1 **Title: Resurrection of the island rule – human-driven extinctions have obscured a basic**

2 **evolutionary pattern**

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4 **Keywords:** anthropocene, body size, evolution, islands, mammals

5

6 The manuscript contains five supplementary figures and a supplementary excel sheet containing

7 information on body size and island status of all mammals.

8 This manuscript is intended to be a "Note."

9

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17

18   **Abstract**

19   Islands are or have been occupied by unusual species, such as dwarf proboscideans and giant rodents.

20   The discussion of the classical but controversial "island rule," which states that mammalian body sizes

21   converge on intermediate sizes on islands, has been stimulated by these unusual species. In this paper,

22   we use an unprecedented global data set of the distributions and the body sizes of mammals and a novel

23   analytical method to analyze body size evolution on islands; the analyses produced strong support for

24   the island rule. Islands have suffered massive human-driven losses of species, and we found that the

25   support for the island rule was substantially stronger when the many late-Quaternary extinct species

26   were also considered (particularly, the tendency for dwarfing in large taxa). In this study, the decisive

27   support generated for the island rule confirmed that evolution is markedly different on islands and that

28   human impact may obscure even fundamental evolutionary patterns.

29

Introduction

30

31 Before the arrival of humans, many oceanic islands housed bizarre mammal faunas. Dwarf

32 proboscideans used to occur on Mediterranean islands, the Channel Islands in California, and the island

33 of Timor in Southeast Asia, but all are extinct (Faurby and Svenning 2015). Similarly, giant rats were

34 frequent on islands, with only a few species that are extant (Faurby and Svenning 2015), although in

35 some cases with much reduced ranges, e.g., the Malagassy giant rat (*Hypogeomys antimena*) (Burney et

36 al. 2008). In addition to these clades with numerous deviant island forms, many other clades also had a

37 single or a few odd-sized island species, e.g., the extinct dwarf hippos of Crete and Madagascar and the

38 extinct Sardinian giant pika (Stuenes 1989, Angelone et al. 2008).

39   These bizarre island mammals stimulated the proposal of the island rule, which states that

40 mammalian body sizes converge on intermediate sizes on islands (Van Valen 1973). However, the

41 island rule has been intensely debated in recent years and is viewed as both a near universal rule

42 (Lomolino et al. 2011) and a sample or publication artifact (Meiri et al. 2008, Raia et al. 2010), with

43 intermediate positions also argued (Welch 2009). Both the opponents and the proponents of the island

44 rule acknowledge the apparent abundance of giants and dwarfs on islands (Meiri et al. 2008, Lomolino

45 et al. 2011). The two schools have strongly argued whether the island rule represents a general

46 evolutionary pattern, the idiosyncratic changes in individual lineages or even the human tendency to

47 see patterns in all datasets (Van Valen 1973, Meiri et al. 2008, Raia et al. 2010, Lomolino et al. 2011).

48   Critics of the island rule argue two primary points, both of which we overcome in the

49 present study. The first point concerns sampling bias. The studies that support the island rule have

50 generally been meta-analyses of published comparisons between the mainland and island populations

51   of the same species (Van Valen 1973, Lomolino et al. 2011). As discussed for the related Bergmann's

52   rule (Meiri et al. 2004), these studies may be a nonrandom subset of all populations and therefore a

53   significant pattern matching expectation may be generated by a reporting bias. In this study, we

54   removed the possibility for such sampling bias by generating and analyzing a database that contained

55   the body sizes for approximately 99% of all extant and recently extinct species of mammals (see

56   Materials and Methods).

57   The second critique of the basis for the island rule is that of phylogenetic

58   nonindependence, because previous studies showed diminished support for the rule when the

59   phylogeny was accounted for in the intraspecific analyses (Meiri et al. 2008, McClain et al. 2013). This

60   problem is a form of pseudo-replication that inflates the estimates of precision and thereby potentially

61   generates false significances. The magnitude (or existence) of this problem, however, depends on what

62   model is used as the null model. The classical studies, which compared only sister lineages (e.g.,

63   Lomolino 1985), are compatible with body sizes that evolved via simple models such as the Brownian

64   motion (Felsenstein 1985) or the Ornstein-Uhlenbeck (OU) models (Hansen 1997). The studies that

65   analyzed the ratios between the sizes of island and mainland mammals in a phylogenetic context (e.g.,

66   Meiri et al. 2008) might also be compatible with such models, when one assumes an identical age for

67   all island populations or that the island populations have reached a new equilibrium size.

68   However, with the assumption that the rate of evolutionary change is a function of traits,

69   which are also evolving, i.e., via the correlation between generation length and evolutionary rate

70   (Welch et al. 2008, Thomas et al. 2010), phylogenetic nonindependence is a problem for studies that do

71   not integrate phylogeny. Such a correlation is not a problem for studies that incorporate phylogeny and

72   that focus on the ratios between the island and mainland species, but these studies also require an

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73   identical age of all island populations or that the island populations have reached a new equilibrium

74   size. Imagine, for example, an analysis that contained two sets of rodent mainland /island sister pairs

75   with short generation times and therefore potentially fast evolutionary rates and that contained two sets

76   of elephant mainland/island species pairs with longer generation times and therefore potentially lower

77   evolutionary rates. If the rate is evolving over time, the comparisons of the magnitude of change

78   between the species pairs will need phylogenetic correction because larger relative differences between

79   the mice species pairs than the elephant species pairs could be a null expectation. Irrespective of

80   whether the rate is evolving, however, the null expectations would remain a 50% decrease in size in

81   both the mice and the elephants. To solve the potential problem of phylogenetic nonindependence

82   without requiring an identical age of all island populations or that the island populations have

83   previously reached a new equilibrium size, we restricted the analyses to focus only on the directionality

84   and not on the magnitude of change (see the Materials and methods). We stress that this restriction did

85   not imply that body size did not evolve as a Brownian motion process (there are strong indications that

86   it often does (Blomberg et al. 2003)) but that our analysis (explained below) did not make that

87   assumption. Moreover, the analysis was almost independent of the assumed model of body size

88   evolution.

