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Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach

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We analyze the distribution of body masses for 701 species of South American terrestrial mammals at different spatial resolutions from continental to biome, to local habitat scales. Previous studies on North American mammals suggest that body size distributions are highly modal and right skewed at continental scales, but become more uniform as spatial scale decreases. We show, in general, that these patterns also hold for the body size distribution of South American terrestrial mammals. However, we also found some striking differences attributable to the history of this biota and related to the Great American Biotic Interchange (GABI). At continental scales the distribution of body masses for South American mammals is highly right skewed and possesses several modes. One mode corresponds to species derived from North American ancestors, while a second mode, towards larger size, is characteristic of the South American stock. The same pattern is apparent at biome and local habitat scales. We found support for the progressive flattening of the distributions as spatial scale decreases, but they do not become as flat (indistinguishable from log-uniform) as they do in North America. However, the pattern is stronger for species of South American origin. Our results indicate that there is a strong historical component affecting the macroecological structure of contemporary assemblages at different spatial scales. Body size distributions can provide valuable information on the ways biotas built up.

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Many of the relevant questions concerning the structure of natural communities can be fruitfully approached at the interface between ecology and biogeography (e.g., Ricklefs 1987, 1989, Brown 1984, Brown and Maurer 1989, Jackson and Harvey 1989, Lawton 1990, Tonn et al. 1990, Wiens 1990, Hinch et al. 1991, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Maurer 1994). It has become clear in recent years that the composition and organization of species assemblages is the result of processes that occur along a wide spectrum of temporal and spatial scales. Current assemblages are not only embedded and affected by processes operating at larger spatial scales, but also carry with them the signature of events that occurred in the distant past.

An increase in the spatial scale of analysis beyond the local scale makes it possible to understand large scale biogeographic patterns that emerge as the result of the interaction among individual level physiological characteristics, species' tolerances to biotic and abiotic conditions, and the large temporal and spatial scale process of dispersal, extinction and speciation (e.g., Brown 1984, 1987, 1995, Brown and Maurer 1989, Roughgarden 1989, Brown and Nicoletto 1991, Brown et al. 1993, Marquet et al. 1993, 1995, Ricklefs and Schluter 1993, Marquet 1994, Rosenzweig 1995). This approach has been recently applied by Brown and Nicoletto (1991) to understand the factors affecting the composition of biotas at different spatial scales by focussing on

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the spatial scaling of body size distributions for North American land mammals.

Body size is known to be related to a variety of physiological, ecological, and evolutionary characteristics of organisms (e.g., Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Bonner 1988), hence body size patterns can in principle be explained by the interaction among processes acting at these three levels. Under this scenario it is expected that body size distributions will be highly variable in both time and space. Surprisingly, they show some striking similarities (e.g., Blackburn and Gaston 1994, Brown 1995). Body size distributions have elicited considerable interest in recent years (see Blackburn and Gaston 1994 for a review). Much of this interest stem from their practical and theoretical importance. Body size distributions have been used to estimate species diversity (e.g., May 1988, Siemann et al. 1996), and their shape is thought to result from size-related extinction and speciation biases (e.g., Dial and Marzluff 1988, Martin 1992, Maurer et al. 1992, Marquet and Taper 1998) associated to basic processes of energy acquisition and convertion (Brown et al. 1993).

In this paper we analyze the body size distribution of South American terrestrial mammals at different spatial scales, from continental down to local habitat scales. Because this biota has been subjected to a long history of isolation, punctuated by episodes of biotic interchanges, it provides an opportunity to assess the legacy and importance of these large scale phenomena at different spatial resolutions. We show that while it has some similarities with the patterns reported for North American mammals, it has some major differences attributable to the history of the South American biota. For South American mammals, one of the most important events that drastically changed the composition of the actual biota, and the course of species evolution and subsequent interactions at local scales, was the so-called Great American Biotic Interchange (GABI). This event, which occurred about 2.5 Ma, after the formation of the Isthmus of Panama, allowed the invasion of the South American continent by 17 families of land mammals, most of which diversified and became well represented in local communities across the continent. Thus, this historical event not only altered the composition of the South American biota as a whole, but also had enormous ecological impact in changing the pool of potential species to form local communities. In this paper we characterize the consequences of this event upon the current composition of mammalian assemblages at different spatial scales from continental to local. We show the importance of considering processes occurring at large temporal and spatial scales to understand the structure and composition of mammalian assemblages in South America.

Material and methods

We compiled data on species occurrences, and body size of terrestrial South American mammals for three different spatial scales: 1) the entire South American continent, 2) the biomes of South America ($n = 10$) as defined by Udvardy (World Conservation Monitoring Centre 1992) and 3) 14 small patches (10–1000 ha) of relatively homogeneous habitat. Species lists for these patches of local habitat were obtained from the literature. We tried to ensure that each faunal list was derived from an exhaustive sampling of all species that utilize the habitat. For most species we used names following Wilson and Reeder (1993). We followed throughout the criteria proposed by Brown and Nicoletto (1991), thus the analysis included all species of native terrestrial mammals (i.e., we excluded bats, pinnipeds, cetaceans, and sea otters). Similarly, we used a single value of body mass for each species, ignoring intraspecific variation. Body mass values and distributional records were obtained from the literature (Damuth 1987, unpubl., Eisenberg 1989, Arita et al. 1990, Emmons 1990, Redford and Eisenberg 1992, Cofré and Marquet 1998) and field guides. In the few cases where masses were unavailable we estimated them based on length figures using regressions for the family. As in most previous studies of body size distributions, values were transformed to their logarithms (base 2).

