

1 The island rule explains consistent patterns of body size  
2 evolution in terrestrial vertebrates

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21 **Abstract**

22 Island faunas can be characterized by gigantism in small animals and dwarfism in large animals,  
23 but the extent to which this so-called ‘island rule’ provides a general explanation for  
24 evolutionary trajectories on islands remains contentious. Here we use a phylogenetic meta-  
25 analysis to assess patterns and drivers of body size evolution across a global sample of paired  
26 island-mainland populations of terrestrial vertebrates. We show that ‘island rule’ effects are  
27 widespread in mammals, birds and reptiles, but less evident in amphibians, which mostly tend  
28 towards gigantism. We also found that the magnitude of insular dwarfism and gigantism is  
29 mediated by climate as well as island size and isolation, with more pronounced effects in  
30 smaller, more remote islands for mammals and reptiles. We conclude that the island rule is  
31 pervasive across vertebrates, but that the implications for body size evolution are nuanced and  
32 depend on an array of context-dependent ecological pressures and environmental conditions.

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## 37 **Introduction**

38 From giant pigeons to dwarf elephants, islands have long been known to generate evolutionary  
39 oddities<sup>1</sup>. Understanding the processes by which island lineages evolve remains a prominent  
40 theme in evolutionary biology, not least because they include many of the world's most bizarre  
41 and highly threatened organisms<sup>2</sup>. The classic insular pattern of both small-animal gigantism and  
42 large-animal dwarfism in relation to mainland relatives has been described as a macro-  
43 evolutionary or biogeographical rule – the ‘island rule’<sup>3-5</sup> (Fig. 1). However, previous research  
44 has cast doubt on the generality of this pattern<sup>6</sup>, suggesting that body size shifts are  
45 asymmetrical, with reduced size in some clades (e.g. carnivores, heteromyid rodents, and  
46 artiodactyls) or increased size in others (e.g. murid rodents)<sup>7,8</sup>. Even in these cases, the  
47 underlying mechanisms driving patterns of insular gigantism and dwarfism remain unclear.

48 Several mechanisms have been proposed to explain the island rule, including reduced predation,  
49 relaxed competition and resource limitation in island environments<sup>9</sup>. In theory, each of these  
50 factors may be accentuated in smaller, more isolated islands, where lower levels of interspecific  
51 competition and predation could lead to ‘ecological release’, allowing small-bodied species to  
52 increase in body size<sup>5,9</sup>. Conversely, among large-bodied species, limited resource availability  
53 could select for smaller body sizes with reduced energy requirements, leading to insular  
54 dwarfism. Climatic conditions may also influence body size evolution on islands since primary  
55 productivity and associated resource availability are strongly influenced by climate<sup>9,10</sup>. Although  
56 previous studies of body size evolution on islands have tested the effects of these different  
57 mechanisms, many have focused on relatively restricted geographic and taxonomic scales and  
58 did not directly address the island rule in its broad sense across multiple species within a taxon<sup>10-  
59 13</sup>, with notable exceptions<sup>9,14-16</sup>.

60 Most work on the island rule has been restricted to mammals (e.g.<sup>4,7,14,17</sup>), although the  
61 hypothesis has also been tested in amphibians<sup>18</sup>, reptiles<sup>19-21</sup>, birds<sup>15,22</sup>, fish<sup>23</sup>, insects<sup>24</sup>,  
62 molluscs<sup>25</sup>, and plants<sup>26</sup>. The highly inconsistent results of these studies (e.g.<sup>5,6,27</sup>) are perhaps  
63 unsurprising because they typically deal with single species or pool together data on different  
64 traits from numerous sources without controlling for variation in study design or accounting for  
65 sampling variance. Accordingly, a recent systematic review based on a simplified scoring  
66 system<sup>27</sup> concluded that empirical support for the island rule is not only potentially biased but

67 also generally low, particularly for non-mammalian taxa. However, scoring approaches provide  
68 only limited information as they do not account for heterogeneity between studies, taxonomic  
69 representativeness, sample size, or precision in the estimates.

70 These limitations are best addressed with formal meta-analyses<sup>28,29</sup>, hence we tested the island  
71 rule hypothesis by applying phylogenetic meta-regressions to a global dataset of 2,479 island-  
72 mainland comparisons for 1,166 insular and 886 mainland species of terrestrial vertebrates  
73 (Supplementary Dataset 1, Fig. 2). Our analytical framework allows us to control for multiple  
74 types of variation, including data source, sample size imbalance, intraspecific and intra-  
75 population variability, and phylogenetic relatedness (see Methods). For each island-mainland  
76 comparison, we calculated the log response ratio ( $lnRR$ ) as the natural logarithm of the ratio  
77 between the mean body size of individuals from an insular population  $M_i$  and that of mainland  
78 relatives  $M_m$  ( $lnRR = \log[M_i/M_m]$ )<sup>30</sup>. Then, we regressed  $lnRR$  against the body mass of the  
79 mainland population ( $M_m$ )(Fig.1).

80 This framework provides a clear set of predictions in the context of evolutionary trajectories on  
81 islands<sup>4,6,14</sup>. Specifically, since negative values of  $lnRR$  indicate dwarfism and positive values  
82 indicate gigantism, a positive intercept and negative slope of the  $lnRR$ -mainland mass  
83 relationship supports the island rule (Fig. 1). Given the contentiousness of the generality in the  
84 island rule, we assessed the robustness of our results against potential biases derived of  
85 regressing ratios<sup>31,32</sup>, using small samples, imputing missing data, or the influence of using data  
86 from the island rule literature or derived from other studies focused on unrelated questions (i.e.  
87 publication bias; see Methods). Finally, we use our framework to assess how body size shifts are  
88 related to island size, island isolation, island productivity and climate, as well as species diet.  
89 The extent to which these different factors explain insular body size shifts allows us to re-  
90 evaluate a range of hypotheses for the mechanisms underlying “island rule” effects on body size,  
91 including ecological release<sup>9</sup>, immigrant selection<sup>9</sup>, resource limitation<sup>9,33,34</sup>,  
92 thermoregulation<sup>9,15,35</sup>, water availability<sup>36,37</sup> and starvation resistance<sup>9,33</sup> (Supplementary Table  
93 1, Extended Data Fig. 1).

## 94 **Results**

### 95 **The generality of the island rule**

96 We found that  $\ln RR$  and mainland body mass were negatively related for mammals, birds and  
97 reptiles, with small species tending to gigantism and large species to dwarfism (Fig. 3). The  
98 relationship was weakly negative but statistically non-significant for amphibians, with a  
99 tendency towards gigantism across all body sizes (Fig. 3, Table 1). We obtained similar results  
100 using size ratios corrected for small sample size ( $\ln RR^d$ ), or by regressing island mass against  
101 mainland mass, with support for the island rule across all groups except for amphibians  
102 (Supplementary Table 3-4). This indicates that our analyses are robust to small sample size bias<sup>38</sup>  
103 or any potential spurious correlation associated to ratio regression models<sup>31,32</sup> (Extended Data  
104 Fig. 2). Further, neither imputation nor publication bias influenced our results (Supplementary  
105 Table 5-6), with no apparent differences between island-mainland comparisons sampled from  
106 studies formally testing the island rule or compiled from unrelated data sets.

107 Mainland body mass explained 11.4, 7.0 and 17.6% of the variance in mammals, birds and  
108 reptiles, respectively. The amount of further variance accounted for by phylogeny (0.0–29.8%),  
109 data source (1.8–25.1%), and species (25.9–53.2%) fluctuated widely among taxa (Extended  
110 Data Fig. 3). Phylogeny accounted for a relatively large amount of variance in mammals (20.1%)  
111 and reptiles (29.8%), but even in these cases the overall patterns were not driven by large effects  
112 in particular clades. Some groups tended towards gigantism and others towards dwarfism, while  
113 others contained both dwarfs or giants depending on body size (e.g., Primata, Rodentia, and  
114 Carnivora in mammals, and Viperidae, Scincidae and Iguanidae in reptiles; Extended Data Fig.  
115 4).

### 116 **Ecological mechanisms underlying body size evolution on islands**

117 The pattern of body size evolution in our island-mainland comparisons provides some insight  
118 into the likely mechanisms driving “island rule” effects (Extended Data Fig. 5-8, Supplementary  
119 Table 7, Supplementary Dataset 2). Overall, insular size shifts arise through some combination  
120 of ecological release from predation and competition, resource limitation, biased colonization  
121 (i.e. immigrant selection), and starvation resistance. The fact that no single factor explained  
122 island effects on body size is not surprising because some hypotheses shared overlapping  
123 predictions, making them difficult to disentangle.