89   In addition to the potential problems with the studies that support the island rule, the

90   primary interspecific study that dismisses the island rule (Raia et al. 2010) also has potential problems.

91   The study used a somewhat incomplete body size database (Smith et al. 2003) and a partially outdated

92   phylogeny (Bininda-Emonds et al. 2007). Raia et al. (2010) also included bats, whereas the classic

93   studies that support the island rule focused on non-flying mammals (Lomolino 1985) or analyzed bats

94   separately (Lomolino 2005). If supported, the island rule is likely a consequence of island isolation, and

95   the substantially lower levels of endemism in bats than in non-flying mammals (Weyeneth et al. 2011)

96   indicates that the island bat fauna is less isolated compared to non-flying mammalian fauna. Thus, the

97   island rule would be expected to establish a weaker pattern for bats than for non-bats.

98   In this paper, we reanalyzed the magnitude of the island rule in an interspecific context

99   using a novel, near-complete body size database and a recent mammalian phylogeny (Faurby and

100   Svenning 2015) solely focusing on the directionality and not on the magnitude of body size changes in

101   island lineages. To determine the potential importance of the factors responsible for the apparent lack

102   of support for the island rule in the earlier studies that integrated phylogenetic relationships between

103   species, we estimated the effects of including or excluding bats and extinct species and different

104   definitions of islands.

105

106   **Materials and methods**

107   **Data generation**

108   For all analyses, we used the taxonomy and the phylogeny of a recent mammalian phylogeny, which

109   included all species with dated occurrences within the last 130,000 years, but no likely chronospecies

110   (Faurby and Svenning 2015). Notably, most extant mammal species existed throughout this period and

111   therefore coexisted with the extinct species, and there is increasing evidence that Homo sapiens were

112   the primary cause of these extinctions (Sandom et al. 2014), particularly on islands (Turvey and Fritz

113   2011).

114   We generated a new body size database, which included almost all species of mammals (5673

115   of 5747 species; of the 74 species without data, 8 represented extinct, but undescribed, species). The

116   new database was partly based on an older database (Smith et al. 2003) but was heavily modified. The

117   information for 3629 of the 5673 species was used from the older database, but our complete database

118   contained information from a total of 709 separate data sources (644 articles published in 146 separate

119   journals, 55 books, 8 web resources and personal information from 2 experts; the complete database is

120   available in the Supplementary Data, in addition to information on which islands all island endemic

121   species are found). For the species for which the weight data were not available, the weights were

122   generally estimated with the assumption of strict isometries for related similar sized species. The

123   isometry was generally assumed for forearm length in bats and body length (excluding tail) for the

124   remaining species, but other measures were also used occasionally.

125   We scored island endemic or remainder as a binary character and defined island endemics based

126   on three definitions. The loose and classical definition was any species endemic to any area, which are

127   the oceanic islands at the current sea levels. The species that are currently restricted to islands (or were

128   restricted until their extinction in historical times) but with former Holocene occurrences on the

129   mainland, e.g., the Tasmanian devil (*Sarcophilus harrisii*) and the Tasmanian tiger (*Thylacinus*

130   *cynocephalus*) (Johnson and Wroe 2003), were not scored as island endemics. The strict definition was

131   for any species that was not found on any continent or any island connected to a continent during the

132   ice ages (i.e., any island for which the deepest water-level between the island and a continent was less

133   than 110 meters deep). Using this restricted definition, the island endemics were species for which the

134   majority of their evolutionary history were restricted to islands instead of species that happened to be

135   on islands with the current sea levels. For the few species that evolved by rapid speciation since the last

136 ice age on land-bridge islands (e.g., Anderson and Hadley 2001), this definition may be overly

137 restrictive because the species would have been island endemics for their entire evolutionary history.

138 Therefore, we also used a semi-strict definition, which was a relaxation of the strict island definition,

139 and any species that did not occur on large land-bridge islands (larger than 1000 km^2) were also scored

140 as island endemics. We acknowledge that this threshold was somewhat arbitrary, but rapid speciation

141 since the end of the last ice age likely required a small population size and therefore a limited area. The

142 largest island with a strong candidate for such recent speciation would be Coiba (503 km^2) with the

143 endemic agouti *Dasyprocta coibae*, whereas the colobus monkey *Procolobus kirkii* from Zanzibar

144 (1658 km^2, the smallest land-bridge island above 1000 km^2 that contained an endemic species)

145 appeared to have been isolated for substantially longer than the end of the last ice age (Ting 2008).

146

Analyses

148 The phylogeny used in this study consisted of the 1000 separate, random fully bifurcating trees from a

149 posterior distribution of trees that represented the phylogenetic uncertainty from Faurby and Svenning

150 (2015). Separate analyses were initially performed for each of the 1000 trees after which the results

151 from each tree were combined.

152   For each island endemic species (IE), we found the largest clade that contained only island

153 endemics (C_{Island}) and the smallest clade that contained both island endemics and nonendemics and

154 removed all members of C_{Island} from this clade (hereafter $C_{Mainland}$). We then estimated ancestral

155 $\log_{10}$(Weight) for all C_{Island} and $C_{Mainland}$, assuming Brownian motion. With the removal of the island

156 endemics for the calculation of $C_{Mainland}$, we allowed body size evolution to differ between island and

157   mainland clades but did not enforce such differences. Following this procedure, we sampled all the

158   island endemic species in random order, listed all members of C_{Island} and, if the sampled species was

159   not a member of the C_{Island} of any previously sampled species, noted the size of the (Size$_{Mainland}$) and

160   whether this size was smaller or larger than Size$_{Island}$. Therefore, our end products were a vector of

161   ancestral mainland weights for independent island invasions and a corresponding vector with binary

162   information on whether the island invaders were smaller than the mainland ancestors. To reduce the

163   effects of measurement errors on weight, we discarded from further analyses all island invasions for

164   which the difference in weight between Size$_{Mainland}$ and Size$_{Island}$ was smaller than 10%. Supplementary

165   analyses were performed using 0%, 5%, 15% and 20% weight difference thresholds, but the results

166   changed very little, although there was a tendency for a weaker island rule with the 0% threshold,

167   which was likely a consequence of the increased noise in the data (see Supplementary Figures S1-S5)

