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The asymmetry in the Great American Biotic Interchange in mammals is consistent with differential susceptibility to mammalian predation

Running title: Predation and biotic interchange in mammals

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Abstract

Aim One of the most famous natural experiments in biogeography is the Great American Biotic Interchange (GABI). Here, we re-assess the famous asymmetry in the exchange for mammals, with North American lineages much more successful in South America than vice versa to see if this directionality could reflect higher susceptibility to predation in South American mammals rather than low competitive ability as usually believed.

Location North and South America.

Methods Prior to the GABI, South America lacked effective mammalian predators and since its fauna did not co-evolve with such predators, colonization of North America may only have been possible for species whose natural history makes them less susceptible to mammalian predation. To investigate this we used phylogenetic regressions to investigate species traits associated with the
ability of originally South American lineages to colonize North America and vice versa during the GABI. Analyses were conducted both with and without late-Quaternary extinct species.

**Results** When extinct species were included, traits associated (large body size, arboreality) with lower predation risk were associated with greater success in colonizing North America for South American lineages. This pattern was not visible based in the current fauna, since most of the mammals that invaded North America went extinct at the end of the Pleistocene, likely due to human predation. The pattern for northern colonizers of South America was similar whether or not extinct species were included and was not linked to predation risk.

**Conclusions** Our findings are consistent with the asymmetric GABI in mammals being explained by predation and not consistent with expectations from competition. The GABI hereby illustrates that trophic interactions can be a powerful driver of long-term dynamics of biotic interchange, just as seen in many human-driven invasions of formerly isolated regions.

**Keywords:** Competition, GABI, Macroecology, Mammals, Megafauna Extinction, Predation
For most of the Paleogene and Neogene (66-2.6 mya) South America was an isolated continent. The main exception was that cold-adapted lineages could migrate between Australia and South America through Antarctica until the opening of the Drake Passage, with low seas possibly already reducing dispersal from ~55 million years ago (Reguero et al., 2014). During this time, South America’s fauna developed mostly by in-situ evolution, though a few groups managed to colonize South America from Africa, notably New World Monkeys (Ceboidea) and hystricognath rodents, both with their earliest South American fossils from the Eocene (Antoine et al., 2012; Bond et al., 2015).

South America’s isolation ended abruptly with the collision of North and South America, allowing intense faunal interchange via the Panama land bridge from approximately 3.5 million years ago (the Great American Biotic Interchange, GABI), with exchanges increasing from ~10 million years (Bacon et al., 2015).

Colonization rates for most animal groups were symmetrical or slightly higher for south-to-north migrants (Bacon et al., 2015; Weir et al., 2009). In contrast, north-to-south colonization was much more common than south-to-north colonization for non-flying mammals (Marshall, 1988). As already noted by Marshall (1988), almost 50% of the families and genera of non-flying mammals in South America, or 465 of the 945 species based on the ranges and taxonomy of Schipper et al. (2008), are descendants of North American immigrants, while continental United States and Canada includes only 3 out of 322 species belonging to families of South American origin.

Competition has been the classical explanation for this asymmetric exchange (Simpson, 1980). South America is rather island-like relative to North America, which throughout much of the Paleogene and Neogene was connected to Eurasia, and islands have historically had a high extinction rate following the introduction of continental mammals (Turvey & Fritz, 2011).
However, competition fails to explain why competitiveness would only be low for South American non-flying mammals, with other animal groups exhibiting more symmetrical exchanges (e.g., Bacon et al., 2015; Weir et al., 2009). In this paper we re-assess the mechanisms underlying the asymmetrical GABI pattern for mammals and focus on an alternative to competition, namely predation. Our findings suggest that the asymmetrical pattern is not caused by low competitiveness, but rather by inefficient (non-placental) mammalian carnivores in South America prior to the GABI, causing many South American lineages to struggle to coexist with the placental carnivores, such as felids and canids, arriving with the GABI. Predation has previously been suggested to be part of the explanation (Webb, 2006), but we here suggest that it may be the main driver. This would also be in concordance with the strong role of human-introduced predators in driving recent extinctions on oceanic islands (Blackburn et al., 2004).

