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

3 **Running title:** Predation and biotic interchange in mammals

4 **Authors**

5 Søren Faurby^a, Jens-Christian Svenning^b

6 ^a Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC,
7 Calle José Gutiérrez Abascal 2, Madrid 28006, Spain

8 ^b Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Ny
9 Munkegade 114, DK-8000 Aarhus C, Denmark

10 **Corresponding author**

11 Søren Faurby. Department of Biogeography and Global Change, Museo Nacional de Ciencias
12 Naturales, CSIC, Calle José Gutiérrez Abascal 2, Madrid 28006, Spain.
13 Email:faurby@mncn.csic.es. Tel. + 34 914 111 328. Fax + 34 915 645 078.

14 **Abstract**

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

20 **Location** North and South America.

21 **Methods** Prior to the GABI, South America lacked effective mammalian predators and since its
22 fauna did not co-evolve with such predators, colonization of North America may only have been
23 possible for species whose natural history makes them less susceptible to mammalian predation. To
24 investigate this we used phylogenetic regressions to investigate species traits associated with the

25 ability of originally South American lineages to colonize North America and vice versa during the
26 GABI. Analyses were conducted both with and without late-Quaternary extinct species.

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

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

37

38

39 **Keywords:** Competition, GABI, Macroecology, Mammals, Megafauna Extinction, Predation

40

41 **Introduction**

42 For most of the Paleogene and Neogene (66-2.6 mya) South America was an isolated continent. The
43 main exception was that cold-adapted lineages could migrate between Australia and South America
44 through Antarctica until the opening of the Drake Passage, with low seas possibly already reducing
45 dispersal from ~55 million years ago (Reguero *et al.*, 2014). During this time, South America's
46 fauna developed mostly by in-situ evolution, though a few groups managed to colonize South
47 America from Africa, notably New World Monkeys (Ceboidea) and hystricognath rodents, both
48 with their earliest South American fossils from the Eocene (Antoine *et al.*, 2012; Bond *et al.*, 2015).
49 South America's isolation ended abruptly with the collision of North and South America, allowing
50 intense faunal interchange via the Panama land bridge from approximately 3.5 million years ago
51 (the Great American Biotic Interchange, GABI), with exchanges increasing from ~10 million years
52 (Bacon *et al.*, 2015).

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

61 Competition has been the classical explanation for this asymmetric exchange
62 (Simpson, 1980). South America is rather island-like relative to North America, which throughout
63 much of the Paleogene and Neogene was connected to Eurasia, and islands have historically had a
64 high extinction rate following the introduction of continental mammals (Turvey & Fritz, 2011).

65 However, competition fails to explain why competitiveness would only be low for South American
66 non-flying mammals, with other animal groups exhibiting more symmetrical exchanges (e.g.,
67 Bacon *et al.*, 2015; Weir *et al.*, 2009). In this paper we re-assess the mechanisms underlying the
68 asymmetrical GABI pattern for mammals and focus on an alternative to competition, namely
69 predation. Our findings suggest that the asymmetrical pattern is not caused by low competitiveness,
70 but rather by inefficient (non-placental) mammalian carnivores in South America prior to the GABI,
71 causing many South American lineages to struggle to coexist with the placental carnivores, such as
72 felids and canids, arriving with the GABI. Predation has previously been suggested to be part of the
73 explanation (Webb, 2006), but we here suggest that it may be the main driver. This would also be in
74 concordance with the strong role of human-introduced predators in driving recent extinctions on
75 oceanic islands (Blackburn *et al.*, 2004).

76 Prior to the GABI, the mammalian predator fauna in South America was less
77 developed and made up of exclusively non-placental mammals, in particular the extinct order
78 Spassodonta. This likely caused a less intense predatory regime for the larger South American
79 mammals than where placental carnivores were present, leaving local mammals overall ill-adapted
80 to the post-GABI predation regime. There are strong indications that metatherians (marsupials and
81 their extinct relatives) make worse vertebrate predators than placental mammals (as also argued in
82 Faurby & Svenning, 2015a). Potential evolutionary reasons include a lower specialization potential
83 due to having only one set of teeth (Werdelin, 1987) and a stronger developmental constraint on the
84 metatherian skull (Bennett & Goswami, 2013, but cf. Sánchez-Villagra 2013). Further evidence
85 comes from the former predatory guild in South America and Australia, where large non-
86 mammalian terrestrial predators were important: terror birds (Phorusrhacidae) in South America,
87 and giant goanas and likely terrestrial crocodiles in Australia (REFS). The extinction of
88 sparassodonts and terror birds has been suggested to be caused by competition with invading