To assess the existence of differences in body size distributions across spatial scales, distributions were compared with null models that assumed that species were assembled at random from appropriate larger-scale species pools. For each biome we randomly drew the observed number of species from the South American pool (for local habitats the same procedure was carried out but using the biome where the site was located as the source pool). This procedure was repeated 1000 times. For each simulation the median of the body size distribution was recorded. To assess the null hypothesis that the biome was a random sample from the continental species pool we compared the observed median against the 1000 simulated random samples. The same procedure was repeated for local habitats.

Brown and Nicoletto (1991) found that body size distributions become progressively more uniform as spatial scale is reduced. Following their lead, we quantified this change in shape by comparing all distributions to a log-uniform distribution, with the same range as the South American distribution, by using the Kolmogorov-Smirnov D_n statistic and test.

In order to assess the present day impact of the biotic interchange between the Americas we repeated the analysis, but this time we separated species according to their origin (i.e., the South or North American source of the family before the beginning of the interchange) following Lessa and Fariña (1996). As did these authors, we classified sigmodontine rodents as of North American origin, although this is still a vexing problem for paleobiologists (see Webb 1985).

Results

We assembled data for 701 species of terrestrial South American mammals. Statistics for the frequency distributions of body masses at different spatial scales are presented in Tables 1 and 2. At the continental and biome scales distributions are positively skewed. The same is true at the level of local habitats but for three cases (Table 2) which showed negative skewness. In general, standard skewness tended to decrease from continental to biome to local habitat scales, whereas quartile range (the width of the range about the median that includes 50% of the cases) increases. However, no apparent trend was observed in the median of distributions. The distribution of the entire South American fauna was highly modal and significantly right skewed (Fig. 1). The mode was in class 5 to 7, approximately 30 to 150 g. A kernel smoothing, which allows us to discern the density of data points or areas where the data are most concentrated in the sample (Silverman 1986), shows the existence of two other modes located at 130–1050 g and 2050–8200 g (Fig. 1). The distribution of body masses for North American mammals do not show the second (130–1050 g) modal size class.

The distribution of body masses at the level of biomes show modal classes which in most cases correspond to either the first or the second mode of the continental distribution (Fig. 2). At this spatial scale, distributions were highly modal and all of them were significantly different from log-uniform distributions (Fig. 2, Table 3). Most biomes were random samples of the continental distribution (Table 1). The exceptions were the Tropical humid forest, Savanna, and the Mountain biomes. The first two had significantly larger medians while the third had a significantly smaller median. In general, body size distributions at the biome level tended to have larger quartile ranges than the continental distribution.

At the level of local habitat patches (Fig. 3), body size distributions tended to be less skewed, and have larger medians and quartile ranges than those observed for their corresponding biomes (Table 2).This implies that body size distributions at local scales are flatter than those at the biome level. However, eight out of 14 distributions were random samples of their respective biome pools (Table 2), and the other six distributions had medians that were significantly larger than expected under random sampling. Most of these latter local habitats ($n = 4$) were located in the Tropical humid forest biome. As observed at the biome level, most distributions at the level of local habitat patches ($n = 9$) were significantly different from log-uniform distributions (Table 3). These results suggest that, in relative terms, as we change spatial scale from biomes to local habitat patches distributions tend to become flatter, as implied by the

Table 1. Summary statistics for the distribution of body masses for South American mammals at the continental and biome scales. *P* value indicates the probability associated with the null hypothesis that the biome was a random sample from the continental species pool.

Biome number	Biome	*N*	Median	Minimum	Maximum	Quartile range	Standard skewness	*P*
All	South America	701	7.3	2.93	18.19	3.85	9.73	
1	Tropical humid forest	324	8.25	2.93	18.19	4.09	4.00	0.0009
2	Savanna	78	8.15	3.64	15.61	5.47	1.76	0.018
3	Mountain system	218	6.27	3.46	17.46	4.21	6.73	0.0009
4	Tropical dry forest	155	7.45	3.62	18.19	5.23	4.14	0.345
5	Temperate rain forest	95	7.75	4 37	16.1	4.83	2.98	0.2
6	Temperate grassland	78	6.65	3.69	17.86	4.95	3.64	0.15
7	Warm semi-desert	75	7.23	3.5	16.04	3.69	3.23	0.48
8	Sclerophyllus forest	21	6.66	4.8	12.85	4.78	1.21	0.29
9	Temperate broadleaf forest	19	7.08	4.39	16.1	6.03	1.96	0.43
10	Cold winter desert	44	7.27	4.04	16.87	4.65	2.87	0.49
	Biome mean	110.7	7.28	3.84	16.53	4.79	3.25	

Table 2. Summary statistics for frequency distribution of body masses for South American mammals in 14 local habitats. *P* value indicates the probability associated with the null hypothesis that the local habitat was a random sample from the biome species pool. Biome number as in Table 1.