Prior to the GABI, the mammalian predator fauna in South America was less developed and made up of exclusively non-placental mammals, in particular the extinct order Spassodonta. This likely caused a less intense predatory regime for the larger South American mammals than where placental carnivores were present, leaving local mammals overall ill-adapted to the post-GABI predation regime. There are strong indications that metatherians (marsupials and their extinct relatives) make worse vertebrate predators than placental mammals (as also argued in Faurby & Svenning, 2015a). Potential evolutionary reasons include a lower specialization potential due to having only one set of teeth (Werdelin, 1987) and a stronger developmental constraint on the metatherian skull (Bennett & Goswami, 2013, but cf. Sánchez-Villagra 2013). Further evidence comes from the former predatory guild in South America and Australia, where large non-mammalian terrestrial predators were important: terror birds (Phorusrhacidae) in South America, and giant goanas and likely terrestrial crocodiles in Australia (REFS). The extinction of sparassodonts and terror birds has been suggested to be caused by competition with invading...
Carnivora, although doubts have been raised about this explanation (Prevosti et al., 2013). Non-mammalian carnivores were never important in the Neogene anywhere where representatives of the placental order Carnivora were present. There were giant predatory birds and likely terrestrial crocodiles in Europe and North America in the Paleogene (Brochu, 2012; Angst et al., 2013), but these alternate types of predators disappeared thereafter, likely due to competition with Carnivora. Similarly, a recent study attributes the high diversity of ground-dwelling birds in the Eocene Messel bird fauna relative to contemporary tropical faunas to a scarcity of placental carnivores (REF).

If mammalian predation explains why the GABI in non-flying mammals deviates from other organism groups, the asymmetric colonization pattern should be less strong in mammals whose natural history makes them less susceptible to mammalian predation. Two such natural history characteristics are arborealism and body size. Arboreal mammals should be less susceptible to predation from terrestrial predators, including mammals (Shattuck & Williams, 2010). Therefore, South American mammals should be relatively more successful among arboreal than terrestrial species. Predation risk should also decrease with increased body size, and adult herbivores larger than ~1 ton should be largely safe from non-human predation (Owen-Smith, 1987). Small mammals are subject to heavy predation from both non-mammalian predators, such as birds of prey and snakes, and mammalian predators. As the non-mammalian predator fauna was well-developed in South America already prior to GABI (Chiappe, 1991; Tambussi, 2011; Scheyer et al., 2013), the region’s small-sized mammals should be well-adapted to predation. Medium-sized species, such as deer, are generally too big to be the prey for most non-mammalian predators, but the optimal size prey for large mammalian predators (Carbone et al., 1999). Thus, the importance of mammalian predation may be greatest at intermediate sizes; hence, the asymmetric exchange should be most pronounced for this size class. Analogously, human-introduced invasive placental carnivores have selectively removed middle-sized native mammals in Australia (Hanna & Cardillo, 2014).
The largest species of both North and South American origin went extinct during the Late Pleistocene/Holocene megafauna extinction (Barnosky et al., 2004), a likely mainly anthropogenic event (Sandom et al., 2014). These extinctions may have masked any size-related selectivity in relation to the outcome of GABI and we therefore carried out the analyses with and without the Late Pleistocene and Holocene extinct species.

Materials and methods

Input data

Our analyses used the most recent information on mammalian phylogeny and taxonomy (Faurby & Svenning, 2015b), mammalian body sizes (Faurby & Svenning, Accepted), estimated present-natural (sensu Peterken (1977)) distributions (hereafter ‘natural distributions’) (Faurby & Svenning, 2015a), and current distributions (Schipper et al., 2008). We also generated a new database of arborealism for all mammals that have occurred naturally in continental North or South America within the last 130,000 years, scoring mammals likely to spend the majority of their time in trees as ‘arboreal’ and species likely to be mainly terrestrial, fossorial, or aquatic as ‘terrestrial’ (Supplementary materials and methods; Appendix A). All island endemics were excluded from analyses.