124 Shifts in body mass of mammals were mostly explained by island size and spatial isolation ( $Q_m =$   
125 12.20,  $P = 0.002$ , Fig. 4a), resulting in more pronounced gigantism or dwarfism in small and  
126 remote islands. Birds showed similar size shifts in relation to spatial isolation and island area, but  
127 these were not statistically significant (Supplementary Table 7). In both mammals and birds,  
128 temperature had similar effects across the size range, with body size consistently larger in cool  
129 islands and smaller in warm islands (Extended Data Figs. 5e, 6e). Hence, in these groups, even  
130 large species that had undergone dwarfism were significantly larger in cool insular environments  
131 than in warm ones. Contrary to the starvation resistance hypothesis, small-sized birds did not  
132 become larger in highly seasonal islands, but large-sized birds had reduced dwarfism on islands  
133 with high seasonality in temperatures ( $Q_m = 12.33$ ,  $P < 0.001$ , Extended Data Fig. 6).

134 In reptiles, the combination of island area and spatial isolation were the most important factors  
135 explaining variation in body size (Fig. 4c), with productivity and seasonality also supported but  
136 with weaker effects (Extended Data Fig. 7). Similar to mammals, the tendency towards dwarfism  
137 or gigantism in large-bodied or small-bodied reptiles was more apparent in isolated small-sized  
138 islands, with stronger effects of area than isolation (Supplementary Table 7). The effects of  
139 productivity and seasonality were only partially in line with predictions, as small-sized species  
140 were larger on islands with high seasonality, but smaller on islands with high productivity  
141 (Extended Data Fig. 7). In turn, large-bodied reptiles were smaller on islands with low  
142 productivity and high seasonality.

143 Finally, the relationship between size ratio and mainland mass in amphibians was slightly steeper  
144 in small and remote islands (Fig. 4d), with island area being marginally more important than  
145 spatial isolation (Extended Data Fig. 8). The effect of seasonality was clearer, with amphibian  
146 species inhabiting islands with high seasonality (unpredictable environments) tending toward  
147 gigantism, whereas those from islands with low seasonality (predictable environments) being  
148 similar in size to mainland counterparts (Extended Data Fig. 8). We found no effects of diet for  
149 any of the four taxa, or precipitation for amphibians, contrary to the water availability  
150 hypothesis.

## 151 **Discussion**

152 Based on comprehensive morphometric data from a worldwide sample of island fauna, we show  
153 consistent patterns of body size evolution across terrestrial vertebrates in accordance with  
154 predictions of the island rule. This finding was robust to alternative modelling approaches (island  
155 mass vs mainland mass regressions), small sample bias, data imputation, and publication bias.  
156 Moreover, we have demonstrated that insular size shifts are contextual and depend not only on  
157 the body size of mainland relatives (island rule *sensu stricto*) but also on the physiographic and  
158 climatic characteristics of particular island environments<sup>9</sup>.

### 159 **Repeated evolutionary trajectories on islands**

160 We found a clear negative relationship between insular body size variation and the body mass of  
161 mainland individuals in mammals, birds, and reptiles. Mainland body mass explains between 7.0  
162 and 17.6% of the variation in insular size divergence in these three taxonomic groups, which is  
163 similar to that reported in smaller-scale studies of bats (15%), birds (13%), snakes (42%), non-  
164 volant and terrestrial mammals (11–21%), and turtles (8%)<sup>5,14,15,39,40</sup>. Contrary to these earlier  
165 studies, our analyses are corrected not only for phylogenetic relatedness, but also for variability  
166 between species and intrapopulation variability, thereby strengthening the evidence for  
167 predictable evolutionary trajectories on islands. Nevertheless, the island rule provides only a  
168 partial explanation for these trajectories because substantial variation around the trend line  
169 remains unexplained. We also conducted the first multispecies test of island rule effects in  
170 amphibians, showing that the relationship goes in the expected direction but with a weak effect  
171 (1.4 %), possibly because the body mass range in amphibians is narrower and limited to small  
172 sizes (~ 0.5-50 g) and thus most amphibians tend to gigantism on islands with reduced predation  
173 risk.

174 Our findings are in contrast with a number of studies rejecting the island rule, including a recent  
175 review of evidence from across mammals, birds and reptiles<sup>27</sup>, as well as other taxon-specific  
176 studies focused on lizards<sup>20,41</sup> and turtles<sup>21</sup>. On the other hand, the patterns we detect are  
177 consistent with analyses supporting the island rule in snakes<sup>19</sup>, mammals<sup>4,9</sup> and birds<sup>5,15</sup>. We  
178 conclude that the contradictory results of previous studies may have been related to sampling  
179 bias, heterogeneity between sources and species, and phylogenetic relatedness (i.e. statistical  
180 non-independence). By accounting for these effects in our global models we are able to

181 demonstrate that vertebrate animals evolve in largely consistent ways on islands. Further, we  
182 have shown that the island rule is not clade-specific and instead applies to numerous clades  
183 within major taxonomic groups, particularly in mammals and birds.

184 A corollary that emerges from the island rule is that body size converges on islands. Specifically,  
185 if insular environments select for intermediate body sizes, closer to the optimal size of the focal  
186 clade, then the size spectrum of organisms found on islands should be narrower compared to the  
187 mainland<sup>42,43</sup>. Theoretically, the optimal body size towards which small and large species may  
188 converge in low-diversity systems such as islands should correspond to the point where the trend  
189 intersects the horizontal dashed line in the relationship between size ratio and mainland mass, at  
190 which point fitness is maximized<sup>42</sup> (but see<sup>44</sup>). Interestingly, the shift between dwarfism and  
191 gigantism in our models occurred at approximately 100-250 g in endotherms, slightly larger than  
192 the 100 g adult body mass proposed for mammals<sup>42</sup> (but see<sup>43</sup>), and the mode of the global body  
193 size distribution of birds that separate between small- and large-bodied species (60 g)<sup>22,45,46</sup>.  
194 Additionally, our analyses suggest that the optimal body size for island reptiles should be ca. 20  
195 g, which is marginally higher than the modal body size of Lepidosaurians (14.1 g)<sup>47</sup>. Whether there  
196 is an optimal body size in island biotas has been the subject of much debate<sup>44</sup>, but overall we  
197 expect that phenotypic variability in morphometric traits will be substantially narrowed if  
198 directional selection is operating in island assemblages, a feature that warrants further  
199 investigation. Additionally, optimal phenotypes should vary with the environmental  
200 characteristics of islands, in particular their area and isolation, climate, productivity and  
201 seasonality. For example, in mammals, our results suggest that the optimal body size would be  
202 ca. 100 g and ca. 900 g in warm and cold islands, respectively.

### 203 **Ecological mechanisms influencing body size variation**

204 Because body size is intimately linked to many physiological and ecological characteristics of  
205 vertebrates, it may be associated with a variety of environmental factors. As a consequence, the  
206 body size of colonizing species may predictably evolve as the result of selective pressures  
207 associated with insular environments (e.g., low food resources, few competitors, no predators)  
208 and others that act across larger geographic scales (e.g., climate). For mammals and reptiles, our  
209 results suggest that insular body size shifts are indeed governed by spatial isolation and island  
210 size, with individuals becoming dwarfs or giants in remote islands of limited size. Furthermore,



211 the slope of the relationship between size ratio and mainland mass was slightly steeper for birds  
212 and amphibians in small remote islands than in large islands near continental land masses (Fig.  
213 4). This points to a combination of resource limitation (with small islands having fewer resources  
214 to maintain large-sized organisms<sup>48,49</sup>) along with release from interspecific competition and  
215 predation pressure in small, species-poor islands. The pattern is also consistent with biased  
216 colonization favoring larger individuals with higher dispersal abilities (immigration selection<sup>50</sup>).  
217 Conversely, our results showed that body size divergence on islands close to the mainland was  
218 minimal, reflecting two non-mutually exclusive processes. First, many of these islands were  
219 connected to the continent by land bridges so recently that phenotypic differences have not had  
220 time to accumulate. Second, regular dispersal between mainland and island populations promotes  
221 gene flow, with introgression counteracting divergent selection<sup>51,52</sup>.

222 Besides island physiography (area and isolation), other relevant factors were temperature  
223 conditions in endotherms and resource availability and seasonality in ectothermic organisms.  
224 Mammals and birds both responded to island temperature in line with the heat conservation  
225 hypothesis, with small- and large-sized species exhibiting exacerbated gigantism and diminished  
226 dwarfism, presumably to conserve heat in colder, harsher insular environments. Additionally,  
227 temperature seasonality was an important determinant of the size of large-bodied birds, with  
228 populations on highly seasonal islands being similar in size to mainland populations. One  
229 possibility is that larger size in these cases may help maintain energy reserves during periods of  
230 low food availability, allowing them to thrive in otherwise hostile environments. Another  
231 possibility is that bird populations on highly seasonal islands – which tend to be situated at  
232 relatively high latitudes – are more often seasonally mobile or even migratory, potentially  
233 increasing gene flow with mainland populations or weakening adaptation to the local  
234 environment<sup>53</sup>. These findings add new insights to previous results regarding the role of thermal  
235 and feeding ecology on morphological divergence in island birds<sup>54,55</sup>. Traditionally, changes in  
236 feeding ecology were thought to be the prime force in driving morphological divergence in  
237 island birds<sup>54,55</sup>. Yet, our results imply that physiological mechanisms related to heat  
238 conservation (‘thermoregulation hypothesis’) and energy constraints (‘starvation resistance  
239 hypothesis’) may also shape body size evolution in island birds.