168   We then fitted zero to the 4th degree polynomial models of the probability of size decrease as a

169   function of the Size$_{Mainland}$ using a logistic regression $\left(M_{0_{Tree\ i}}, M_{1_{Tree\ i}}, M_{2_{2Tree\ i}}, M_{3_{Tree\ i}}, M_{4_{Tree\ i}} \right)$ and

170   calculated their respective AIC weights $\left(w_{0_{Tree\ i}}, w_{1_{Tree\ i}}, w_{2_{2Tree\ i}}, w_{3_{Tree\ i}}, w_{4_{Tree\ i}} \right)$. For all the

171   potential values of Size$_{Mainland}$ between 0.0 and 6.0 (i.e., untransformed weights between 1 g and 1 ton)

172   in steps of 0.1 for all models, we then calculated the means and the variances,

173    $\left(\mu_{M_{0\,0.0_{Tree\ i}}} \dots . \mu_{M_{0\,6.0_{Tree\ i}}} \right)$ and $\left(\sigma^2_{M_{0\,0.0_{Tree\ i}}} \dots . \sigma^2_{M_{0\,6.0_{Tree\ i}}} \right)$, respectively, for the untransformed fitted

174   values for all five models.

175   The results were thereafter combined for all five models for each potential value of $C_{Mainland}$ as a

176   mixture of the normal distributions from the five models, with the weight of each model equal to the

177   AIC weight. Therefore, the combined result was that the predicted effect for any k would be in the

178   distribution $\text{Predict}_{k\,Tree\,i} = \sum_{j=0}^{4} w_{j\,Tree\,i} \times N\left(\mu_{M_{j_{k\,Tree\,i}}}, \sigma^2{}_{M_{j_{k\,Tree\,i}}}\right)$. Following this procedure, the

179   results were combined for all trees as $Combined_k = \sum_{i=1}^{1000} \text{Predict}_{k\,Tree\,i}$. Finally, the median and

180   several quantiles for the *Combined*~k~ were transformed into probabilities.

181   We tested the effect of the definition of an island endemic, the potential effect of the

182   anthropogenic extinctions to bias the results and the effect of including bats in the analysis. The

183   analysis was performed separately for each of the twelve combinations of the three definitions of island

184   endemics (classical, semi-strict, strict), for the exclusion or inclusion of bats and for the exclusion or

185   inclusion of extinct species.

186   All analyses were performed in R 3.0.2 (R Core Team. 2013) using functions from the libraries

187   ape (Paradis et al. 2004), phylobase (R Hackathon et al. 2014) and qpcR (Spiess 2014).

188

189   **Model justification**

190   Because our analysis included approximately 99% of all mammal species, the issue of publication bias

191   was dismissed. However, we acknowledge that small biases might remain because of taxonomic

192   practices, e.g., whether island populations that diverged more in size from their mainland relatives were

193   more likely to be classified as separate species. One example of such a small bias is the island endemic

194   pygmy sloth (*Bradypus pygmaeus*) (Anderson & Handley, 2001). These questionable populations or

195   species are generally found on land-bridge islands (as with the pygmy sloth), and therefore, this type of

196   bias is a problem that should affect only the classical or semi-strict but not the strict island endemic

197   definition.

198   However, a problem noted by Meiri et al. (2008) might have affected our analysis. For the

199   two vectors A and B, the correlation between B and B/A is significantly negative the majority of the

200   time when A and B are independent. Meiri et al. (2008) extended this basic mathematical result to the

201   island rule and argued that the island rule pattern would occur when the body sizes of the populations

202   or species on the islands were independent of the body sizes of their mainland relatives. To assess the

203   effect of this relationship, we randomized the body sizes of all species, of all species within families, or

204   of all species within genera for the analysis with the apparent strongest island rule (i.e., strict island

205   endemic definition, excluding bats and including extinct species). For this analysis, the body sizes were

206   randomized anew for each of the 1000 trees.
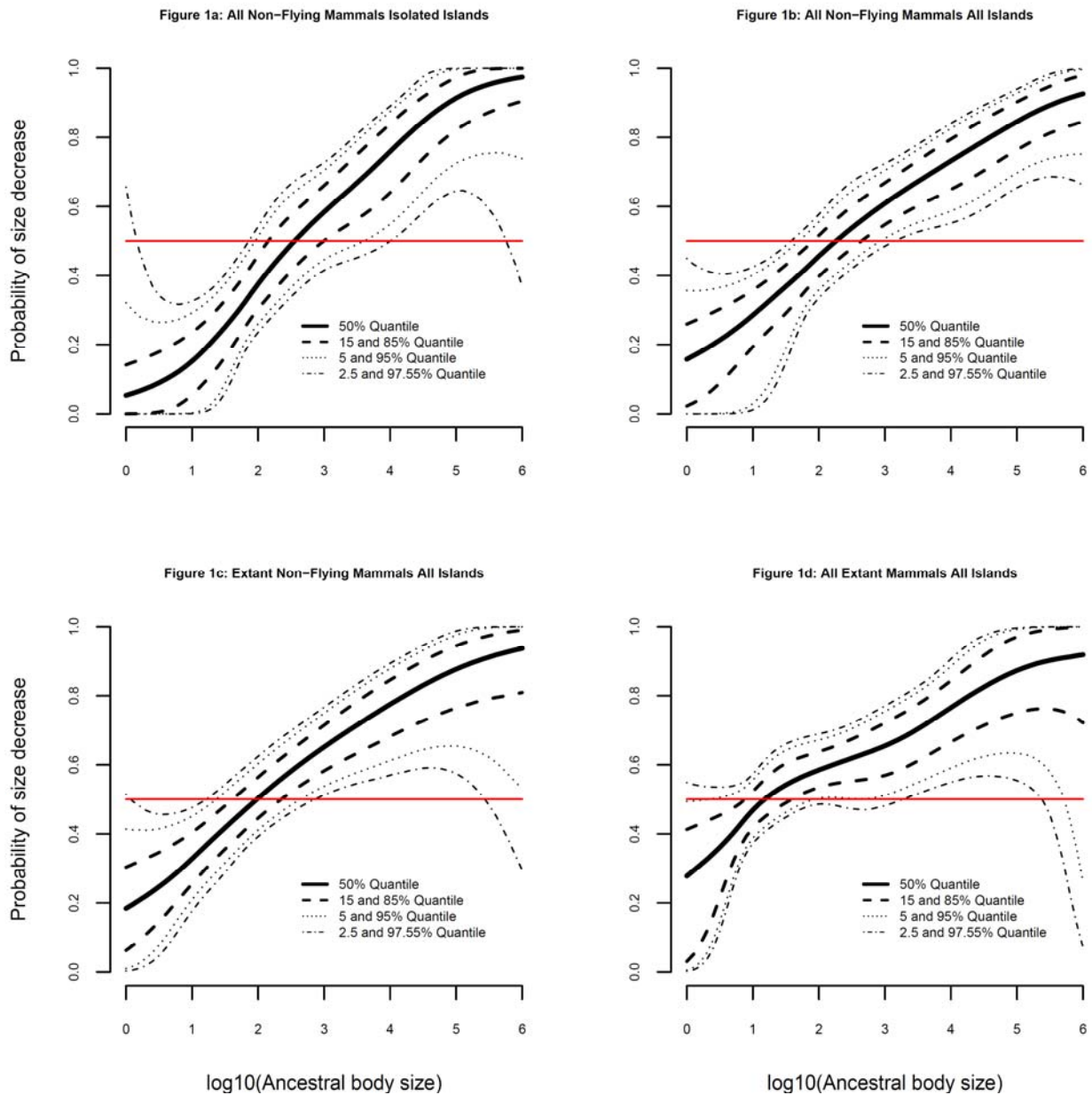
207