Analyses

We analyzed the latitudinal distribution range of all species based on rasterizations of the ranges in 1°×1° cells using both the current and natural distributions. From these results, we plotted three different patterns. First, we plotted the raw diversities of species from families restricted to North America prior to the GABI (‘northern origin’), and from families restricted to South America prior to the GABI (‘southern origin’). Second, we plotted the proportion of arboreal and all species in
various size classes of southern origin. Third, we plotted the proportion of species of southern origin among different size classes, from medium-sized to very large, terrestrial species.

As a more explicit test of our hypotheses, we analyzed the colonization success of each family (with the exception that we used the order Cingulata rather than the families Dasypodidae, Glyptodontidae, and Pampatheridae because the phylogeny used considers Glyptodontidae and Pampatheridae to be nested within Dasypodidae (Porpino et al., 2009)). For each species belonging to a family of northern origin we scored how far (in degrees latitude) it had colonized into South America (0 = species of northern origin still endemic to North America).

Similarly, for each species belonging to a family of southern origin we scored how far it had colonized into North America. In both cases we set the limit between North and South America as the Panama Canal. We then retained the maximum value for each family (‘colonization success’) and tested which factors were related to the colonization success of each family.

Two separate analyses were performed: a classical phylogenetic generalized least squares (pgls) regression fitting Pagel’s lambda, λ (Pagel, 1999; Freckleton et al., 2002), and one based on the phylogenetic logistic regression approach of Ives & Garland (2010). In both cases we used the new fast implementation of Ho & Ané (2014). We performed analyses both at the family and the subfamily level and furthermore tested if there was any effect of excluding species which never occurs in tropical regions (Supplementary materials and methods). In the main text we focus on the pgls at the family level and only discuss these other analyses in terms of the stability of our conclusions. Separate analyses were conducted for all 1000 trees from Faurby & Svenning (2015b) using version 1.002 of the phylogeny, and the results were combined by weighting the results from each tree based on AIC weight (supplementary materials and methods). We used three potential parameters related to our main hypothesis: maximum body size (log transformed) of the family (‘body size’), body size squared (only used in models also containing body size), and percentage of
arboreal species in a family (‘arborealism’). As a fourth potential parameter we used the number of species (log-transformed) in each family to account for sampling artifacts. All else being equal, families with larger numbers of species should have a broader total distribution and would, on average, have colonized a larger part of each continent (values for each family can be seen in Supplementary Tables 8-9). To reduce the likelihood of overfitting, no models with more than two parameters were fitted. Since the sample size is insufficient to include all parameters in the same model, we interpret AIC improvement by the addition of a parameter. To improve interpretability, all potential parameters and colonization success were normalized to a mean of 0 and standard deviation of 1. All analyses were performed in R 3.2.2 (R Development Core Team 2015 R).

Results

Geographic patterns

Lineages of northern origin are dominant throughout North America (Fig. 1). The diversity of southern lineages decreases linearly with increasing latitude, whereas the diversity of northern lineages peaks at intermediate latitudes (i.e., where North America is widest). In South America, lineages of northern and southern origin are approximately equally represented, though lineages of northern origin are relatively more common at southern latitudes. The same overall patterns exist for current and natural distributions, though diversity is consistently lower for the former (Fig. 1).