240 In reptiles, we find some evidence that resource availability and seasonality are important factors  
241 explaining body size evolution, with some deviations from the patterns predicted. As  
242 hypothesized, large species are much smaller on islands with low resource availability, and small  
243 species are larger on islands with high seasonality. Yet, unexpectedly, small species are larger on  
244 islands with low productivity, perhaps because increased intraspecific competition favors large  
245 individuals under the high population densities that reptiles often attain on islands<sup>56,57</sup>.

246 Overall, most amphibians tended to gigantism, presumably as a result of increased growth rate or  
247 lower mortality due to reduced predation pressure on islands<sup>58</sup>. Additionally, we found that body  
248 size of amphibians consistently increased on islands where resources were highly seasonal and  
249 unpredictable, perhaps to maximize energy reserves and withstand long periods without food, for  
250 example during aestivation or hibernation<sup>59</sup>. We did not find a clear relationship between  
251 precipitation and body size, suggesting that water availability is not a key factor. It appears that  
252 gigantism in island amphibians is mostly driven by physiological mechanisms that maximize  
253 growth rate, particularly in smaller, more isolated islands. These findings should be further  
254 explored when more data on island-mainland pairwise populations of amphibians become  
255 available.

### 256 **Body size evolution in extinct species**

257 Our analyses focused on extant species for which we could gather information on the variation  
258 around the morphometric estimates, along with sample size (essential for meta-analyses). The  
259 widespread extinction of large species on islands, including dwarf morphotypes of large species  
260 such as insular elephants in Sicily and the Aegean islands<sup>60,61</sup>, may have masked the historical  
261 pattern of phenotypic variation on islands<sup>62</sup>. Giant insular birds<sup>54,63</sup>, primates<sup>64,65</sup>, and lizards<sup>66</sup>,  
262 along with large insular turtle species, went extinct during the Holocene and late Pleistocene<sup>67</sup>,  
263 most likely because of overhunting and the introduction of invasive species<sup>68,69</sup>. Overall, it is  
264 estimated that human colonization of oceanic islands was followed by the extinction of 27% of  
265 insular endemic mammals<sup>70</sup>, as well as over 2000 bird species in the Pacific region alone<sup>71</sup>, with  
266 these losses biased towards large-bodied, flightless, ground-nesting species<sup>68</sup>. Extinct species  
267 may shed new light on size evolution in insular vertebrates because species extinctions have  
268 substantially altered the biogeography of body size in island faunas, potentially leading to  
269 downsized insular communities<sup>72,73</sup>. For example, the predominance in our dataset of smaller-

270 bodied organisms could reflect the extinction of large species on islands<sup>68</sup>, or simply the fact that  
271 few islands support large species. Either way, further studies should include data from extinct  
272 species as this may alter or strengthen the signal that we report for extant species<sup>39</sup>.

273 We foresee that, under global change, the extinction of insular species and the introduction of  
274 novel (invasive) species may trigger new equilibria, with concomitant shifts in the composition  
275 of insular communities and the opening of novel niches to which species may respond via  
276 genetic adaptations and phenotypic plasticity. Recent evidence indicates that even introduced  
277 species on islands, which were not included in our analysis, predictably evolve towards dwarfism  
278 or gigantism<sup>74-76</sup>. In theory, as the Anthropocene gathers pace, further extinctions will drive a  
279 decline in mean body size of the overall island community, pushing optimal body sizes towards  
280 the lower end of body size ranges in the different vertebrate groups.

## 281 **Conclusions**

282 Of the many evolutionary implications of living on islands – together known as the ‘island  
283 syndrome’<sup>2</sup> – the effects on body size are the most widely known and controversial. We have  
284 shown that these ‘island rule’ effects are widespread in vertebrate animals, although the evidence  
285 for amphibians is inconclusive. Morphological changes were directional for species at the  
286 extremes of the body size range in mammals, birds and reptiles, following the predicted pattern  
287 of convergence towards intermediate “optimum” body sizes, in line with optimal body size  
288 theory<sup>42,43,45</sup>. Although this convergence towards morphological optima may result from natural  
289 selection or phenotypic plasticity, the exact mechanism producing these changes on islands is  
290 still not well understood. Nonetheless, we found that consistent transitions towards intermediate  
291 body sizes were associated with a combination of factors, indicating a range of different  
292 ecological mechanisms. Our results highlight the contextual nature of insular size shifts, where  
293 island physiographic, climatic and ecological characteristics play a fundamental role in shaping  
294 body size evolution, reinforcing the idea that large-scale macroevolutionary patterns do not arise  
295 from single mechanisms but are often the result of multiple processes acting together<sup>77,78</sup>.

## 296 **Methods**

### 297 **Data collection**

298 We collected baseline morphometric data from articles included in a recent assessment of the  
299 island rule<sup>27</sup>, as well as other compilations assembled to test the hypothesis in reptiles<sup>20</sup>,  
300 mammals<sup>6</sup>, and birds<sup>15</sup>. To expand this sample, we then performed a literature search (February  
301 2020) in Web Of Science Core Collection (WOS) using the following search string: (“island  
302 rule” OR “island effect” OR “island syndrome” OR island\*) AND (gigantism OR dwarfism OR  
303 “body size” OR weight OR SVL OR snout-vent length OR length OR size) AND (mammal\* OR  
304 bird\* OR avian OR amphibia\* OR reptile\*) (Appendix 1). Because this search was  
305 complementary to the data we have gathered from previous compilations<sup>6,15,20,27</sup>, we only  
306 downloaded the first 500 hits out of a total of 33,431 hits ordered by relevance, and removed  
307 duplicates already included in our dataset. We reviewed every island-mainland comparison  
308 reported in published studies and traced primary source data when possible to extract original  
309 measurements. We also extracted data from all studies containing morphometric measurements  
310 for insular populations when these could be matched with equivalent data published elsewhere  
311 for relevant mainland taxa. We excluded problematic data, such as comparisons that were not  
312 supported by taxonomic or phylogenetic evidence, or which reported morphometric data  
313 restricted to single specimens or without sample size. In addition, we excluded comparisons  
314 based on extinct taxa since they are often known from very few or incomplete specimens  
315 (Supplementary Dataset 3).

316 It has been argued that research on the island rule might be prone to ascertainment bias, where  
317 researchers are more likely to notice and measure animals of extreme body size when conducting  
318 research on islands<sup>41</sup>. To help overcome this problem, we collected body size data not only from  
319 studies testing the island rule, or reporting dwarfism and gigantism in island fauna, but also from  
320 studies that did not specifically test hypotheses related to the island rule. We matched unpaired  
321 insular populations with independent data from mainland populations by performing species-  
322 specific searches in WOS and Google Scholar. We also compiled morphometric data for 442  
323 insular and 407 mainland bird species from an independent global dataset of avian functional  
324 traits<sup>79</sup>.

325 Large islands may be more ‘mainland like’ in relation to factors that are thought to affect body  
326 size (i.e. competition, resource availability and predation<sup>5</sup>). Thus, when major islands were at  
327 least 10 times larger than a nearby island, we treated the large island as the mainland  
328 comparison, following previous studies testing the island rule<sup>4,5,20</sup>. Consequently, a single mid-  
329 sized island can simultaneously be treated as the continent in comparisons with smaller islands,  
330 and the island in comparisons with larger continents. When authors reported data referring to an  
331 entire archipelago instead of a specific island (3.2% of cases), we used the size of the largest  
332 island as island area. Removing these cases from our analyses did not qualitatively affect our  
333 results (Supplementary Table 8).

334 Our final dataset contained 529 data sources and 2,479 island-mainland comparisons<sup>7,10,36,58,79-</sup>  
335 <sup>602</sup>. In total, we collated morphometric measurements for 63,561 insular and 154,875 mainland  
336 specimens representing mammals (1,058 island-mainland comparisons), birds (695  
337 comparisons), reptiles (547 comparisons) and amphibians (179 comparisons) from across the  
338 globe (Fig. 2). 2,068 island-mainland comparisons (83.4%) were within species (e.g. subspecies)  
339 comparisons, and 411 (16.6%) were between-species comparisons. Insular populations were  
340 sampled from an array of islands varying widely in size (0.0009–785,753 km<sup>2</sup>), climate, and  
341 level of spatial isolation (0.03–3,835 km from mainland). To explore the drivers of body-size  
342 shifts in insular populations, we also sampled species with a wide range of average body masses  
343 (0.18–234,335 g). We collated data on body size indices (body mass, body length, cranial and  
344 dental measurements) of different taxa in island and mainland populations following strict  
345 morphological, phylogenetic and biogeographic criteria. Specifically, we always compared the  
346 same body size index for island and mainland populations. For within-species comparisons, we  
347 compared island and mainland populations based on the information given by the authors of the  
348 relevant study (e.g. taking note of which mainland source populations are likely to inhabit a  
349 particular island because of colonization history or isolation via rising sea levels<sup>89,101,240,386,548</sup>).  
350 When we matched comparisons independently, we used information published in the study  
351 reporting the insular form, selecting the geographically closest mainland population whenever  
352 possible. In addition, we prioritized latitudinal alignment of mainland and island populations to  
353 avoid confounding effects of latitudinal variation in body size. In the case of island endemics, we  
354 compared island populations to their closest mainland relative whenever these were identifiable  
355 by phylogenetic data or other information reported in each particular study. This usually meant

356 selecting their sister species or the geographically closest representative of a sister clade or  
357 polytomy (Supplementary Dataset 1). If we could not reliably establish the closest mainland  
358 relative, we discarded the data (see Supplementary Dataset 3).