208   **Results**

209   Strong support for the island rule was provided when bats were excluded from the analysis but only

210   weak support when the bats were included. Among the 12 combinations of island-type definitions and

211   included species, the strongest support for the island rule (measured as the difference between the

212   predicted probability for size increase species for species with a size of 1 ton and 1 gram) was with the

213   strict island definition and the exclusion of bats but the inclusion of extinct species (Table 1, Figure 1,

214   Figures S1-S5). The inclusion of bats in the analysis consistently led to markedly lower support for the

215   island rule, and the addition of the bats removed or at least reduced the tendency for small mammals to

216   increase in size on islands. The inclusion of the extinct species and the application of the strict or semi-

217   strict island definitions provided stronger support for the island rule, but only when bats were excluded.

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Figure 1. Relationships between ancestral body size and directionality of evolutionary size change after island invasion.

The estimated probability of a size decrease as a function of the ancestral body size of the island invading clade. The thick black line shows the median of the distribution of potential predicted values, whereas the three stippled lines show the 2.5/97.5%, 5/95% and 15/85% quantiles. Because the response variable is binary, the values below the horizontal line indicate that a clade is most likely to increase in size, and the values above the horizontal line indicate that a clade is most likely to decrease in size. The first panel shows the relationship for non-flying mammals, including both extinct and extant species for isolated islands. The last panel shows the relationship for both flying and non-flying mammals but only for extant species and using all islands. The three differences between the panels are changed one by one; the last three panels use all the islands, the last two panels only analyze extant species and the last panel analyzes all mammals without restricting the analysis to non-flying species.

Figure 1a: All Non−Flying Mammals Isolated Islands

Figure 1b: All Non−Flying Mammals All Islands

Figure 1c: Extant Non−Flying Mammals All Islands

Figure 1d: All Extant Mammals All Islands

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The definitions of island endemics and the exclusion or inclusion of bats and extinct species also changed the shape of the relationship between body size and body size change on islands, in addition to influencing the magnitude of the island rule. For the strict island definition, when bats were excluded but extinct species were included, the apparent optimal size (the body size for which

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224   size increases and decreases are equally likely) was 500 gram ($10^{2.7}$ g). On the other hand, for the

225   classical island definition, when bats were included and, extinct species were not included, the optimal

226   size was only 20 gram. (Table 1).

227   Our analysis of the effect of randomization of body sizes showed no support for the island

228   rule under realistic randomization scenarios. Of the average of 143.3 independent island invasions from

229   each of the 1000 separate trees, an average of 38.5 consisted of island endemic genera. When these

230   genera were removed from the analysis with randomization within genera, almost no relationship

231   between the body size and the directionality of size change was detected (Figure 2a). A slightly

232   stronger but still weak pattern was found when the island endemic genera were included in the analysis

233   (Figure 2b); however, randomization at the family level (Figure 2c) was required to falsely generate a

234   pattern with substantial support for the island rule (the pattern with complete randomization was almost

235   identical to the pattern for randomization at the family level, results not shown). The results of these

236   randomizations strongly suggested that the support for the island rule was not an analytical artifact.

237

Figure 2. Relationships between ancestral body size and directionality of evolutionary size change for randomized body sizes.

All panels show the effect of randomization of body sizes for the strict island rule, when

extinct species are included but bats are excluded (analogous to Figure 1d). In Figure 2a, body

sizes are randomized across all genera but with all island endemic genera excluded from the

analysis, whereas in Figure 2b, body sizes are randomized across all species within genera and

the island endemic genera are included in the analysis. In Figure 2c, body sizes are randomized

across all species within families.