This overall pattern masks large differences in the relative dominance of southern and northern lineages among different ecologies and size (Figs. 2 and 3). In both North and South America, southern lineages are much more prevalent among arboreal species. This pattern holds for all size classes and is especially evident among the largest size class containing arboreal species (Fig. 2). A pattern of greater dominance of southern lineages is also evident among larger terrestrial species (Fig. 3). Looking at the natural patterns, approximately equal numbers of southern and
northern lineages are found among the largest species (> 1 ton) in North America, whereas lower frequencies of southern lineages are found in the smaller size classes. Looking at the natural patterns in South America, southern lineages are dominant among the largest species, of equal importance to northern lineages among species 1-10 kg and 100-1000 kg in size, and unimportant for species 10-100 kg in size. Thus, migrants from South to North America have been more important for the largest species (>1 ton), while migrants from North America to South America have been most important for the other size classes. These patterns are not visible in the current fauna due to the late-Quaternary megafauna extinctions in which all southern species ≥100 kg and all northern species ≥1 ton went extinct, along with many smaller species.

Drivers of colonization success

For analyses of natural distribution patterns, there were consistently substantial improvements in AIC in the optimal models relative to the models only including an intercept (e.g., ΔAIC 12.1 for southern lineages and 13.7 for northern lineages in Table 1). Considering only current distributions, there were a substantial reduction in the benefit of adding explanatory parameters for southern lineages (e.g., ΔAIC 0.4 in Table 1), suggesting a more random pattern in which southern lineages managed to colonize North America, if extinct species are ignored, and a similar but smaller reduction for northern lineages (e.g., ΔAIC 11.8 vs 13.7 in Table 1). A similar apparent randomness for southern lineages based on current distributions is suggested by Pagel’s λ, which is generally near 0.0 in these analyses, but near 1.0 for analyses of natural distributions for southern lineages, and intermediate for northern lineages for both current and natural distributions (Table 1).

The model including body size and number of species was generally preferred (Table 1). Out of 32 analyses (all combinations of southern/northern origin, natural/current distributions,
family/subfamily, PGLS/binomial regressions, all lineages/anti-tropical lineages excluded). The model was the preferred based on AIC for 26 analyses. Even though the same model was generally preferred for southern and northern lineages, the relative strength of the two parameters was substantially different. The relative importance of body size in the model (the ratio between the standardized parameter values for body size and number of species) was much higher for natural distributions for lineages of southern origin (median 1.88; tables 1 and S1-S7) than for their current distributions (median 0.91; tables 1 and S1-S7) or for northern origin natural distributions (median 1.00; tables 1 and S1-S7).

Differences in the effect of body size are also evident in comparisons of models containing both a linear and squared terms of body size vs. just a linear term. The former models were preferred in 5 of the 32 analyses (all of these were based on binomial regressions of lineages of northern origin, tables S3, S6, S7). More importantly, the addition of a squared term to a model only including a linear term of body size never caused an improvement in AIC for analyses of southern lineages, but did so in 7 out of 8 analyses for northern lineages for both current or natural distributions (Tables 1, S1-S7). The difference in the shape of the nonlinear effect of body size between the northern and southern lineages was consistent for all eight different analyses (Figure 4, Table 1; Supplementary Tables 1-7, splines of raw data is shown in Figure S1). Colonization success for northern lineages whether based on natural or current distributions always peaked at intermediate sizes, colonization success for southern lineages based on natural distributions was always highest for the very largest sizes. The particularly high colonization success among intermediate-sized animals from northern lineages and the stronger effect size of number of species in the family for northern lineages can potentially be seen as two sides of the same pattern size, since the number of species in families is moderately negatively correlated with body sizes for northern families (p=-0.40).
Unlike the strong support for the effect of body size, the support for an effect of arborealism was moderate. Models including arborealism were never optimal according to AIC and in only 10 out of 32 analyses produced inclusion of arborealism a lower AIC than models just containing body size (four for southern lineages’ natural distributions and three each for northern lineages’ current and natural distributions). Effect sizes of arborealism were generally strongest for models of lineages of southern origin based on natural distributions, and the only two cases with a significant effect of arborealism were found for these (Tables S2, S5).