359 When more than one body size index was reported in published studies, we prioritized those  
360 indices related most closely to body mass (Supplementary Table 2). For mammals, we selected  
361 indices in this order of preference: body mass, body length, cranial length (greatest skull length  
362 or condylobasal length), and dentition (e.g. canine length)<sup>5</sup>. For birds, preferred indices were  
363 body mass, wing length, tarsus length and bill length. Finally, for amphibians and reptiles, size  
364 was reported as body mass, snout-vent-length (SVL), carapace length (CL, for turtles) and total  
365 length (TL, including SVL and tail length). In all cases, we included measurements for adults  
366 only. To avoid size biases attributable to sexual size dimorphism, we calculated the pooled mean  
367 for both sexes and the combined SD using standard formulae for combining groups<sup>603</sup>. When  
368 information was only available for one sex (male or female), we restricted our size comparisons  
369 to the sex for which we had morphometric data in both mainland and island populations. Data  
370 from zoos or studies that could not be georeferenced were discarded.

371 To overcome the problem that different authors report size using different indices, we used  
372 allometric relationships to convert island and mainland size to body mass equivalents, thereby  
373 enabling cross-taxa and cross-study comparisons. Although this conversion is imprecise,  
374 morphological indices and body mass are nonetheless highly correlated across the global scale  
375 and wide range of body sizes within our samples (providing more accurate predictions than  
376 simply assuming an exponent  $\sim 3$ , as in previous studies testing the island rule<sup>5,9</sup>). We used  
377 published allometric relationships where available (see Supplementary Table 2), or derived them  
378 based on published datasets<sup>47,179,604-609</sup> and other data sources (Supplementary Dataset 4). To  
379 calculate allometric relationships, we used OLS (Ordinary Least Square) models of the  $\log^{10}$   
380 transformed body mass against the  $\log^{10}$  transformed body size index (e.g. condylobasal length,  
381 Supplementary Table 2, Supplementary Dataset 4).

382 For birds, we complemented published data with standardized morphometric measurements from  
383 3,618 museum specimens and live individuals of 436 insular and 404 mainland bird species  
384 (see<sup>79</sup>). We used wing length in the main analyses instead of tarsus length because the former is a  
385 better predictor of body mass in our dataset ( $R^2_{wing} = 0.89$  vs  $R^2_{tarsus} = 0.69$ , Supplementary Table

386 2) (see also<sup>610</sup>). Although wing length may change during moult or thereafter because of wear,  
387 these effects are negligible in relation to interspecific differences<sup>79</sup> and minimized by calculating  
388 averages across multiple individuals. Further, interobserver differences between measurements  
389 may explain some variation in wing length estimates, but again this bias was shown to have  
390 negligible effects in our dataset by comparing repeated measures from different observers  
391 (see<sup>79</sup>). To assess the consistency in our results, we repeated analyses using tarsus length, another  
392 popular proxy of overall body size in birds<sup>611</sup>. Our results were unchanged (Fig. S2).

393 To select suitable comparisons for museum specimens, we first classified species as either  
394 insular or continental by overlapping IUCN range polygons with a GIS land layer including  
395 continental land masses. For each insular species we then identified continental sister species  
396 from avian phylogenies<sup>612</sup>, using the method described above. We excluded bird species that are  
397 highly pelagic or aerial (e.g. swifts) and fully migratory species because in these groups it is  
398 unclear whether insular and mainland forms experience different environments<sup>15</sup>. Further, we  
399 also excluded flightless bird species, because morphological changes may be due to  
400 flightlessness rather than island dwelling per se<sup>15</sup>.

401 We calculated the response ratio ( $\ln RR$ , eq. 1) as effect size in our meta-regressions, where we  
402 divided the mean body mass of individuals from an insular population  $\bar{M}_i$  by that of the nearest  
403 mainland relative,  $\bar{M}_m$ , and then applied the natural logarithm. Unlike unlogged ratios, the  
404 sampling distribution of  $\ln RR$  is normal, particularly for small samples<sup>30</sup>, and thus less prone to  
405 statistical artefacts associated with ratio-based regressions.

$$406 \quad \ln RR = \ln \left( \frac{\bar{M}_i}{\bar{M}_m} \right) \quad (\text{Eq. 1})$$

407

408 Response ratios greater than zero indicate a shift towards larger sizes (gigantism) whereas ratios  
409 less than zero indicate shifts towards smaller sizes (dwarfism). Besides mean measurements, we  
410 recorded measures of variation, i.e. standard deviation (SD), standard error (SE) or coefficient of  
411 variation (CV), and sample sizes of the body size indices in island and mainland organisms. SD  
412 and sample sizes were used to calculate sampling variances (Eq. 2), which were then used to  
413 weight each response ratio (coupled with the amount of heterogeneity, i.e. the variance in the  
414 underlying effects)<sup>30</sup>.

$$415 \quad \hat{\sigma}^2(\ln RR) = \frac{SD_i^2}{N_i \bar{x}_i^2} + \frac{SD_m^2}{N_m \bar{x}_m^2} ; \quad (\text{Eq. 2})$$

416

417 SDs were extracted from raw data when possible. If ranges were provided instead of SD (or SE  
418 or CV), we calculated SD following<sup>613</sup>. If neither ranges nor measures of variation were reported,  
419 but the reported sample size was > 1, we imputed SD based on the coefficient of variation from  
420 all complete cases (“Bracken approach”<sup>614</sup>). Imputation was done for 22% of all cases in  
421 mammals, 1.1% in birds, 11% in reptiles and 7.3% in amphibians, all within the upper limit of  
422 imputations (<30% of all cases per group) advised in previous studies<sup>90</sup>.

423 For each study and island-mainland comparison, we compiled the mainland and island names,  
424 the study reference, the body size index used, the geographic coordinates, the distance to the  
425 closest mainland (spatial isolation, km) and the island area (km<sup>2</sup>). We completed missing data on  
426 island characteristics using the UNEP island database (<http://islands.unep.ch/>) and the  
427 Threatened Island Biodiversity Database (TIB, <http://tib.islandconservation.org/>). Missing  
428 information was calculated using Google Earth. Additionally, we extracted the Normalized  
429 Difference Vegetation Index (NDVI) as a proxy for resource availability on islands<sup>615</sup>. We also  
430 calculated the standard deviation of NDVI to assess seasonality in leaf or vegetation cover, as an  
431 index of seasonality in available resources. NDVI was downloaded from NASA Ames  
432 Ecological Forecasting Lab (<https://lpdaacsvc.cr.usgs.gov/appears/task/area>).

433 Because climate influences both resource requirements and primary productivity, body size  
434 evolution should also be influenced by climatic conditions on islands. We thus extracted island  
435 climatic conditions from WorldClim v. 2.0 (<http://worldclim.org><sup>616</sup>). Specifically, we used  
436 variables that are more closely associated with the proposed underlying mechanisms of  
437 Bergmann’s rule (i.e. thermoregulation and starvation resistance): mean annual temperature,  
438 annual precipitation, and seasonality of temperature and precipitation<sup>617</sup>. We assumed that the  
439 time period for these bioclimatic variables (1970–2000), although not necessarily matching the  
440 actual time period of body size evolution in the insular populations, roughly represents the  
441 climatic conditions in the Holocene, a period relatively climatically stable where most of our  
442 populations became isolated (i.e., after the last glacial maximum; see also<sup>9</sup>). Because climatic  
443 variability across cells substantially exceeds variation within cells in the Holocene, current layers  
444 are considered adequate for geographic comparisons. All spatial variables were downloaded at



445 0.1-degree resolution, and we averaged all cells per island to obtain a mean value of each  
446 environmental variable (e.g., temperature, NDVI, precipitation, etc.). Finally, for each species  
447 included in our dataset, we collated diet information from EltonTraits for birds and mammals<sup>618</sup>,  
448 and from other sources for reptiles<sup>608,619</sup>, and classified species as carnivores (> 50% diet  
449 consisting of vertebrates) or non-carnivores (< 50% diet consisting of vertebrates), following  
450 previous studies<sup>79,620</sup>. As all amphibians in our dataset are carnivores<sup>621</sup>, we did not record their  
451 diet.