89 Carnivora, although doubts have been raised about this explanation (Prevosti *et al.*, 2013). Non-
90 mammalian carnivores were never important in the Neogene anywhere where representatives of the
91 placental order Carnivora were present. There were giant predatory birds and likely terrestrial
92 crocodiles in Europe and North America in the Paleogene (Brochu, 2012; Angst *et al.*, 2013), but
93 these alternate types of predators disappeared thereafter, likely due to competition with Carnivora.
94 Similarly, a recent study attributes the high diversity of ground-dwelling birds in the Eocene Messel
95 bird fauna relative to contemporary tropical faunas to a scarcity of placental carnivores (REF).

96 If mammalian predation explains why the GABI in non-flying mammals deviates
97 from other organism groups, the asymmetric colonization pattern should be less strong in mammals
98 whose natural history makes them less susceptible to mammalian predation. Two such natural
99 history characteristics are arborealism and body size. Arboreal mammals should be less susceptible
100 to predation from terrestrial predators, including mammals (Shattuck & Williams, 2010). Therefore,
101 South American mammals should be relatively more successful among arboreal than terrestrial
102 species. Predation risk should also decrease with increased body size, and adult herbivores larger
103 than ~1 ton should be largely safe from non-human predation (Owen-Smith, 1987). Small mammals
104 are subject to heavy predation from both non-mammalian predators, such as birds of prey and
105 snakes, and mammalian predators. As the non-mammalian predator fauna was well-developed in
106 South America already prior to GABI (Chiappe, 1991; Tambussi, 2011; Scheyer *et al.*, 2013), the
107 region's small-sized mammals should be well-adapted to predation. Medium-sized species, such as
108 deer, are generally too big to be the prey for most non-mammalian predators, but the optimal size
109 prey for large mammalian predators (Carbone *et al.*, 1999). Thus, the importance of mammalian
110 predation may be greatest at intermediate sizes; hence, the asymmetric exchange should be most
111 pronounced for this size class. Analogously, human-introduced invasive placental carnivores have
112 selectively removed middle-sized native mammals in Australia (Hanna & Cardillo, 2014).

113 The largest species of both North and South American origin went extinct during the
114 Late Pleistocene/Holocene megafauna extinction (Barnosky *et al.*, 2004), a likely mainly
115 anthropogenic event (Sandom *et al.*, 2014). These extinctions may have masked any size-related
116 selectivity in relation to the outcome of GABI and we therefore carried out the analyses with and
117 without the Late Pleistocene and Holocene extinct species.

118 **Materials and methods**

119 **Input data**

120 Our analyses used the most recent information on mammalian phylogeny and taxonomy (Faurby &
121 Svenning, 2015b), mammalian body sizes (Faurby & Svenning, Accepted), estimated present-
122 natural (*sensu* Peterken (1977)) distributions (hereafter ‘natural distributions’) (Faurby & Svenning,
123 2015a), and current distributions (Schipper *et al.*, 2008). We also generated a new database of
124 arborealism for all mammals that have occurred naturally in continental North or South America
125 within the last 130,000 years, scoring mammals likely to spend the majority of their time in trees as
126 ‘arboreal’ and species likely to be mainly terrestrial, fossorial, or aquatic as ‘terrestrial’
127 (Supplementary materials and methods; Appendix A). All island endemics were excluded from
128 analyses.

129 **Analyses**

130 We analyzed the latitudinal distribution range of all species based on rasterizations of the ranges in
131 1°×1° cells using both the current and natural distributions. From these results, we plotted three
132 different patterns. First, we plotted the raw diversities of species from families restricted to North
133 America prior to the GABI (‘northern origin’), and from families restricted to South America prior
134 to the GABI (‘southern origin’). Second, we plotted the proportion of arboreal and all species in

135 various size classes of southern origin. Third, we plotted the proportion of species of southern
136 origin among different size classes, from medium-sized to very large, terrestrial species.

