08$, $P > .05$ for South American; $z = 3.82$, $P < .01$ for North American.
27. D. M. Raup, *Paleobiology* **1**, 333 (1975). The mathematical technique used here was that applied by Raup to higher taxa.
28. M. C. McKenna, in *Implications of Continental Drift to the Earth Sciences*, D. H. Tarling and S. K. Runcorn, Eds. (Academic Press, New York, 1973), p. 21; R. H. Tedford, in *Paleogeographic Provinces and Provinciality*, C. A. Ross, Ed. (Soc. Econ. Paleontol. Mineral. Spec. Publ. 21, 1974), p. 109.
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38. Alternatively, the higher average turnover rates for South America may simply represent the need for a refined synthetic systematic review of these faunas [D. M. Raup and L. G. Marshall, *Paleobiology* **6**, 9 (1980)], and rate differences between the continental faunas may be due to different approaches to taxonomic treatment (lumpers versus splitters). We consider only potential mammal-mammal interactions yet recognize that nonmammalian groups may be involved as well [J. H. Brown and D. W. Davidson, *Science* **196**, 880 (1977)].
39. This subdivision of immigrants into primary and secondary groups has never before been formally attempted, although many workers have noted existence of these categories. Several caveats should accompany such an interpretive subdivision, the first being our wholly inadequate knowledge of late Cenozoic mammalian evolution in the American tropics, regarded as an undocumented source area for many of the immigrants (*8*). Nevertheless, our criteria for subdivision are simple and can be easily tested by further fossil discoveries. Primary immigrant genera are native genera (those that belong to native families) with members that occur on the other continent or are genera with members so closely related to known genera on the other continent that further taxonomic studies will probably show them to be congeneric (a criterion based on the observations of L.G.M. and S.D.W.). Secondary immigrant genera are those that belong to families native to the other continent but are unknown on that continent and apparently lack possible congeneric forms. By these criteria, the primary South American immigrants to North America are *Didelphis*, *Kraglievichia*, *Dasypus*, *Glyptotherium*, *Pliometanastes*, *Nothrotheriops*, *Eremotherium*, *Thinobadistes*, *Glossotherium*, *Hydrochoerus*, *Neochoerus*, and *Mixotoxodon*; and the primary North American immigrants to South America are *Calomys*, *Canis*, *Felis*, *Leo*, *Smilodon*, *Conepatus*, *Galera*, *Lutra*, *Mustela*, *Cyonasua*, *Nasua*, *Arctodus*, *Hemiauchenia*, *Odocoileus*, *Dicotyles*, *Platygonus*, *Equus*, *Hippidion*, *Tapirus*, *Cuvieronius*, and *Stegomastodon*. The remaining immigrant taxa listed in (*22*) for North America and in (*18*) for South America are regarded as secondary.
40. A z-test for differences in proportions [G. W. Snedecor and W. G. Cochron, *Statistical Methods* (Iowa State Univ. Press, Ames, ed. 6, 1967, p. 220)] applied to total numbers of primary immigrants moving north and south as proportions of the total size of their respective native faunas over the whole of the last 9 million years reveals no significant difference between North and South America ($z = 0.719$, $P > .05$). However, significant differences do occur within the Ensenadan-Lujanian interval (≈ Rancholabrean), when approximately 2 percent of available South American genera move north compared to 11 percent of available North American genera which move south ($z = 2.278$, $P < .05$).
41. It is possible that the comparatively low extinction rate for immigrant taxa in Table 1, row g may involve multiple immigrations rather than any special quality of the immigrants. If all members of a taxon endemic to continent A died out on that continent, it is for all practical purposes, regarded extinct. (Members of this taxon may have dispersed to continent B before their extinction on A, and then may have been able to reinvade A from B after the population on A died out, but the chance of this happening is regarded as having a very low probability.) If, on the other hand, an immigrant from continent B to continent A died out on A, its extinction would not be universal so long as it survived on continent B. This population from B could then reestablish itself on A by subsequent and repeated invasions from B and create the impression that the original population in A never really "became extinct." Such reestablishments of populations would result in lower extinction rates for immigrants relative to native taxa (that is, Table 1, row g) even if actual extinction rates in both groups were the same on each continent.
42. B. S. Vuilleumier, *Paleobiology* **1**, 273 (1975).
43. For applicability to mammalian evolution, see J. A. Lillegraven, *Taxon* **21**, 261 (1972).
44. We thank W. Burger, J. Cracraft, G. McGhee, K. Luchterhand, J. M. Savage, G. G. Simpson, S. Stanley, and W. D. Turnbull for reading the manuscript. Supported in part by NSF grant EAR 7909515 and DEB 7901976 (to L.G.M.), NSF grant DEB 7810672 (to S.D.W.), and NSF grant EAR 75-03870 (to D.M.R.).