## 452 **Data analyses**

453 To test the island rule hypothesis, we used phylogenetic meta-regressions between  $\ln RR$  and  
454 body mass of mainland relatives, following most previous studies of the island rule (e.g. <sup>4,5,7</sup>  
455 <sup>6,622,623</sup>). A negative slope for this relationship would support the island rule (Fig. 1).

456 The use of multiple populations of the same species can overestimate the actual number of  
457 degrees of freedom, generating type-1 errors. We controlled for this by adding ‘Species’ as a  
458 random effect intercept in our analyses. Additionally, body size evolution in insular vertebrates  
459 is heavily influenced by phylogenetic effects, with species within entire clades seemingly  
460 showing either dwarfism or gigantism<sup>6</sup>. Thus, we accounted for phylogeny by including the  
461 phylogenetic relatedness correlation matrix as a random effect. The species term captures the  
462 similarities of effect sizes within the same species, while the phylogenetic term represents the  
463 similarity due to relatedness<sup>624</sup>. We also added ‘Source’ as a random effect intercept to account  
464 for between-source variability and the fact that we had multiple response ratios per study. In  
465 some cases, ‘Source’ represented the combination of two sources of data, one for the island size  
466 and one for the mainland size. Finally, we included an observation level random effect, which  
467 represents the residual variance that needs to be explicitly modelled in a meta-analysis<sup>29</sup>. Total  
468 heterogeneity, and heterogeneity due to phylogeny, source and species identity were computed  
469 following Nakagawa & Santos (2012)<sup>29</sup>.

470 We tested the robustness of our results against several potential limitations. Because multiple  
471 island populations were often compared with a single mainland population, we accounted for  
472 these repeated measures in a variance-covariance matrix where the diagonal includes the  
473 sampling variances, and the off-diagonals of the matrix represent the shared variance  
474 (covariance) among the response ratios due to the common mainland population<sup>625</sup>. Further, we

475 compared our main results to models fitted with  $\ln RR$  and sampling variances corrected for small  
476 sample size<sup>38</sup>. Another potential problem is that regressions using ratios may lead to spurious  
477 correlations<sup>31,32</sup>. Thus, we conducted an additional analysis testing the statistical significance of  
478 body size trends by regressing island mass against mainland mass, following previous  
479 studies<sup>4,5,20,41</sup>. Phylogenetic meta-regressions were run using island mass as the response  
480 variable, and mainland mass as the predictor (both transformed with natural-log), with random  
481 effects as specified above, and sampling variance  $sd_i^2/mass_i^2 * N_i$ . This approach has some  
482 limitations in being harder to visualize and less effective in considering the sampling variance of  
483 measurements (representing intrapopulation variability), yet nonetheless provides an alternative  
484 approach for assessing the robustness of our results, in line with previous studies<sup>4,5,20,41</sup>. Finally,  
485 we assessed publication bias by testing the influence of data source on the relationship between  
486 size ratio and mainland mass. This involved comparing whether patterns differed in island-  
487 mainland pairs extracted from studies testing the island rule (38.6% of cases) versus pairs  
488 extracted from studies not testing the island rule (61.4% of cases).

#### 489 **Testing ecological hypotheses explaining insular size shifts**

490 To evaluate the relative role of key mechanisms proposed to influence body size evolution in  
491 island fauna, we compiled a further range of variables (Supplementary Table 1, Extended Data  
492 Fig. 1). These included island area (linked to both resource limitation and to ecological release  
493 from both predation and competition) and spatial isolation (linked to reduced colonization from  
494 mainland populations for smaller taxa, i.e. immigration selection<sup>50</sup>). In addition, we included  
495 climatic and resource seasonality, which are linked to the starvation resistance hypothesis, and  
496 productivity and species diet, each of which are linked to resource limitation. Because body size  
497 evolution may be influenced by climate (e.g. Bergmann's rule)<sup>9,626</sup>, we also included mean  
498 temperature, which is linked to body size adaptations for enhancing heat conservation or  
499 dissipation (thermoregulation hypothesis). For amphibians, we included precipitation as a proxy  
500 for water supply linked to aquatic habitats, moisture and humidity (water availability  
501 hypothesis).

502 We modelled interactions between body size and each of the explanatory variables because we  
503 expected these factors to differentially affect species of different sizes, thus producing different  
504 effects in small, medium-sized and large species. In line with the ecological release and resource

505 limitation hypotheses, we expected the slope of the *lnRR*-mainland mass relationship to be  
506 steeper in smaller islands, isolated from the mainland and with fewer or no predators (Fig. 1).  
507 Further, if resource availability is a key factor, we also expected large species to undergo  
508 dwarfism on islands with low productivity<sup>48,49</sup>, and for dwarfism to be accentuated in dietary  
509 niches with high energy requirements, including carnivory<sup>9</sup>. In addition, high seasonality in  
510 resources and in temperature was expected to result in increased gigantism in small-sized  
511 species, because energy reserves increase faster than energy depletion as body size increases  
512 (starvation resistance hypothesis)<sup>9,627</sup>. We hypothesized that smaller species would benefit  
513 comparatively more by increasing in size than larger species. Because amphibians are generally  
514 small-sized, we also fitted a model for this group with only additive terms (mainland mass +  
515 sdNDVI) where seasonality in resources would result in larger body sizes for all species. Finally,  
516 mechanisms driven by thermoregulation and water availability predict that body size shifts are  
517 associated with temperature and rainfall, respectively. Mean temperature was expected to  
518 predominantly affect endotherms and small ectotherms with good thermoregulating abilities  
519 (reptiles and anurans) living on cold islands which, compared to similar-sized species on islands  
520 with a mild climate, would exhibit more pronounced gigantism to enhance heat conservation. We  
521 fitted the effect of temperature as an interactive (mainland mass × Tmean) or additive term  
522 (mainland mass + Tmean) to assess whether only small species or all species would increase in  
523 size in low temperature islands (see details in Supplementary Table 1, Extended Data Fig 1,  
524 Supplementary Table 7).

525 Prior to modeling, all the moderators (explanatory variables) were inspected and log<sub>10</sub>-  
526 transformed if necessary to meet normality assumptions in model errors. We considered a result  
527 to be significant when the 95% confidence interval (CI) did not cross zero. We assessed the  
528 explained heterogeneity using Omnibus test for moderators ( $Q_m$ ) and the percentage of variance  
529 explained by the moderators using  $R^2$  marginal<sup>628</sup>. All figures show the relationship between size  
530 response ratio and body mass, and how this might be altered by the mechanisms explained  
531 above.

532 All analyses were performed in R 3.5.3<sup>629</sup> using the packages *metafor* v2.0<sup>630</sup> and *metagear*  
533 v0.4<sup>631</sup> for the meta-regression models and data imputation, *metaDigitise* v1.0<sup>632</sup> for data  
534 extraction from plots, *ape* v5.2<sup>633</sup> for estimating branch lengths and resolving polytomies, *rotl*

535 v3.0.4<sup>634</sup> for building the phylogenies for our species by searching the Open Tree Taxonomy<sup>635</sup>  
536 and retrieving the phylogenetic relationships from the Open Tree of Life<sup>636</sup>, *sf* v0.7-3<sup>637</sup> and  
537 *raster* v2.7-15<sup>638</sup> for spatial analyses, *dplyr* v0.8.0.1<sup>639</sup> and *reshape2* v1.4.3<sup>640</sup> for data  
538 manipulation and *ggplot2* v 3.3.0.9000<sup>641</sup> and *ggpubr* v0.1.8<sup>642</sup> for data visualization. ArcMap  
539 10.5 was used for Figure 2. Silhouettes in figures were extracted from ‘phylopic’  
540 (<https://phylopic.org>). The PRISMA Checklist for systematic reviews is available in Appendix 3.

## 541 Data availability

542 All data are available at [https://github.com/anabenlop/Island\\_Rule](https://github.com/anabenlop/Island_Rule) and  
543 [https://figshare.com/projects/Body\\_size\\_evolution\\_in\\_insular\\_vertbrates/89102](https://figshare.com/projects/Body_size_evolution_in_insular_vertbrates/89102).

## 544 Code availability

545 The code to conduct the analyses is available at [https://github.com/anabenlop/Island\\_Rule](https://github.com/anabenlop/Island_Rule).

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2116

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## 2127 **Author Contributions**

2128 AB-L conceived and coordinated the research, led the analyses and wrote the first draft; AB-L,  
2129 LS, JG-Z, MAJH and JAT helped to develop the conceptual framework; LS compiled the  
2130 environmental rasters; JAT, PW and BM provided morphometric data. All authors contributed to  
2131 the data collection from the literature and to the writing of the final manuscript.