Habitat number	Locality	*N*	Biome	Median	Minimum	Maximum	Quartile range	Standard skewness	*P*	Source
1	Fray Jorge N. P.	13	8	6.66	4.8	12.85	5.4	1.1	0.41	Schamberger and Fulk 1974
2	La Campana N. P.	19	8	7.97	4.8	16.04	5.86	0.65	0.06	Zunino 1990
3	Cuzco Amazónico N. R.	56	1	9.69	3.91	17.44	5.32	0.38	0 0009	Woodman et al. 1991
4	Cocha Cashu Biological Station	65	1	11.03	4.64	17.44	4.72	0.04	0.00001	Terborgh et al. 1984
5	Torres del Paine N. P.	25	10	6.4	4.04	16.87	6.3	1.84	0.0697	Johnson et al. 1990
6	Torres del Paine N. P	16	5	6.255	4.64	16.1	7.56	1.71	0.247	Johnson et al. 1990
7	Rancho Acurizal	40	4	12.11	3.91	17.44	5.89	−1.17	0.00001	Schaller 1983
8	Ticoporo N. R.	32	1	12.06	4.64	17.44	4.66	−0.95	0.00001	Ochoa et al. 1988
9	Los Pijiguaos N. R.	32	1	9.965	4.7	17.44	5.83	0.87	0.00001	Ochoa et al. 1988
10	Nahuelbuta N. P.	16	9	8.58	4.67	16.04	6.68	0.58	0.0959	Murua 1995
11	Manu N. P.	21	3	6.57	3.75	17.61	7.4	0.9	0.281	Pacheco et al. 1993
12	Valle de la Paz	23	3	6.01	3.9	16.07	5.32	2.4	0.11	Mercado and Miralles 1991
13	Pairumani	16	3	5.93	4.69	16.07	5.27	2.08	0.113	Pearson 1951
14	Ecological Reserve (IBGE)	28	2	10.515	4.7	15.46	6.12	−0.09	0.019	Fonseca and Redford 1984
	Habitat mean	28.7		8.55	4.41	16.45	5.88	0.74		

observed increase in medians and quartile ranges, but they are still highly modal and different from log-uniform distributions (Fig. 3, Table 3).

Effects of origin

The total number of mammal species for the South American continent was 701. Of this 349 are of South American origin, while 352 species are of North American origin. The number of species in each category is remarkably similar and not significantly different from the expected under equal proportions ($\chi^2 = 0.013$, df = 1, $P > 0.6$, Table 4). However, at the level of biomes this pattern changes. The number of species of North American and South American origin are significantly and positively correlated across biomes (Pearson's $r = 0.79$, df = 8, $P = 0.006$). However, species of North American origin are significantly more common in three biomes (Temperate grassland, Cold winter desert, and especially in the Mountain biome, Chi-square test, df = 1, $P < 0.04$ in all cases), while species of South American origin are more common in one biome (Tropical humid forest, $\chi^2 = 17.8$, df = 1, $P = 0.00002$). In the other six biomes the proportion of species in each category was not significantly different from what is expected under the null hypothesis of equal proportions (Chi-square test, df = 1, $P > 0.13$ in all cases). Similarly, at the local habitat scale a positive correlation between number of species of North American and South American origin was found (Pearson's $r = 0.793$, df = 12, $P = 0.001$). However, in five local habitats the number of species of North American origin was significantly larger than the number of species of South American origin (Table 5). These habitats are located in four different biomes: the Cold winter desert, Temperate rainforest, Mountain system, and Temperate broad-leaf forest. Interestingly, species in both categories occur in very similar proportions in the other nine local habitats, including those within the Tropical humid forest biome, which harbors a significantly larger number of species of South American origin.

In relation to the body size distribution of species we assessed the potential effect of species' origin by analyzing first the continental distribution of body masses. In Fig. 1 we showed that in contrast to the North American distribution of body masses, South America shows three modes. However, when the distribution of body masses for South American mammals is analyzed, distinguishing between species of North American and South American origin (Fig. 4), it is apparent that the latter species contribute the most to this second mode, while the first mode is produced mostly by species derived from North American ancestors. This same pattern was evident at the biome level (Fig. 5).

Because we are interested in the effect of species' origin on patterns in body size distributions, we restricted our analysis of body size distributions at different spatial scales only to those biomes and local habitats whose distributions were found to be significantly different from what it would be expected under random sampling of species from the continental and biome pools respectively (i.e., the Tropical humid forest, Savanna, and the Mountain biomes, see Table 1). However, this time species pools were separated according to species origin. The results of this analysis show that regarding species origin, both the Mountain and Savanna biomes are random samples of their respective continental pools ($P = 0.26$ and 0.44 for the North American and South American species, respectively, in the Mountain biome, and $P = 0.18$ and 0.27 for the Savanna biome). This result underscores the importance of species origin in understanding patterns of body size distributions at the biome level. However, species of South American origin show a distribution of body masses with a median significantly larger than expected from random sampling from its continental pool for the Tropical humid forest biome ($P = 0.0009$), which suggests that these species account for the observed non-randomness in the distribution of body sizes for this biome (Table 1).