137 As a more explicit test of our hypotheses, we analyzed the colonization success of
138 each family (with the exception that we used the order Cingulata rather than the families
139 Dasypodidae, Glyptodontidae, and Pampatheridae because the phylogeny used considers
140 Glyptodontidae and Pampatheridae to be nested within Dasypodidae (Porpino *et al.*, 2009)). For
141 each species belonging to a family of northern origin we scored how far (in degrees latitude) it had
142 colonized into South America (0 = species of northern origin still endemic to North America).
143 Similarly, for each species belonging to a family of southern origin we scored how far it had
144 colonized into North America. In both cases we set the limit between North and South America as
145 the Panama Canal. We then retained the maximum value for each family ('colonization success')
146 and tested which factors were related to the colonization success of each family.

147 Two separate analyses were performed: a classical phylogenetic generalized least
148 squares (pgls) regression fitting Pagel's lambda, λ (Pagel, 1999; Freckleton *et al.*, 2002), and one
149 based on the phylogenetic logistic regression approach of Ives & Garland (2010). In both cases we
150 used the new fast implementation of Ho & Ané (2014). We performed analyses both at the family
151 and the subfamily level and furthermore tested if there was any effect of excluding species which
152 never occurs in tropical regions (Supplementary materials and methods). In the main text we focus
153 on the pgls at the family level and only discuss these other analyses in terms of the stability of our
154 conclusions. Separate analyses were conducted for all 1000 trees from Faurby & Svenning (2015b)
155 using version 1.002 of the phylogeny, and the results were combined by weighting the results from
156 each tree based on AIC weight (supplementary materials and methods). We used three potential
157 parameters related to our main hypothesis: maximum body size (log transformed) of the family
158 ('body size'), body size squared (only used in models also containing body size), and percentage of

159 arboreal species in a family ('arborealism'). As a fourth potential parameter we used the number of
160 species (log-transformed) in each family to account for sampling artifacts. All else being equal,
161 families with larger numbers of species should have a broader total distribution and would, on
162 average, have colonized a larger part of each continent (values for each family can be seen in
163 Supplementary Tables 8-9). To reduce the likelihood of overfitting, no models with more than two
164 parameters were fitted. Since the sample size is insufficient to include all parameters in the same
165 model, we interpret AIC improvement by the addition of a parameter. To improve interpretability,
166 all potential parameters and colonization success were normalized to a mean of 0 and standard
167 deviation of 1. All analyses were performed in R 3.2.2 (R Development Core Team 2015 R).

168 **Results**

169 **Geographic patterns**

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

176 This overall pattern masks large differences in the relative dominance of southern and
177 northern lineages among different ecologies and size (Figs. 2 and 3). In both North and South
178 America, southern lineages are much more prevalent among arboreal species. This pattern holds for
179 all size classes and is especially evident among the largest size class containing arboreal species
180 (Fig. 2). A pattern of greater dominance of southern lineages is also evident among larger terrestrial
181 species (Fig. 3). Looking at the natural patterns, approximately equal numbers of southern and

182 northern lineages are found among the largest species (> 1 ton) in North America, whereas lower
183 frequencies of southern lineages are found in the smaller size classes. Looking at the natural
184 patterns in South America, southern lineages are dominant among the largest species, of equal
185 importance to northern lineages among species 1-10 kg and 100-1000 kg in size, and unimportant
186 for species 10-100 kg in size. Thus, migrants from South to North America have been more
187 important for the largest species (>1 ton), while migrants from North America to South America
188 have been most important for the other size classes. These patterns are not visible in the current
189 fauna due to the late-Quaternary megafauna extinctions in which all southern species ≥ 100 kg and
190 all northern species ≥ 1 ton went extinct, along with many smaller species.

191

192 **Drivers of colonization success**

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

203 The model including body size and number of species was generally preferred (Table
204 1). Out of 32 analyses (all combinations of southern/northern origin, natural/current distributions,

205 family/ subfamily, PGLS/ binomial regressions, all lineages/anti-tropical lineages excluded). The
206 model was the preferred based on AIC for 26 analyses. Even though the same model was generally
207 preferred for southern and northern lineages, the relative strength of the two parameters was
208 substantially different. The relative importance of body size in the model (the ratio between the
209 standardized parameter values for body size and number of species) was much higher for natural
210 distributions for lineages of southern origin (median 1.88; tables 1 and S1-S7) than for their current
211 distributions (median 0.91; tables 1 and S1-S7) or for northern origin natural distributions (median
212 1.00; tables 1 and S1-S7).