## 2132 **Competing interests**

2133 The authors declare no competing interests.

2134

## 2135 **Figures and Tables**

2136 **Figure 1.** Conceptual figure showing body size evolution in island populations. According to the  
2137 island rule, changes in body size of island populations are dependent on the body mass of  
2138 mainland relatives, with small species tending to increase in size on islands (gigantism) and large  
2139 species tending to decrease in size (dwarfism). By plotting the log response ratio ( $\ln RR$ ) between  
2140 insular mass and mainland mass, against mainland mass, we can test if insular populations  
2141 adhere to the rule (intercept  $> 0$  and slope  $< 0$ ) (blue line). Mechanisms proposed to drive ‘island  
2142 rule’ effects are mainly based on reduced predation, inter- and intra-specific competition, and  
2143 food availability, suggesting that the relationship will steepen in small, remote islands (red line).

2144 **Figure 2.** Location of island populations included in our analyses for mammals (N = 1058, blue),  
2145 birds (N = 695, orange), reptiles (N = 547, yellow), and amphibians (N = 179, green). The size of  
2146 each point indicates the number of species sampled on each island; some points overlap. See Fig.  
2147 S1 for a 4-panel figure with the location of insular populations separated for each taxonomic  
2148 group.

2149 **Figure 3.** Relationship between  $\ln RR$  (log response ratio between island mass and mainland  
2150 body mass) and body mass in the mainland for (a) mammals (N = 1058), (b) birds (N = 695), (c)  
2151 reptiles (N = 547) and (d) amphibians (N = 179). Models were fitted using phylogenetic  
2152 multi-level meta-regression models with mainland body mass as moderator, and observation-  
2153 level ID, source ID, species ID and phylogeny as random effects.  $\ln RR > 0$  indicates gigantism;  
2154  $\ln RR < 0$  indicates dwarfism; and  $\ln RR = 0$  indicates stasis (no shift in body size from mainland  
2155 to island populations). The size of points represents the inverse of the sampling variance for each  
2156 paired island-mainland response ratio in the model. Shaded areas represent 95% confidence  
2157 intervals. Note that y-axes have different scales.

2158 **Figure 4.** The effect of island area and spatial isolation on insular size shifts in terrestrial  
2159 vertebrates for (a) mammals (N = 1058), (b) birds (N = 695), (c) reptiles (N = 547) and (d)  
2160 amphibians (N = 179). Continuous variables are represented at the 10% and 90% quantile for  
2161 each extreme (close vs remote islands; small vs large islands).  $\ln RR > 0$  indicates gigantism;  
2162  $\ln RR < 0$  indicates dwarfism; and  $\ln RR = 0$  indicates stasis (no shift in body size from mainland  
2163 to island populations). Shaded areas represent 95% confidence intervals.

2164



2165 **Table 1.** Parameter estimates for the phylogenetic meta-regression models testing the generality  
2166 of the island rule in terrestrial vertebrates.  $k$ : number of island-mainland comparisons ( $\ln RR$ ),  
2167  $Q_m$ : test of moderators ( $\log_{10}$ (mainland mass)).  $R^2_m$ : marginal  $R^2$ , estimated percentage of  
2168 heterogeneity explained by the moderator (fixed effects).  $R^2_c$ : conditional  $R^2$ , percentage of  
2169 heterogeneity attributable to fixed and random effects.

2170

Class	$k$	Intercept (CI)	Slope (CI)	$Q_m$ (p-value)	$R^2_m$	$R^2_c$
Mammals	1058	0.208 (0.052 – 0.365)	-0.088 (-0.122 – -0.055)	27.30 ( $p < 0.001$ )	11.4	56.4
Birds	695	0.216 (0.117 – 0.315)	-0.104 (-0.145 – -0.064)	25.40 ( $p < 0.001$ )	7.0	43.4
Reptiles	547	0.410 (0.006 – 0.814)	-0.305 (-0.419 – -0.190)	27.21 ( $p < 0.001$ )	17.6	66.6
Amphibians	179	0.195 (0.012 – 0.377)	-0.107 (-0.320 – 0.107)	0.96 ( $p = 0.328$ )	1.4	67.1