At the level of local habitats, we tested for the effect of species origin in affecting the non-random patterns in body mass distributions for the local habitats found within the Tropical humid forest biome. Our results show that the non-random pattern shown in Table 2 is not affected by species' origin. Species of North American origin had distribution of body masses that were significantly larger ($P < 0.02$ in all cases) than expected for the four local habitats considered. Similarly, species of South American origin had medians significantly larger than expected in three local habitats ($P < 0.03$). The exception was the local habitat number three ($P = 0.36$).

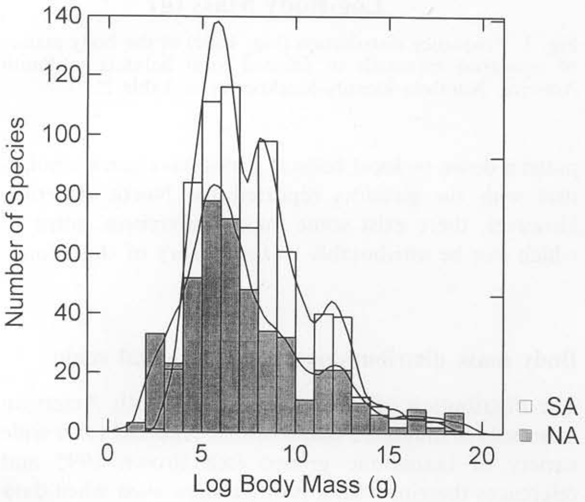

Fig. 1. Frequency distribution ($\log_2$ scale) of the body masses of the 701 species of terrestrial South American mammals (open bars) and of the 465 species of terrestrial North American mammals (shaded bars) reported by Brown and Nicoletto (1991). Continuous lines represent a kernel smoothing (see text).

Table 3. Comparisons of the body mass distributions for South American mammals in ten biomes and 14 local habitats with a log-uniform distribution. D_n is the Kolmogorov-Smirnov statistic, numbers in parentheses identify biomes and local habitats as in Tables 1, 2.

South American biomes		D_n	P
Tropical humid forest (1)		0.280	0.0001
Savanna (2)		0.277	0.0001
Mountain system (3)		0.341	0.0001
Tropical dry forest (4)		0.287	0.0001
Temperate rain forest (5)		0.299	0.0001
Temperate grassland (6)		0.314	0.0001
Warm semi-desert (7)		0.378	0.0001
Sclerophyllous forest (8)		0.361	0.006
Temperate broad-leaf forest (9)		0.328	0.025
Cold winter desert (10)		0.330	0.0001
Local habitats	Biome	D_n	P
Fray Jorge N. P. (1)	8	0.362	0.049
La Campana N. P. (2)	8	0.298	0.054
Cuzco Amazonico N. P. (3)	1	0.185	0.043
Cocha Cashu Biological Station (4)	1	0.157	0.082
Torres del Paine N. P.1 (5)	10	0.399	0.008
Torres del Paine N. P.2 (6)	5	0.293	0.022
Rancho Acurizal (7)	4	0.159	0.265
Ticoporo N. R. (8)	1	0.20	0.154
Los Pijiguaos N. R. (9)	1	0.24	0.050
Nahuelbuta N. P. (10)	9	0.264	0.179
Manu N. P. (11)	3	0.285	0.053
Valle de La Paz (12)	3	0.349	0.005
Pairumani (13)	3	0.367	0.019
Ecological Reserve (IBGE) (14)	2	0.180	0.325

Regarding the shape of the distributions, for species of North American origin and at the biome level, all but one distribution (Temperate broad-leaf forest) were significantly different from a log-uniform distribution, with a positive skew, and a modal class that corresponds to that observed at the continental scale (Fig. 4). At the level of local habitats eight out of 14 were not significantly different from a log-uniform distribution (local habitats 1,2,3,4,8,9,10,14). For species of South American origin, distributions tend to be less skewed, as compared to those for species of North American origin, and seven biomes show distributions significantly different from a log-uniform distribution, including the Temperate broad-leaf forest biome. This suggests that the non-uniform distribution that characterizes this biome (Table 4) is mostly due to species of South American origin. Similarly, species of North American origin contribute to the existence of non-uniform body mass distributions in the Warm semi-desert, Temperate grassland, and Savanna biomes. At the level