213 Differences in the effect of body size are also evident in comparisons of models
214 containing both a linear and squared terms of body size vs. just a linear term. The former models
215 were preferred in 5 of the 32 analyses (all of these were based on binomial regressions of lineages
216 of northern origin, tables S3, S6, S7). More importantly, the addition of a squared term to a model
217 only including a linear term of body size never caused an improvement in AIC for analyses of
218 southern lineages, but did so in 7 out of 8 analyses for northern lineages for both current or natural
219 distributions (Tables 1, S1-S7). The difference in the shape of the nonlinear effect of body size
220 between the northern and southern lineages was consistent for all eight different analyses (Figure 4,
221 Table 1; Supplementary Tables 1-7, splines of raw data is shown in Figure S1). Colonization
222 success for northern lineages whether based on natural or current distributions always peaked at
223 intermediate sizes, colonization success for southern lineages based on natural distributions was
224 always highest for the very largest sizes. The particularly high colonization success among
225 intermediate-sized animals from northern lineages and the stronger effect size of number of species
226 in the family for northern lineages can potentially be seen as two sides of the same pattern size,
227 since the number of species in families is moderately negatively correlated with body sizes for
228 northern families ($p=-0.40$).

229 Unlike the strong support for the effect of body size, the support for an effect of
230 arborealism was moderate. Models including arborealism were never optimal according to AIC and
231 in only 10 out of 32 analyses produced inclusion of arborealism a lower AIC than models just
232 containing body size (four for southern lineages' natural distributions and three each for northern
233 lineages' current and natural distributions). Effect sizes of arborealism were generally strongest for
234 models of lineages of southern origin based on natural distributions, and the only two cases with a
235 significant effect of arborealism were found for these (Tables S2, S5).

236

237 **Discussion**

238 **The importance of arborealism for colonization success**

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

251 for a substantial period of time, is exclusively arboreal (Jones *et al.*, 2009), further supporting our
252 claim.

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

259 **The importance of body size for colonization success**

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

274 according to Brownian motion (Blomberg *et al.*, 2003). Therefore, the high λ for southern lineages
275 could suggest that invasion success was almost entirely governed by body size.

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

290 **Conclusion**

291 Our results are consistent with differential sensitivity to predation among the pre-GABI mammal
292 assemblages in North and South America as the main mechanism behind the asymmetric exchange
293 in the mammal faunas. Notably, South American taxa with characteristics that make them less
294 susceptible to mammalian predation (large body size, arboreality) had much higher success in
295 colonizing North America than other taxa. The case of the very largest mammals (>1 ton) is
296 especially interesting because several of these lineages successfully colonized North America

297 without causing any obvious extinction among the original taxa in the same body size class on that
298 continent. In line with previous findings on frogs (Pinto-Sánchez *et al.*, 2014), our results suggest
299 that the end product of the mixing of previously isolated biota may not always be competitive
300 exclusion, but rather extremely diverse communities. This may further suggest that many
301 communities are not saturated with species. The increased diversification rates among the lineages
302 invading South America where the native lineages diminished due to invading carnivores (as also
303 discussed by Marshall (1988)), but not in the opposite direction, suggest that diversification rates
304 are density-dependent, however. Despite not finding any clear support for competition causing
305 extinctions, we are not stating that competition never leads to extinctions in biotic interchanges, or
306 that high diversity will always be the outcome of contact between formerly isolated members of the
307 same guild. We note, however, that some of the apparently clearest competition-linked extinctions
308 in the paleobiological record, e.g., the canid subfamilies Borophaginae and Hesperocyoninae
309 (Silvestro *et al.*, 2015), have been among carnivores. As intra-guild predation is common (Levi &
310 Wilmers, 2012), these extinctions may also be explained by predation rather than just competition.

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

317

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320 supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC).