Figure 2a: Randomisation within genera
Excluding island endemic genera
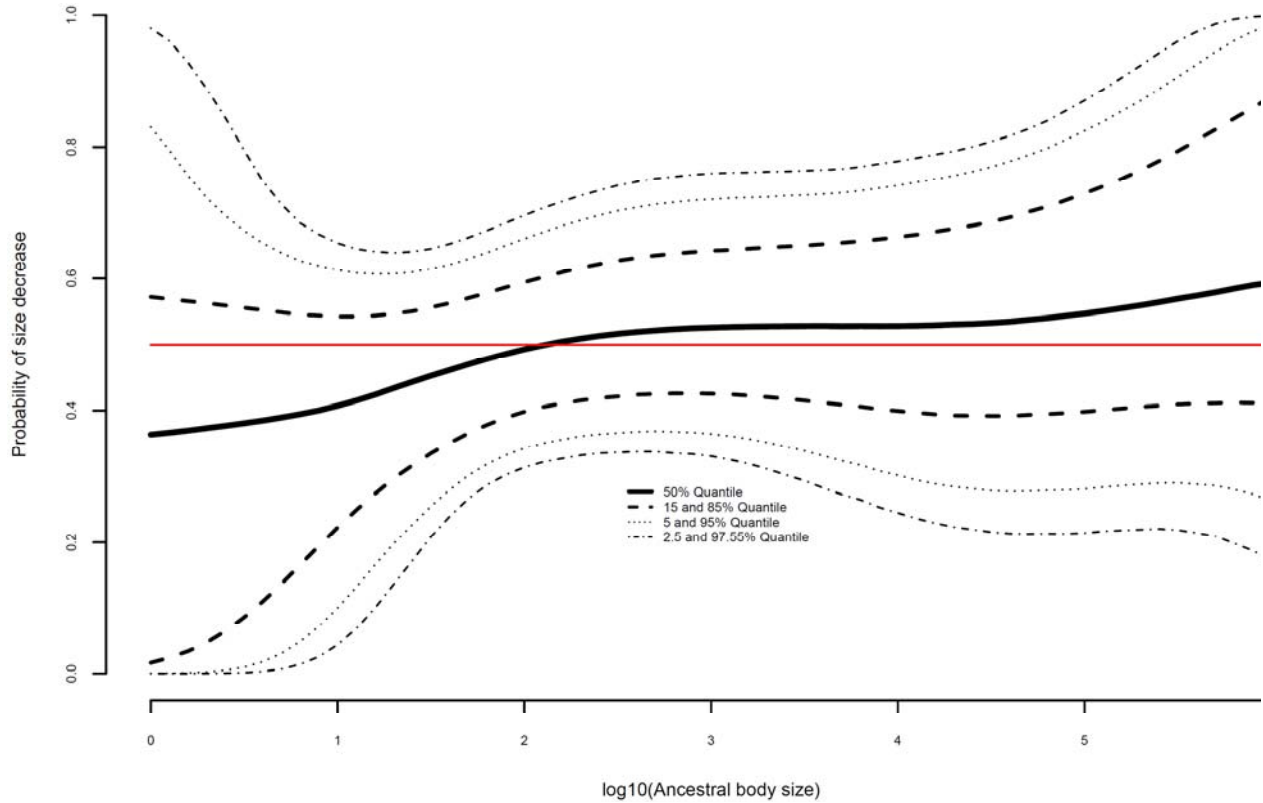

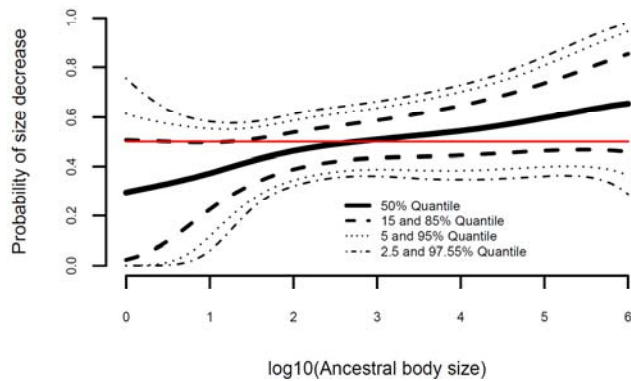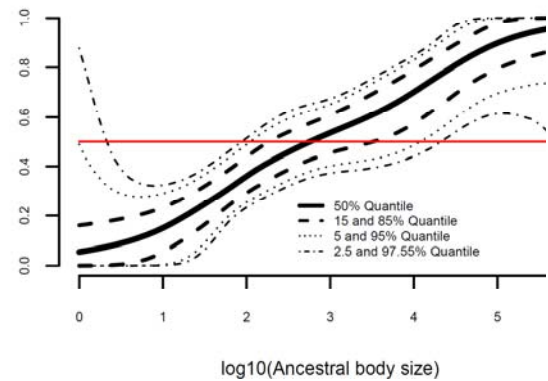### Figure 2b: Randomisation within genera

Figure 2c: Randomisation within families

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Discussion

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241   The validity of the island rule was clearly supported with our results. Therefore, we suggest that part of

242   the explanation for the lack of evidence for the island rule in the earlier interspecific study (Raia *et al.*

243   2010) was not because of the incorporation of the phylogeny, as the authors suggested, but because of

244   the choice to disregard the ecological difference between flying and non-flying mammals and, to a

245   lesser extent, the choice of definition of island endemics and the incomplete inclusion of historically

246   extant species (i.e., species that occurred within the Late Pleistocene or Holocene). In this regard, we

247   do not state explicitly that the models that excluded bats in our analysis provided a better fit to the data

248   than the models that included bats; however, we do state that the estimated effect of body size (i.e., the

249   island rule) is substantially stronger in the models that excluded bats.

250   The effects of including or excluding land-bridge islands and bats into the analysis can

251   potentially be seen as two sides of the same story. If the primary factor for the island rule was

252   ecological release, the rule would only be realized on islands with reduced numbers of predators or

253   competitor species. Therefore, the island rule would not apply or would be much less applicable to the

254   land bridge islands, which were part of the continental mainland during the last glaciation, in addition

255   to many earlier periods during the Pleistocene. The species on the land-bridge islands would have

256   experienced similar faunas as on the current mainland for a large part of their evolutionary history, and

257   therefore these species would not have experienced ecological release, or only relatively brief release.

258   Similarly, island bats were not likely to experience a significant ecological release because the primary

259   predators of bats are birds such as raptors and owls (Rydell and Speakman 1995). These birds are

260   typically strong fliers and therefore even long isolated islands tend to harbor well-developed predatory

261 bird faunas. Thus, for the native bat fauna on land-bridge islands, predator release would be limited or

262 would not occur.