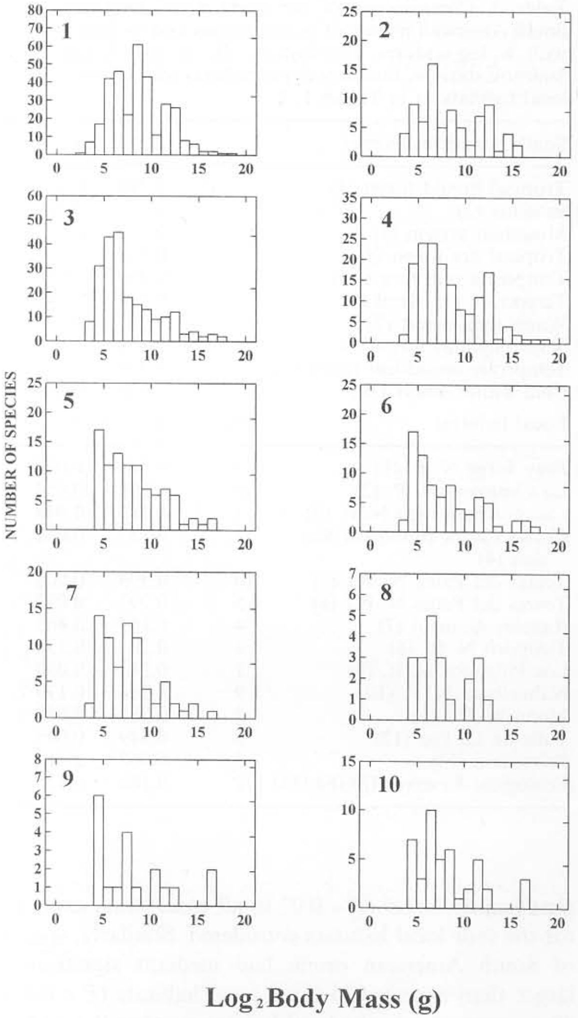

Fig. 2. Frequency distribution (log$_2$ scale) of the body masses of terrestrial mammals inhabiting ten biomes in South America. Numbers identify biomes as in Table 1.

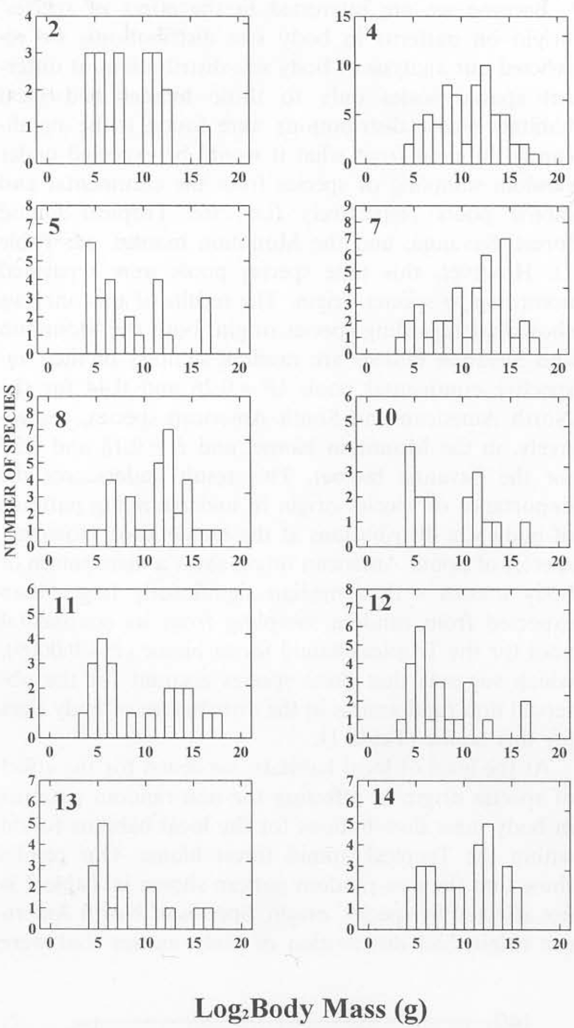

Fig. 3. Frequency distribution (log$_2$ scale) of the body masses of terrestrial mammals in selected local habitats in South America. Numbers identify localities as in Table 2.

of local habitats, only one (local habitat 4) out of 14 has a distribution of body masses significantly different from a log-uniform distribution. This suggests that the progressive flattening in body mass distributions from continental to biome to local habitat scales is most evident for species of South American origin. However, as we go from continental to local scales, distributions for species of North American and South American origin tend to increase their medians and quartile ranges (Tables 4 and 5). Thus, in relative terms, distributions become flatter as we decrease the spatial scale of analysis.

Discussion

We have shown for South American mammals that their distribution of body masses and its spatial scaling pattern down to local habitat scales have some similarities with the patterns reported for North America. However, there exist some major differences, some of which can be attributable to the history of this biota.

Body mass distributions at a continental scale

The distribution of body masses for South American mammals is similar in shape to that reported for a wide variety of taxonomic groups (see Brown 1995 and references therein) with a positive skew even when data are transformed to logarithms. As compared to the distribution of body masses for North American mammals (Brown and Nicoletto 1991), South American mammals encompass a smaller range in body sizes. This is due mostly to the low diversity of soricid species in

South America, which in North America can reach down to 3 g as exemplified by shrews of the genus *Sorex*.