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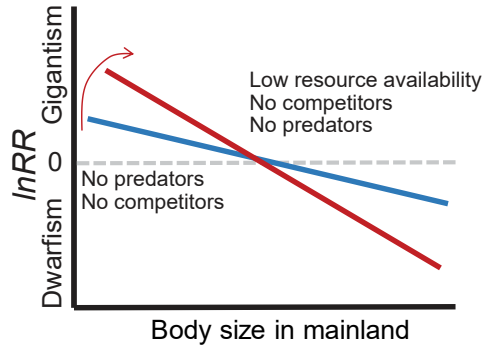
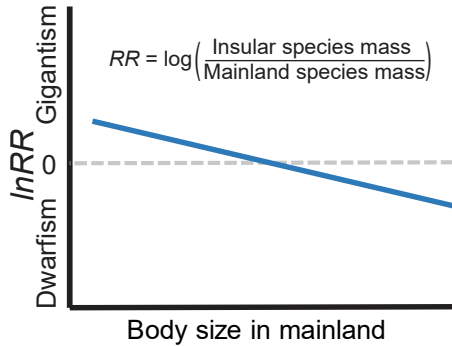
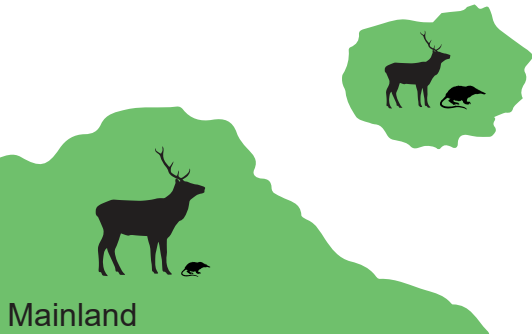
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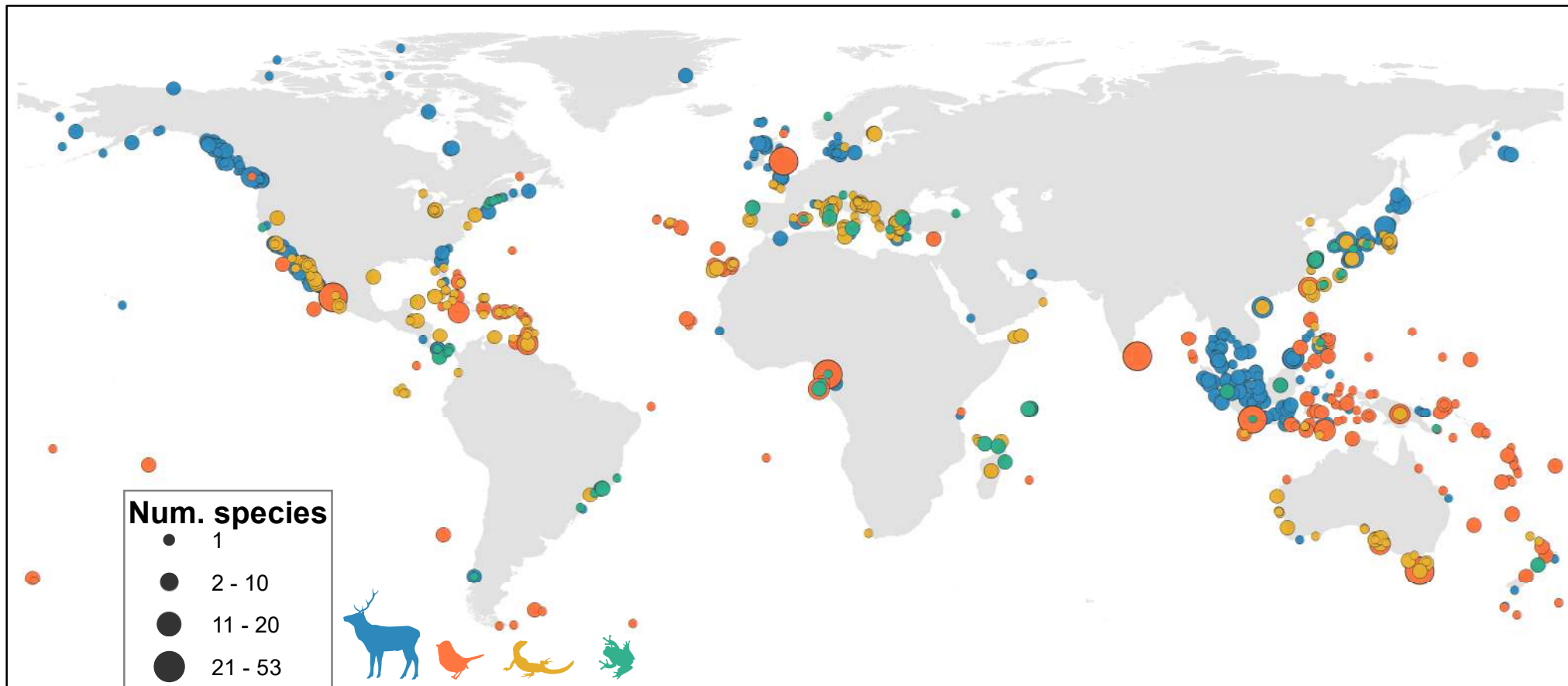
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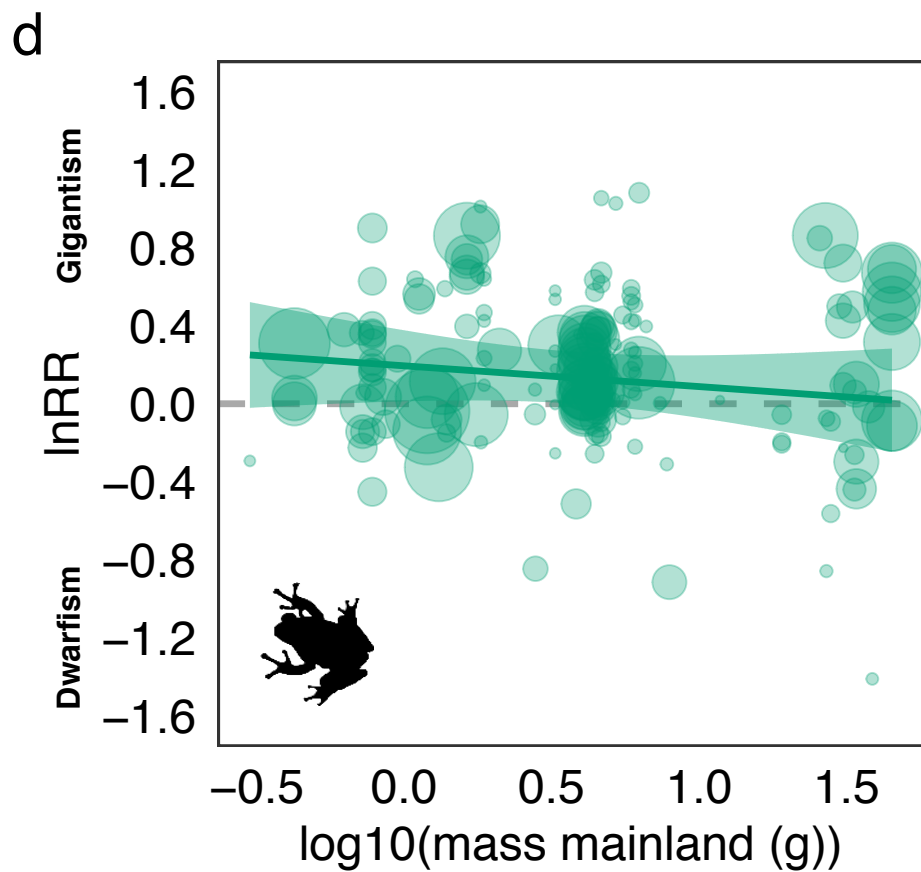