321

322 **Biosketches**

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

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

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

333

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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.				
	Southern origin: Natural	Southern origin: Current	Northern origin: Natural	Northern origin: Current
Number of families	30	24	27	23
Average colonization success	15.7	9.6	31.4	30.3
Intercept only				
AIC/ Δ AIC	86.1/ 12.1	73.1/ 0.4	80.1/ 13.7	69.0/ 11.8
λ	1.00	0.00	0.32	0.30
Intercept	-0.02 (0.99) ^{NS}	0.00 (0.20) ^{NS}	-0.08 (0.29) ^{NS}	-0.06 (0.27) ^{NS}
Body Size				
AIC/ Δ AIC	77.4/ 3.4	72.7/ 0.0	78.8/ 12.4	66.8/ 9.6
λ	0.85	0.00	0.33	0.12
Intercept	0.22 (0.63) ^{NS}	0.00 (0.20) ^{NS}	-0.09 (0.28) ^{NS}	-0.01 (0.21) ^{NS}
Body Size	0.67 (0.18) ^{***}	0.31 (0.20) ^{NS}	0.37 (0.21) ^{NS}	0.44 (0.20) [*]
Arborealism				
AIC/ Δ AIC	88.0/ 14.00	75.0/ 2.3	79.9/ 13.6	68.3/ 11.1
λ	1.00	0.00	0.32	0.31
Intercept	-0.01 (1.01) ^{NS}	0.00 (0.21) ^{NS}	-0.06 (0.28) ^{NS}	-0.05 (0.26) ^{NS}
Arborealism	-0.04 (0.18) ^{NS}	0.06 (0.21) ^{NS}	0.26 (0.18) ^{NS}	0.32 (0.20) ^{NS}
Number of species				
AIC/ Δ AIC	83.9/ 9.9	73.3/ 0.6	74.5/ 8.2	63.4/ 6.2
λ	1.00	0.00	0.58	0.69
Intercept	-0.01 (0.94) ^{NS}	0.00 (0.20) ^{NS}	-0.05 (0.31) ^{NS}	-0.08 (0.30) ^{NS}
Number of species	0.31 (0.14) [*]	0.27 (0.21) ^{NS}	0.50 (0.17) ^{**}	0.54 (0.17) ^{**}
Body Size + Arborealism				
AIC/ Δ AIC	75.3/ 1.3	73.7/ 1.0	78.0/ 11.6	65.8/ 8.6
λ	0.86	0.00	0.29	0.10
Intercept	0.20 (0.62) ^{NS}	0.00 (0.20) ^{NS}	-0.07 (0.26) ^{NS}	-0.01 (0.20) ^{NS}
Body Size	0.91 (0.21) ^{***}	0.39 (0.22) ^{NS}	0.38 (0.20) ^{NS}	0.44 (0.19) [*]
Arborealism	0.37 (0.18) ^{NS}	0.21 (0.22) ^{NS}	0.28 (0.17) ^{NS}	0.31 (0.18) ^{NS}
Body Size + Number of species				
AIC/ Δ AIC	74.0/ 0.0	73.0/ 0.3	66.3/ 0.0	57.2/ 0.0

λ	0.79	0.00	0.44	0.34
Intercept	0.22 (0.54) ^{NS}	0.00 (0.20) ^{NS}	-0.05 (0.24) ^{NS}	-0.01 (0.20) ^{NS}
Body Size	0.65 (0.17) ^{***}	0.29 (0.20) ^{NS}	0.58 (0.17) ^{**}	0.55 (0.17) ^{**}
Number of species	0.31 (0.13) [*]	0.25 (0.20) ^{NS}	0.61 (0.15) ^{***}	0.57 (0.15) ^{**}
Body Size and + Body Size ²				
AIC/ Δ AIC	79.4/ 4.4	74.6/ 2.0	78.0 / 11.7	66.6/ 9.5
λ	0.86	0.00	0.07	0.06
Intercept	0.23 (0.66) ^{NS}	0.00 (0.20) ^{NS}	-0.01 (0.20) ^{NS}	-0.01 (0.20) ^{NS}
Body Size	0.73 (0.89) ^{NS}	0.54 (1.24) ^{NS}	2.25 (1.02) [*]	2.03 (1.14) ^{NS}
Body Size ²	-0.07 (0.86) ^{NS}	-0.24 (1.24) ^{NS}	-1.95 (1.03) ^{NS}	-1.62 (1.15) ^{NS}
Number of species + Arborealism				
AIC/ Δ AIC	88.5/ 11.5	75.2/ 2.6	76.5/ 10.2	65.3/ 8.1
λ	1.00	0.00	0.57	0.66
Intercept	0.02 (0.95) ^{NS}	0.00 (0.21) ^{NS}	-0.05 (0.32) ^{NS}	-0.08 (0.30) ^{NS}
Number of species	0.31 (0.15) [*]	0.27 (0.21) ^{NS}	0.50 (0.20) ^{NS}	0.51 (0.20) [*]
Arborealism	-0.08 (0.17) ^{NS}	0.05 (0.21) ^{NS}	0.01 (0.19) ^{NS}	0.05 (0.20) ^{NS}
^{NS} P>0.05	[*] 0.05>P>0.01	^{**} 0.01>P>0.001	^{***} P<0.001	

485

486

487 **Figure legends**

488 **Figure 1**

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

492

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

498

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

503

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