263 Our focus on interspecific patterns enables us to disentangle the different factors driving

264 the island rule. The selection of immigrants for larger body sizes (as discussed in Lomolino, 2011)

265 could potentially be important for relatively new intraspecific comparisons. Considering the

266 evolutionary rates over small to medium time scales (Gingerich 2001), any effect of immigrant

267 selection would disappear in interspecific analyses unless other selective forces were maintaining the

268 changed body size (see Jaffe et al. (2011) for a similar argument regarding body size evolution in island

269 tortoises). Therefore, our results indicated that selection caused by the novel ecology on islands was

270 driving both the dwarfing and gigantism observed in different lineages.

271 With the arrival of humans, island faunas suffered severe extinctions. Our data set

272 included 589 non-flying and 223 flying island endemics based on the strict island definition, with

273 overall late-Quaternary extinction rates of 20% and 4%, respectively (the corresponding number for all

274 the islands was 916 non-flying and 323 flying species with extinction rates of 13% and 3%,

275 respectively; see Supplementary Data). These extinctions are often tightly linked to human arrival and

276 to evidence of human hunting or other anthropogenic factors (Turvey and Fritz 2011). Based on our

277 analysis, the inclusion of the extinct species strongly increased the support for the island rule. The

278 incorporation of the extinct island species was previously advocated for ecological studies (Griffiths et

279 al. 2009, Hansen and Galetti 2009), but our results highlighted the necessity to also include these

280 species in evolutionary studies. The recent human-driven extinctions most likely obscured signals

281 related to the long-term evolutionary responses to island environments, for example, the elimination of

282 the most specialized of the island lineages (Lomolino et al. 2013). In this regard, we note that we

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283   expect both dwarfing and gigantism to be an evolutionary consequence of predator release. Therefore,

284   the species that showed the largest changes in body size on islands would be expected to be the most

285   sensitive to predation by humans or by our commensal animals.

286   The apparent optimal body size of 500 gram determined in our analysis using the strict

287   island model and excluding bats but including extinct species (the model that showed the strongest

288   support for the island rule) was similar to an estimate of optimal body size derived from the patterns in

289   the intraspecific changes for terrestrial mammals on islands, which was 474 grams (Lomolino, 2005).

290   However, several arguments against a global optimal body size have been developed (discussed in Raia

291   et al. (2010)), and the similarity of the above results was possibly accidental. The potential accidental

292   nature of the similarity of these results was also supported by the variation in the suggested global

293   optimal size, if such an optimal size can be determined, with estimates of both 100 gram and 1 kg

294   suggested previously (Brown et al., 1993; Damuth, 1993).

295   In this study, the decisive support for the island rule highlighted that the function of island

296   ecosystems is fundamentally different from that of mainland systems (cf. Millen 2006) and that these

297   differences drive divergent evolutionary dynamics on islands and the mainland. Notably, our results

298   were consistent with the weakening of ecological interactions on islands that caused body sizes to shift

299   to intermediate biomasses, irrespective of the ancestral body size or the phylogenetic lineage.

300   Conversely, the strong support for the island rule also implied that much of the large variation in body

301   sizes or the repeated evolution of similar maximum body sizes in mainland systems (Smith et al. 2010)

302   was a consequence of the intense ecological interactions in these settings.

303

304   **Supplementary Materials**

305   Figures S1-S5.

306   Supplementary data. A database of body size and island species endemicity.

307

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Table 1. The estimated strength of the island rule under the 12 different analyzed scenarios

| Island definition	Including extinct species	Including bats	log10 of the body size with equal probability of size increase and decrease	Difference between the predicted probability of size increase for species of 1 ton and 1 gram
Classical	No	Yes	1.3	0.641
Classical	No	No	2.1	0.753
Classical	Yes	Yes	1.6	0.602
Classical	Yes	No	2.4	0.769
Semi-strict	No	Yes	1.5	0.578
Semi-strict	No	No	2.4	0.867
Semi-strict	Yes	Yes	2.0	0.583
Semi-strict	Yes	No	2.6	0.893
Strict	No	Yes	1.4	0.589
Strict	No	No	2.4	0.893
Strict	Yes	Yes	2.0	0.616
Strict	Yes	No	2.7	0.922

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Figure S1. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses without any threshold for a minimum size difference between island and mainland clades.