Both South and North American distributions have a mode between 30 and 150 g. This mode, indicating a large number of medium-sized species, has recently been suggested to reflect the existence of an ecological and evolutionary optimum size for mammals, which is close to 100 g (Brown et al. 1993, Brown 1995, Marquet et al. 1995, Marquet and Taper 1998). However, a close examination of Fig. 1 shows the existence of two other modes. The third mode, present in both South and North American mammals, can be explained if the model proposed by Brown et al. (1993) is modified to include energy limitation (Marquet and Keymer unpubl.), which is a realistic assumption for predators and species of large size that feed on poor quality food. But how can we explain the existence of the other two modes only in South American mammals? Our results (Fig. 4) show that the first, or left, mode is composed primarily of species derived from North American ancestors, while the second mode is composed primarily of mammalian species derived from South American ancestors (mostly marsupials, and hystricognath rodents). This led us to propose that this bimodal arrangement reflects a key event in the history of the build up of the South American mammalian biota: the Great American Biotic Interchange (GABI) that occurred around 2.5 Ma and allowed the migration of 17 families of mammals of North American and/or Old World ancestry into South America. However, the mechanisms that gave rise to the presently observed distribution of body masses for species of North American and South American origin are presently unknown. To solve this question requires knowledge of the distribution of body masses for South American mammals prior to the GABI event. If this distribution were similar to the present one, then we could invoke a competitive replacement by which native medium-size South American species would have been driven extinct by North American immigrants. This could be a reasonable scenario if we assume a competitive superiority of North American immigrant taxa, as proposed by several authors (e.g., Webb 1976, 1985, Simpson 1980). However, a recent analysis of this issue by Lessa and Fariña (1996) suggests that mammals of South American origin were no more prone to extinction than their North American counterparts, and that high rates of extinction characterize large-sized species, not medium-sized ones. This evidence renders the hypothesis of competitive replacement as unlikely. However, it should be borne in mind that competition does not need to be immediate, pairwise, or between taxa of similar size to be an important force in shaping biotas. A more plausible hypothesis is that the mode contributed to by species of South American origin was also characteristic

Table 4. Summary statistics for frequency distributions of body masses for South American terrestrial mammals according to their origin in ten biomes. *P* is the probability associated with the null hypothesis of equal number of species of North American (NA) and South American origin (SA).

Biome	Origin	*N*	Median	Minimum	Maximum	Quartile range	Standard skewness	*P*
South America	NA	352	6.02	3.31	18.19	1.83	13.56	0.9
	SA	349	8.55	2.93	15.61	2.44	0.89	
Tropical humid forest	NA	124	6.2	3.31	18.19	3.27	5.89	0.000024
	SA	200	8.92	2.93	15.61	2.75	0.44	
Savanna	NA	40	6.21	3.64	15.05	6.4	2.29	0.82
	SA	38	8.71	4.37	15.61	3.95	0.76	
Mountain system	NA	140	6.09	3.46	17.46	1.56	9.08	0.000027
	SA	78	8.6	3.46	13.29	3.72	−0.44	
Tropical dry forest	NA	84	6.2	3.62	18.19	3.03	5.27	0.3
	SA	71	8.5	4.37	14.87	3.74	0.16	
Temperate rain forest	NA	48	6.52	4.39	16.1	6.27	2.53	0.9
	SA	47	8.15	4.37	12.46	2.83	0.23	
Temperate grasland	NA	48	5.41	3.69	17.86	2.73	4.43	0.041
	SA	30	8.86	4.91	15.61	2.82	1.3	
Warm semi-desert	NA	36	5.62	3.62	16.04	1.80	4.47	0 73
	SA	39	8.16	3.5	14.87	2.51	1.39	
Sclerophyllous forest	NA	14	6.38	4.8	12.85	5 45	0.56	0.127
	SA	7	7.75	4.85	8.77	1.44	−1.16	
Temperate broad leaf forest	NA	12	9.49	4.39	16.1	6.71	0.66	0.251
	SA	7	7.01	4.67	7.75	2.67	−0.36	
Cold winter desert	NA	30	6.36	4.04	16.87	5.65	2.63	0.016
	SA	14	8.53	6.13	12.03	2.63	0.89	

Table 5. Summary statistics for frequency distributions of body masses for South American mammals according to their origin in 14 local habitats. *P* is the probability associated with the null hypothesis of equal number of species of North American (NA) and South American origin (SA).