Discussion

The importance of arborealism for colonization success

The geographic patterns visually supports that South American lineages have done better among arboreal than terrestrial species. Interestingly, the effect is strongest for the largest size group, which is dominated by lineages of southern origin on both continents. However, the explicit analysis of colonization success only provided partial support for the role of arborealism. The models did show a moderately strong effect with greater colonization success for southern arboreal lineages. However, analyses of the lineages of northern origin also revealed a moderate (but generally weaker) effect of greater colonization success for arboreal lineages. Therefore, it is possible that the effect of arborealism may be driven by factors other than predation, such as through a potentially lower dispersal capacity of fossorial lineages (scored as terrestrial here) than non-fossorial lineages. Colonization from Australia is too rare to warrant any generalizations, but it is striking that Phalangeridae (brushtail possums and cuscuses), the only marsupial family to colonize Sulawesi (Ruedas & Morales, 2005) and which has co-occurred with placental carnivores
for a substantial period of time, is exclusively arboreal (Jones et al., 2009), further supporting our
claim.

The greater success among arboreal species compared to terrestrial species for
southern lineages may also explain why southern lineages do well in Central America, which was
part of North America prior to the GABI, but is currently faunistically a part of South America
(Webb, 2006). The dense tree cover of the region means that a large proportion of mammalian
diversity is arboreal, and the southern lineages rapidly diminish in importance to the north as the
climate becomes dryer and the extent of trees and arboreal mammals decreases.

The importance of body size for colonization success

The hypothesized role of body size was strongly supported by the geographic patterns visually, and,
as in arborealism, increased body size led to increased colonization success in both directions when
looking at natural distributions. However, body size was a substantially stronger predictor of the
capacity of southern lineages to colonize North America than vice versa. In addition, colonization
success was maximized at intermediate rather than the largest body sizes for northern lineages
(Figure 4). A potential explanation for this result is that southern lineages did consistently better
when they were larger due to decreased susceptibility to predation. The pattern of the colonization
potential of northern lineages could be the result of two opposing factors. Larger body size may
increase the dispersal ability, potentially enabling the species to invade more of South America, but
may increase the competition with local lineages if the larger South American species cope better
with predation by North American carnivores. The differences in the estimates of λ (high λ for
southern origin and natural distributions and low λ for northern origin) are also striking. A high λ is
only expected when the colonization success of different families has the same underlying
biological reason, especially if the underlying cause, such as body size, is known to evolve
according to Brownian motion (Blomberg et al., 2003). Therefore, the high $\lambda$ for southern lineages could suggest that invasion success was almost entirely governed by body size.

A few researchers still argue a large effect of climate on the massive extinction near the end of the last glaciation (Cooper et al., 2015), but evidence is steadily increasing for a strong human role in the extinctions (Sandom et al., 2014). Notably, it is increasingly clear that much of the South American megafauna survived well into Holocene, 1,000-3,000 years beyond the climate swings of the late-Quaternary (REF). Some studies in consequence attribute the extinctions to the relatively limited Holocene climatic variability and local vegetation shifts (REFS), but these explanatory models ignores the immense variability in climate and vegetation across South America (REFS) and the evidence for diet generalism in many of the extinct species (REF). Here, we hypothesize that none of the formerly medium and large South American lineages could survive substantial mammalian predation, with human predation being an extreme case. Many of the largest species in the lineages initially survived the GABI by being too large to be effectively predated upon by the invading carnivores, but they finally succumbed to predation when *Homo sapiens* arrived. In line with this, the data suggest that many of the lineages that went extinct in the Late Pleistocene or early Holocene had especially low fecundity (Johnson, 2002).