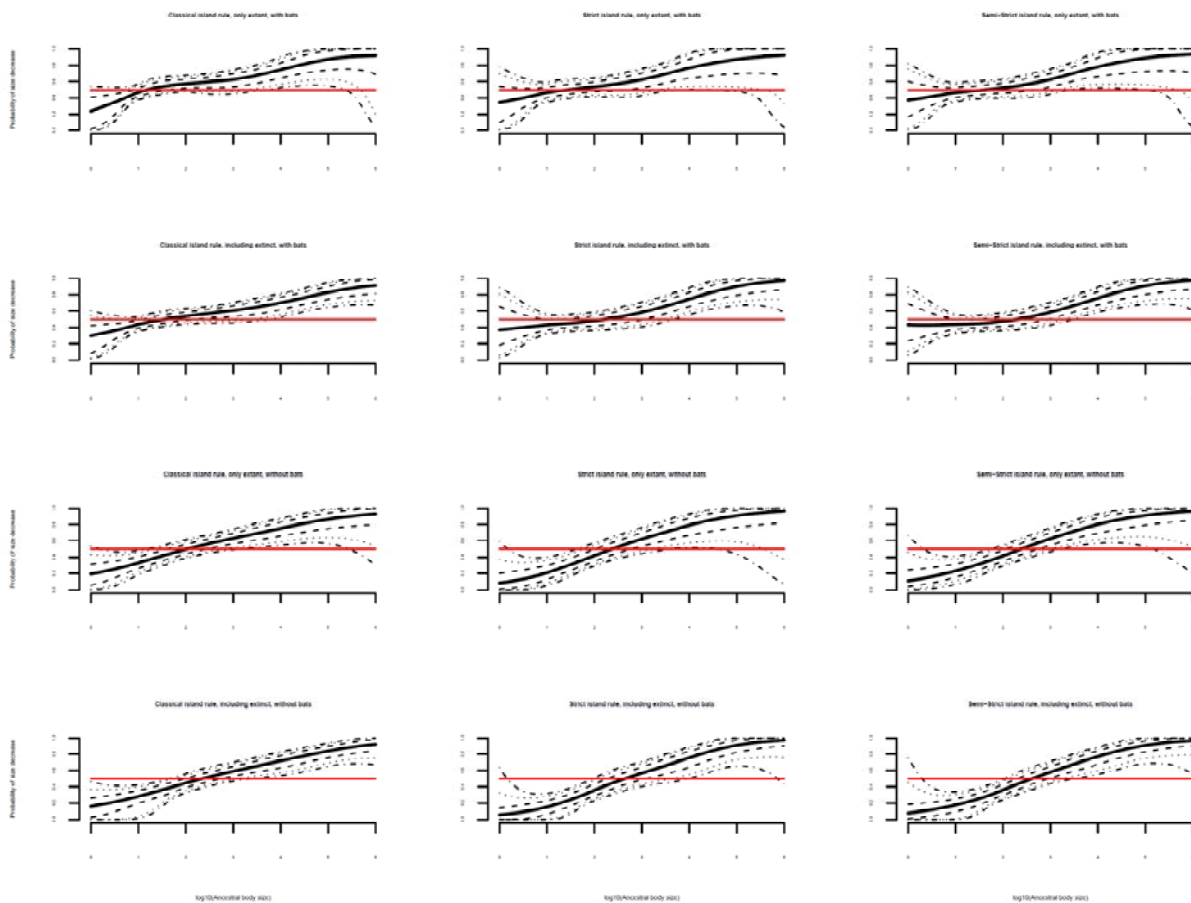The structure and meaning of the individual lines in each panel are identical to those in Figure 1.
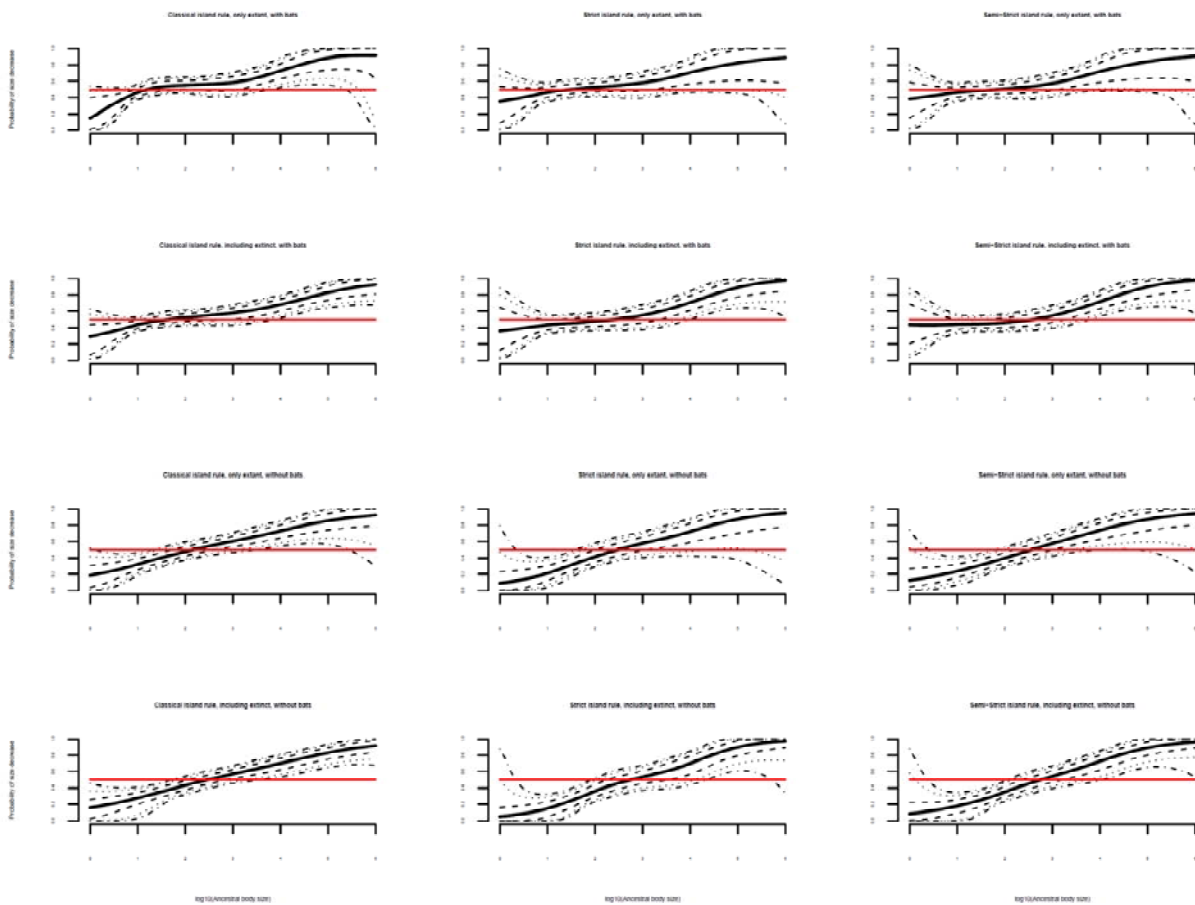
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Figure S2. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 5%.