Habitat number	Origin	*N*	Median	Minimum	Maximum	Quartile range	Standard skewness	*P*
1	NA	9	5.85	4.80	12.85	5.65	0.503	0.17
	SA	4	7.21	4.85	7.97	2.11	−1.16	
2	NA	12	10.76	4.80	16.04	6.30	0.20	0.25
	SA	7	7.86	4.85	12.03	3.93	0.51	
3	NA	28	10.65	3.91	17.44	6.99	0.09	>0.9
	SA	28	9.22	4.39	14.90	3.76	−2.08	
4	NA	31	11.93	4.64	17.44	7.47	−0.35	0.71
	SA	34	10.12	6.13	15.61	3.74	0.63	
5	NA	22	6.27	4.04	16.87	7.0	1.96	0.00014
	SA	3	9.99	8.02	11.21	–	−0.56	
6	NA	16	6.26	4.64	16.10	7.56	1.71	0.00006
	SA	0	–	–	–	–	–	
7	NA	21	13.10	3.91	17.44	6.44	−1.51	0.75
	SA	19	10.10	4.19	14.90	3.62	−0.50	
8	NA	18	12.43	4.64	17.44	6.30	−0.79	0.479
	SA	14	11.80	6.34	14.87	4.15	−1.24	
9	NA	17	7.96	5.55	17.44	6.09	1.11	0.72
	SA	15	10.55	4.70	13.10	4.32	−0.85	
10	NA	14	10.76	4.80	16.04	6.71	0.15	0.003
	SA	2	5.60	4.67	6.53	–	–	
11	NA	17	6.27	3.75	17.61	7.11	0.11	0.004
	SA	4	10.62	4.40	13.29	6.97	−0.59	
12	NA	16	5.84	4.32	16.07	5.68	2.17	0.06
	SA	7	7.97	3.90	10.59	2.21	−1.30	
13	NA	14	5.84	4.69	16.07	5.61	2.11	0.003
	SA	2	9.04	7.82	10.25	–	–	
14	NA	14	8.85	4.95	15.1	7.37	0.33	>0.9
	SA	14	11.33	4.7	15.46	4.15	−0.35	

of the pre-GABI continental distribution of body masses. Under this scenario, mammals of North American origin succeeded in invading South America because of higher speciation rates (Lessa and Fariña 1996). We hypothesize that the extraordinary diversity that medium-sized species (mostly rodents) of North American origin achieved in South America was linked to the evolutionary advantage associated with medium size (around 100 g) in mammals (e.g., Brown et al. 1993), which allowed them to diversify at a higher rate, in comparison with mammals of smaller and larger sizes, through adaptive radiations episodes that enabled them to exploit ecological opportunities in South America. They filled up a size category that had not been explored, or at least had not been filled, by the original South American stock. But, why is it that the mode for species derived from South American ancestors is shifted to the right in relation to the mode for species of North American origin? As proposed by Brown et al. (1993) this probably reflects the existence of different constraints affecting the evolutionary diversification of different lineages, which limit the range and shape of body size distributions.

Body mass distributions at biome and local scales

Only three (Tropical humid forest, Savanna, and the Mountain system) out of the ten biomes considered in our analysis, had body mass distributions that were significantly different from what would be expected under random sampling from the continental pool. This is contrary to what Brown and Nicoletto (1991) showed for North America, where all biome distributions were significantly different from random. This is probably related to the finer definition of biomes used by Brown and Nicoletto (1991). Our biomes are larger in spatial extent than the one used by these authors, which results in body mass distributions that are more similar to the large-scale continental pool. On the other hand, the non-randomness in the body mass distributions found for the Tropical humid forest, Savanna, and the Mountain biomes disappears once the origin of taxa is taken into account. Thus their non-randomness stems from an unequal representation of species of North American (Mountain biome) or South American (Tropical humid forest) origin, which produces distributions with medians that are smaller and larger than the continental pool, respectively. However, for the Tropical humid forest biome, even after taking origin into account, species of South American origin are still characterized by a larger median than the expected under random sampling. The large number of primates, xenarthrans and hystricognath rodent species, restricted to this biome, produces this pattern.

In general, quartile ranges increase as we decrease the spatial scale of analysis, which is evidence that distributions become flatter. However, in most cases they do not become as flat (indistinguishable from a log-uniform distribution) as they do in North America (Brown and Nicoletto 1991). This could be indicative that local communities in South America represent samples of larger or environmentally more diverse areas than in North America, and/or this could be a reflection of the contribution of arboreal species, which have a relatively narrow range of sizes in tropical forest habitats. However, our results indicate that this pattern is affected by origin. When this is taken into account, species of South American origin show a strong support for the flattening pattern, with 13 out of 14 local habitats showing distributions not significantly different from a log-uniform distribution. In contrast, the flattening pattern is not as strong for the body size distribution of species of North American origin, where only eight out of 14 were not significantly different from a log-uniform distribution. Thus, we can claim that at least qualitatively, the pattern observed by Brown and Nicoletto (1991) holds for South American mammals, but is stronger for mammals of South American origin.

Brown and Nicoletto (1991) propose that three mechanisms are necessary and possibly sufficient to produce the flattening pattern they observed: competitive exclusion of similar-sized species within local habitats, greater specialization of modal-sized species owing to energetic and dietary constraints, and differential extinction of species of large size with small geographic ranges. The first two mechanisms are unlikely to underlie the observed pattern because there is no a priori reason to expect that they would apply only to species of South American origin. The third mechanism also seems unlikely to explain the pattern seen for species of South American origin because Lessa and Fariña (1996) showed that there were no extinction biases linked to the origin of taxa. As an alternative hypothesis, we suggest that the pattern arises because species of South American origin have, on average, smaller geographic ranges than their North American counter-