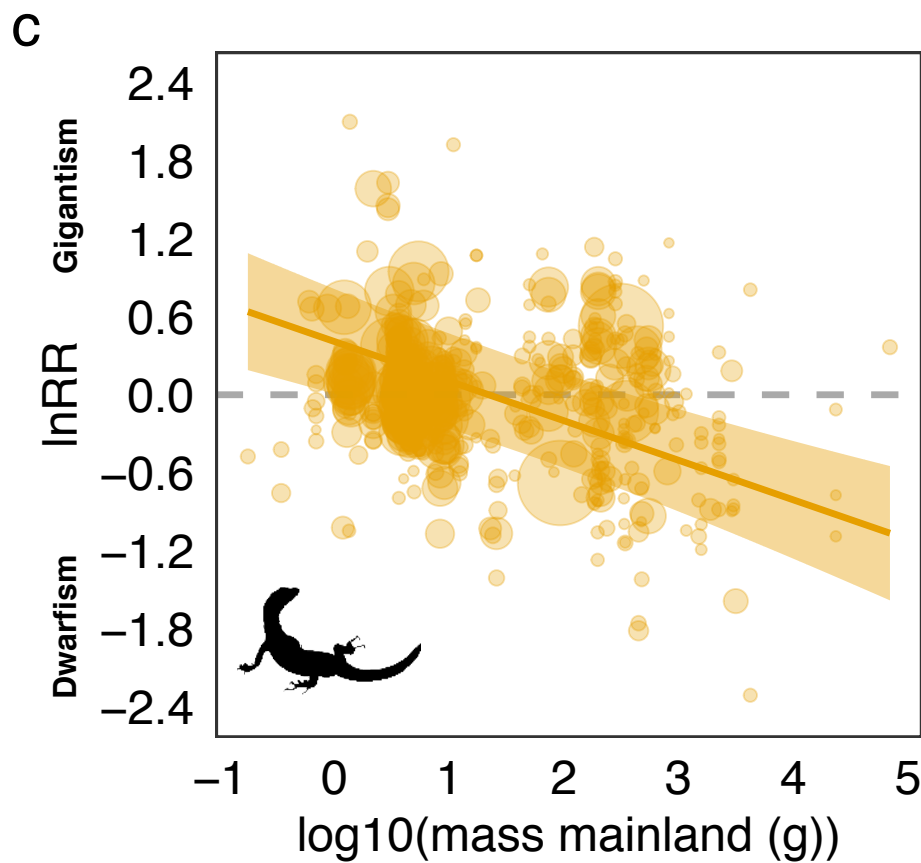
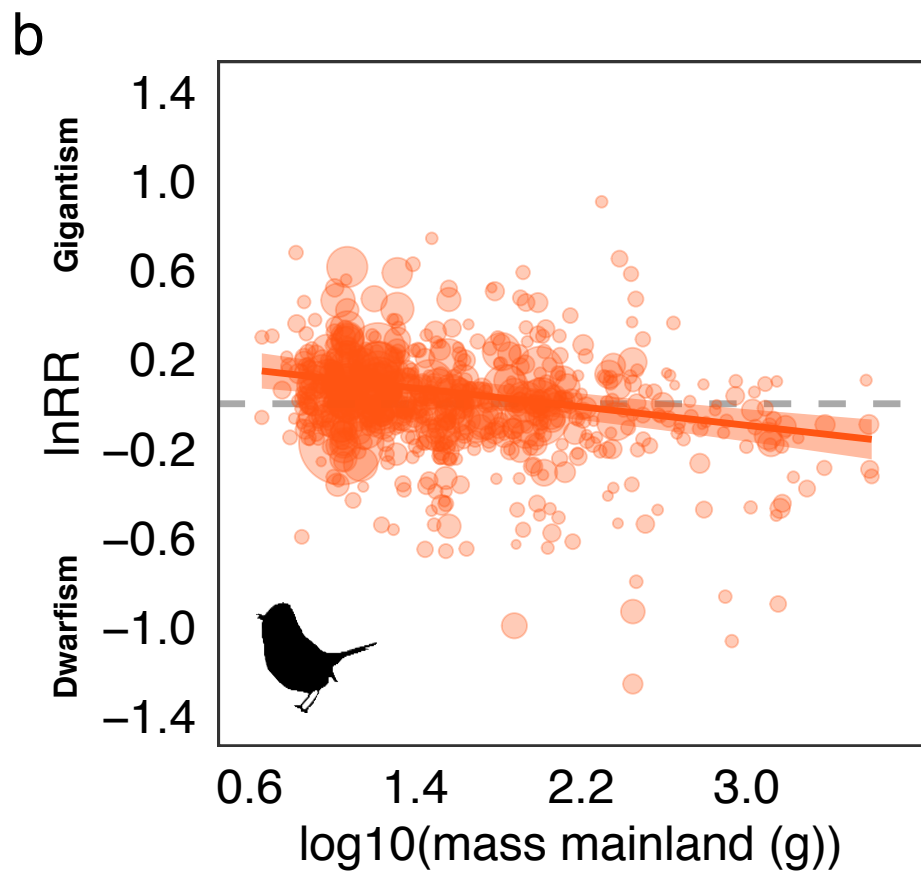
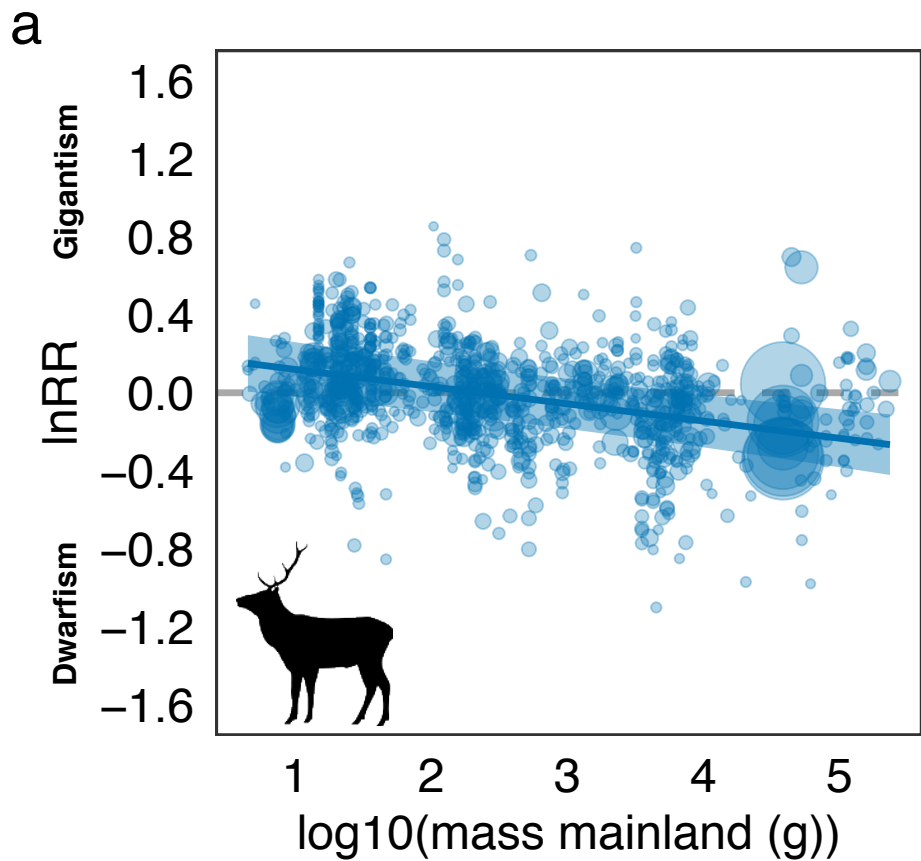
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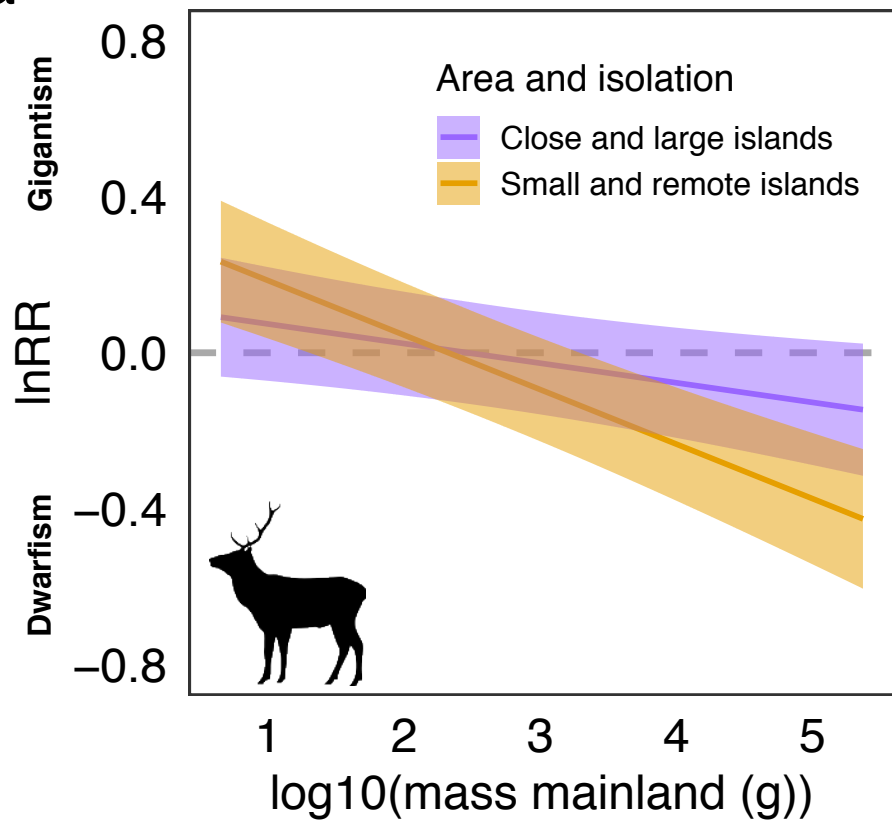
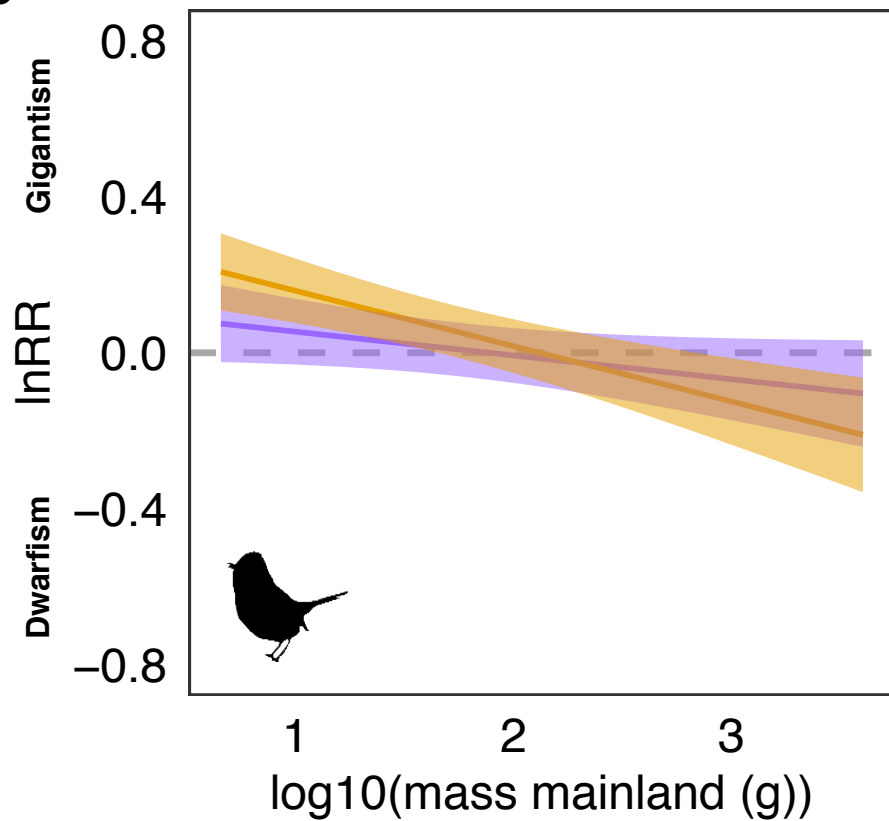
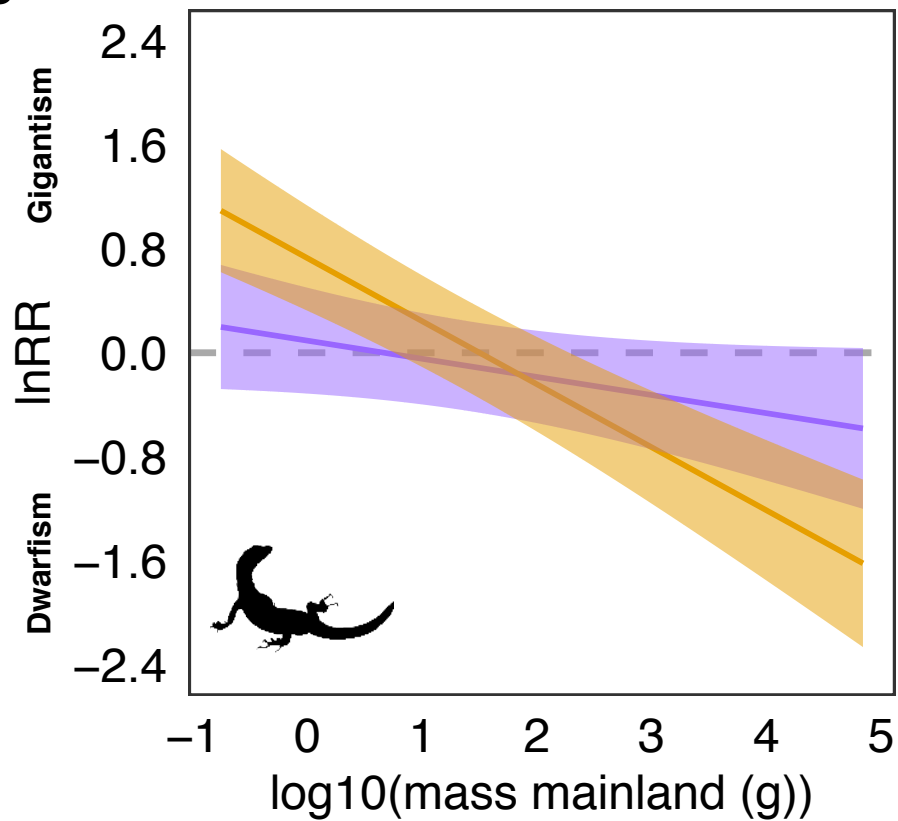
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