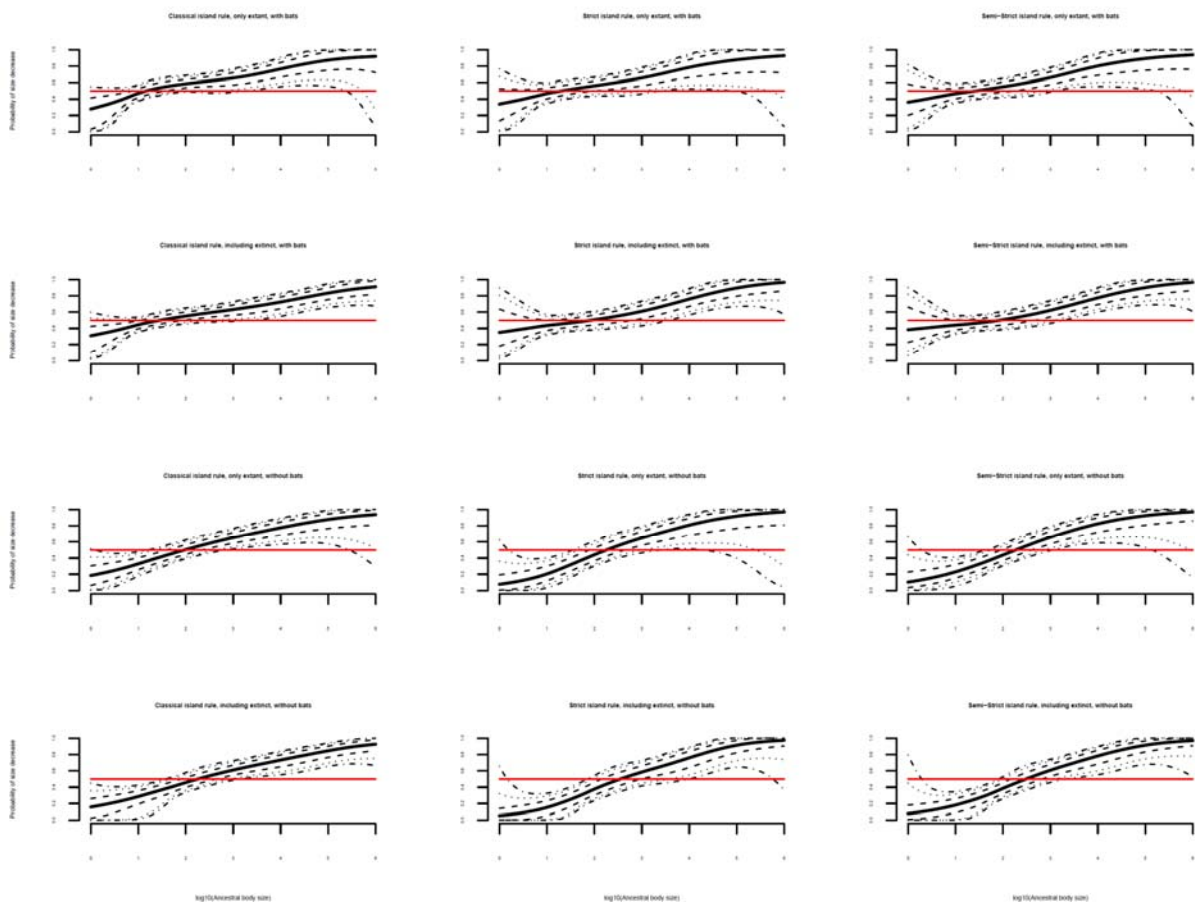The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

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Figure S3. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 10%.
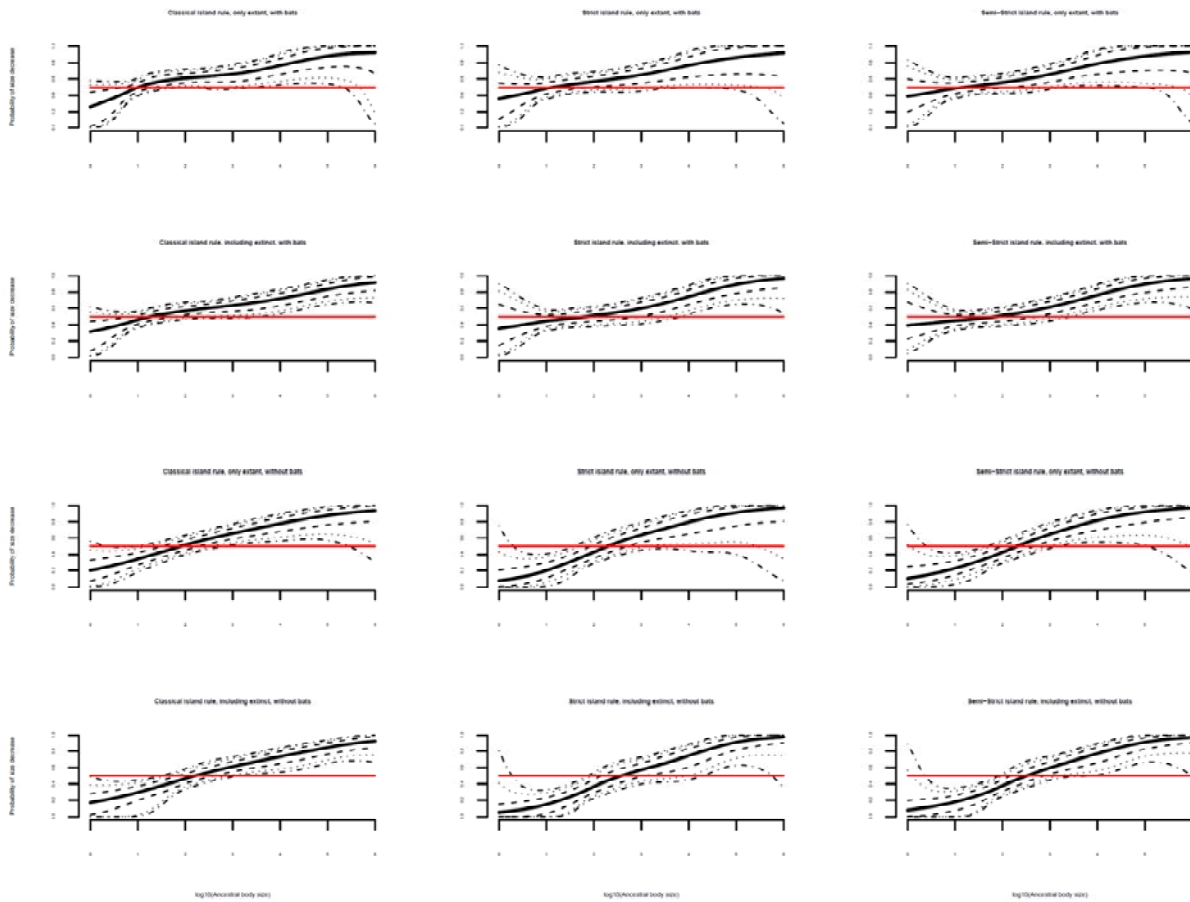The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

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Figure S4. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 15%.
The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

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Figure S5. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 20%.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

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