**Conclusion**

Our results are consistent with differential sensitivity to predation among the pre-GABI mammal assemblages in North and South America as the main mechanism behind the asymmetric exchange in the mammal faunas. Notably, South American taxa with characteristics that make them less susceptible to mammalian predation (large body size, arboreality) had much higher success in colonizing North America than other taxa. The case of the very largest mammals (>1 ton) is especially interesting because several of these lineages successfully colonized North America
without causing any obvious extinction among the original taxa in the same body size class on that continent. In line with previous findings on frogs (Pinto-Sánchez et al., 2014), our results suggest that the end product of the mixing of previously isolated biota may not always be competitive exclusion, but rather extremely diverse communities. This may further suggest that many communities are not saturated with species. The increased diversification rates among the lineages invading South America where the native lineages diminished due to invading carnivores (as also discussed by Marshall (1988)), but not in the opposite direction, suggest that diversification rates are density-dependent, however. Despite not finding any clear support for competition causing extinctions, we are not stating that competition never leads to extinctions in biotic interchanges, or that high diversity will always be the outcome of contact between formerly isolated members of the same guild. We note, however, that some of the apparently clearest competition-linked extinctions in the paleobiological record, e.g., the canid subfamilies Borophaginae and Hesperocyoninae (Silvestro et al., 2015), have been among carnivores. As intra-guild predation is common (Levi & Wilmers, 2012), these extinctions may also be explained by predation rather than just competition.

We note that the drastically different results of the analyses of southern lineages when examining natural versus realized distributions are in accordance with the effects of anthropogenic range contractions and extinctions on analyses of diversity drivers (Faurby & Svenning, 2015a) and body size evolution (Faurby & Svenning, Accepted). Hence, the present study provides further evidence that anthropogenic extinctions may bias assessments of evolutionary and ecological drivers of diversity patterns.

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Biosketches

Søren Faurby is an evolutionary biologist interested in the development, maintenance and consequences of geographic variation within and between species, and he has investigated these subjects in a wide variety of taxa.

Jens-Christian Svenning is a broadly based ecologist, with core research interests including community and vegetation ecology, macroecology, biogeography and physical geography. His work ranges from addressing basic ecological and evolutionary questions to investigating applied ecology, conservation biology and global change.

This paper is part of a long-term collaboration between Søren Faurby and Jens-Christian Svenning looking into the ecological and evolutionary consequences of the mammalian megafauna extinctions.