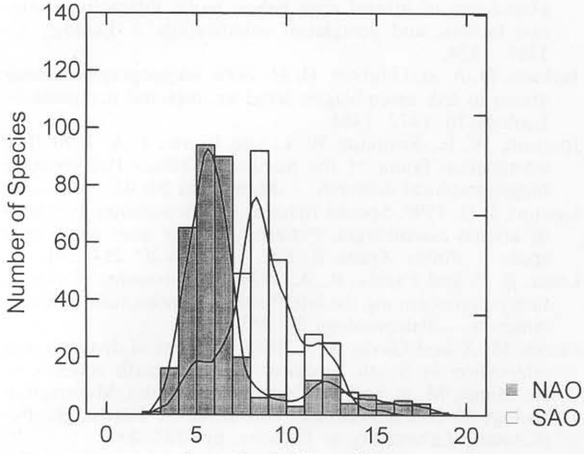

Fig. 4. Frequency distribution (log$_2$ scale) of the body masses of the 701 species of terrestrial South American mammals separated according to their origin. Note that frequency distribution of body masses for the 352 species of South American origin (SAO, open bars) and for the 349 species of North American origin (NAO, shaded bars) are clearly displaced. Continuous lines represent a kernel smoothing.

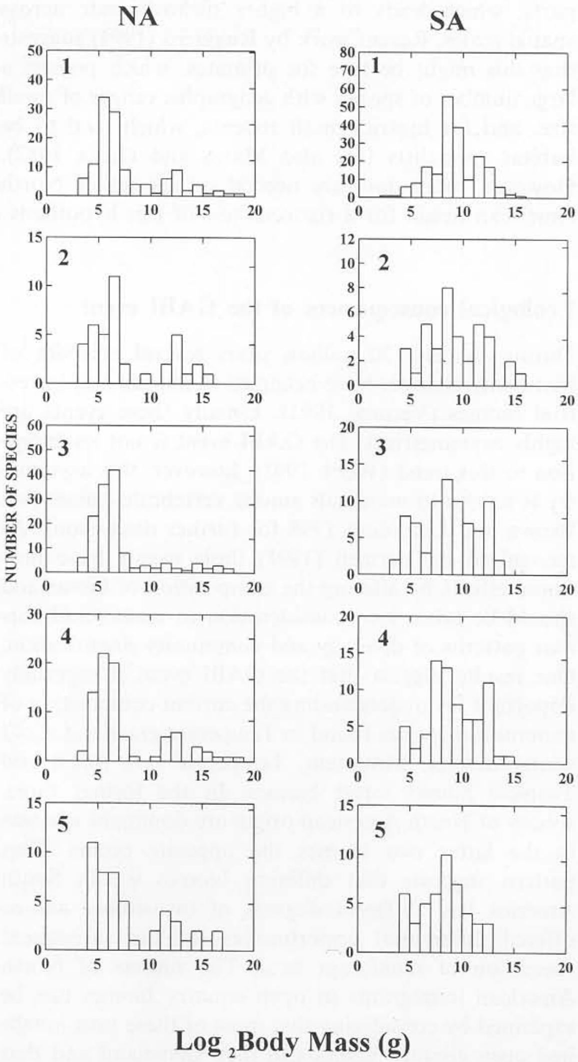

Fig. 5. Frequency distribution (log$_2$ scale) of the body masses of terrestrial mammals inhabiting biomes in South America. Species are separated according to their origin (NA = North America, SA = South America). Numbers identify biomes as in Table 1.

parts, which leads to a higher turnover rate across spatial scales. Recent work by Ruggiero (1994) suggests that this might be true for primates, which possess a large number of species with geographic ranges of small size, and for hystricognath rodents, which tend to be habitat specialists (see also Mares and Ojeda 1982). However, more data are needed on species of North American origin for a rigorous test of this hypothesis.

Ecological consequences of the GABI event

During the last 20 million years several episodes of biotic interchanges have occurred in marine and terrestrial biomes (Vermeij 1991). Usually these events are highly asymmetrical. The GABI event is not an exception to this trend (Webb 1991); however, this asymmetry is unique to mammals among vertebrate classes (see Brown and Lomolino 1998 for further discussion). As recognized by Vermeij (1991) these events have profound effects by altering the composition of biotas and should be taken into consideration to understand current patterns of diversity and community organization. Our results suggest that the GABI event is especially important for understanding the current composition of mammalian species found in Temperate grassland, Cold winter deserts, Mountain, Temperate rain forest and Tropical humid forest biomes. In the former three, species of North American origin are dominant whereas in the latter two biomes the opposite occurs. This pattern suggests that different biomes within South America had different degrees of invasibility and/or offered differential opportunities for the subsequent speciation of immigrant taxa. The success of North American immigrants in open country biomes can be explained by considering that most of these taxa inhabited open country habitats in their homeland and that these biomes provided the major routes for the dispersal of Northerners into South America (Webb 1978, 1985, 1991). The same reasoning can be applied to explain the low representation of taxa of North American origin in the Tropical humid forest and Temperate rain forest biomes. This underscores the importance of historical events in affecting the composition of current mammalian assemblages in South America and points out a fruitful way to understand patterns in body size distributions.

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