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Table 1. PGLS analyses of the factors governing colonization success of families of southern (occurring in South America prior to the GABI) and northern (occurring in North America prior to the GABI) origin.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Southern origin: Natural</th>
<th>Southern origin: Current</th>
<th>Northern origin: Natural</th>
<th>Northern origin: Current</th>
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<tbody>
<tr>
<td>Number of families</td>
<td>30</td>
<td>24</td>
<td>27</td>
<td>23</td>
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<tr>
<td>Average colonization success</td>
<td>15.7</td>
<td>9.6</td>
<td>31.4</td>
<td>30.3</td>
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<table>
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<th>Factor</th>
<th>Intercept only</th>
<th>Body Size</th>
<th>Arborealism</th>
<th>Number of species</th>
<th>Body Size + Arborealism</th>
<th>Body Size + Number of species</th>
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<tbody>
<tr>
<td>AIC/ ΔAIC</td>
<td>86.1/ 12.1</td>
<td>73.1/ 0.4</td>
<td>80.1/ 13.7</td>
<td>69.0/ 11.8</td>
<td>77.4/ 3.4</td>
<td>68.0/ 14.0</td>
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<td>λ</td>
<td>1.00</td>
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<td>0.32</td>
<td>0.00</td>
<td>0.85</td>
<td>0.31</td>
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<tr>
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<td>0.00 (0.20)NS</td>
<td>-0.08 (0.29)NS</td>
<td>-0.06 (0.27)NS</td>
<td>-0.01 (1.01)NS</td>
<td>-0.04 (0.18)NS</td>
</tr>
<tr>
<td>AIC/ ΔAIC</td>
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<td>72.7/ 0.0</td>
<td>78.8/ 12.4</td>
<td>66.8/ 9.6</td>
<td>88.0/ 14.0</td>
<td>79.9/ 13.6</td>
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<td>λ</td>
<td>0.85</td>
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<td>0.00 (0.20)NS</td>
<td>-0.09 (0.28)NS</td>
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<td>-0.06 (0.28)NS</td>
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<tr>
<td>Body Size</td>
<td>0.67 (0.18)***</td>
<td>0.31 (0.20)NS</td>
<td>0.37 (0.21)NS</td>
<td>0.44 (0.20)*</td>
<td>0.06 (0.21)NS</td>
<td>0.26 (0.18)NS</td>
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<td>0.50 (0.17)**</td>
<td>0.54 (0.17)**</td>
<td>0.31 (0.14)*</td>
<td>0.27 (0.21)NS</td>
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<tr>
<td>AIC/ ΔAIC</td>
<td>83.9/ 9.9</td>
<td>73.3/ 0.6</td>
<td>74.5/ 8.2</td>
<td>63.4/ 6.2</td>
<td>75.3/ 1.3</td>
<td>73.7/ 1.0</td>
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<tr>
<td>λ</td>
<td>0.86</td>
<td>0.00</td>
<td>0.58</td>
<td>0.10</td>
<td>0.86</td>
<td>0.58</td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.01 (0.94)NS</td>
<td>0.00 (0.20)NS</td>
<td>-0.07 (0.26)NS</td>
<td>-0.01 (0.20)NS</td>
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<td>-0.07 (0.26)NS</td>
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<tr>
<td>Body Size</td>
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<td>0.39 (0.22)NS</td>
<td>0.38 (0.20)NS</td>
<td>0.44 (0.19)*</td>
<td>0.20 (0.21)NS</td>
<td>0.39 (0.22)NS</td>
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<tr>
<td>Arborealism</td>
<td>0.37 (0.18)NS</td>
<td>0.21 (0.25)NS</td>
<td>0.28 (0.17)NS</td>
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<td>0.37 (0.18)NS</td>
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<tr>
<td>AIC/ ΔAIC</td>
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<td>73.0/ 0.3</td>
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<td>57.2/ 0.0</td>
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<td>73.0/ 0.3</td>
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NS: Not significant
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<th>λ</th>
<th>Intercept</th>
<th>Body Size</th>
<th>Number of species</th>
<th>Body Size and + Body Size²</th>
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<td>0.33 (0.13) *</td>
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<td>78.0/ 11.7</td>
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<th>Arborealism</th>
<th>Number of species + Arborealism</th>
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<td>76.5/ 10.2</td>
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<td>0.01 (0.19) NS</td>
<td>0.05 (0.20) NS</td>
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<th>NS P&gt;0.05</th>
<th>** 0.01&gt;P&gt;0.001</th>
<th>*** P&lt;0.001</th>
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<td>0.10&gt;P&gt;0.05</td>
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Figure legends

Figure 1

Diversity gradients for non-flying mammals in South and North America, broken down into species of northern (1a and 1b) and southern origin (1c and 1d) based on the distribution of mammalian families prior to the GABI. The diversity is the total number of species present at a given latitude.

Figure 2. Role of arborealism in GABI: The proportion of species in different size classes belonging to southern lineages, based on the distribution of mammalian families prior to the GABI among arboreal and all species in North America (2a and 2b) and South America (2c and 2d). No plot is shown for mammals > 100 kg because none are arboreal. The proportions were calculated based on all species present at a given latitude.

Figure 3. Role of body size in GABI: The proportion of species in different size classes belonging to southern lineages in North America (3a and 3b) and South America (3c and 3d), based on the distribution of mammalian families prior to the GABI among medium-sized to large terrestrial species. The proportions were calculated based on all species present at a given latitude.

Figure 4. Predicted relationship between body size and colonization success for models containing both a linear and a quadratic term for body size for each of the eight analyses (Tables 1, S1-S7).