The island rule explains consistent patterns of body size evolution across terrestrial vertebrates

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Abstract

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

Introduction

From giant pigeons to dwarf elephants, islands have long been known to generate evolutionary oddities[1]. Understanding the processes by which island lineages evolve remains a prominent theme in evolutionary biology, not least because they include many of the world's most bizarre and highly threatened organisms[2]. The classic insular pattern of both small-animal gigantism and large-animal dwarfism in relation to mainland relatives has been described as a macro-evolutionary or biogeographical rule – the 'island rule'[3-5] (Fig. 1). However, previous research into island effects on vertebrate morphology has cast doubt on the generality of this pattern, suggesting that body size evolution is often much less predictable[6] and may only follow the 'island rule' in relatively few clades, such as carnivores, ungulates, and heteromyid and murid rodents[7,8]. Even in these cases, the underlying mechanisms driving patterns of insular gigantism and dwarfism remain unclear.

Multiple mechanisms have been proposed to explain the island rule, including reduced predation, relaxed competition and food resource limitation in island environments[9]. In theory, each of these factors may be accentuated in smaller, more isolated islands, where lower levels of competition and predation could lead to 'ecological release', allowing small-bodied species to increase in body size[5,9]. Similarly, among large-bodied species, reduced predation pressure and limited resource availability could select for smaller body sizes with reduced energy requirements, leading to insular dwarfism. Climatic conditions may also influence body size evolution on islands since primary productivity and associated resource availability are strongly influenced by climate[9,10]. The effects of these different mechanisms have rarely been tested by previous studies of body size evolution on islands (but see[9,11,12]), in part because they focused on relatively restricted geographic and taxonomic scales.

Most work on the island rule has been restricted to mammals (e.g.[4,7,11,13]), although the hypothesis has also been tested in amphibians[14], reptiles[15-17], birds[12,18], dinosaurs[19], fish[20], insects[21], molluscs[22], and plants[23]. The highly inconsistent results of these studies (e.g.[5,6,24]) are perhaps unsurprising because they typically deal with single species or pool together data on different traits from numerous sources without controlling for variation in study design or accounting for measurement error. Accordingly, a recent systematic review based on a simplified scoring system[24] concluded that previous studies were undermined by author-related biases and

67 that empirical support for the island rule is generally low, particularly for non-mammalian taxa.
68 However, scoring approaches provide only limited information about the general support for a
69 hypothesis as they do not account for heterogeneity between studies, taxonomic
70 representativeness, sample size, or precision in the estimates. In contrast, formal meta-analyses
71 are able to systematically test ecological hypotheses, while accounting for the multiple sources of
72 heterogeneity mentioned above[25,26].

73 We therefore tested the island rule hypothesis by applying meta-regressions to a global dataset of
74 2,478 island-mainland comparisons for 1,165 insular and 890 mainland species of terrestrial
75 vertebrates, controlling for phylogeny throughout. In total, these phylogenetic meta-analyses
76 included morphometric measurements of 63,048 insular and 155,942 mainland specimens
77 representing mammals (1,046 island-mainland comparisons), birds (706 comparisons), reptiles
78 (548 comparisons) and amphibians (178 comparisons) from across the globe (Fig. 2). Insular
79 populations were sampled from an array of islands varying widely in size (0.04–785,778 km^2),
80 climate and level of spatial isolation (0.03–3,835 km from mainland). To explore the drivers of
81 body-size shifts in insular populations, we also sampled species with a wide range of average
82 body masses (0.17–234,335 g). To avoid the widespread author- or publication-biases detected in
83 previous analyses[24] we sampled body size measurements not only from published studies that
84 formally or partially assessed the island rule, but also those that gathered similar data to address
85 unrelated questions. Similarly, for birds, our sample includes additional morphometric data
86 extracted from an independent global dataset of avian functional traits[27].

87 Our analytical framework has the key advantage of allowing us to control for multiple types of
88 variation, including data source, sample size imbalance, intraspecific and intra-population
89 variability, and phylogenetic relatedness. For each island-mainland comparison, we calculated
90 the log response ratio (*lnRR*) as the natural logarithm of the ratio between the mean body size of
91 individuals from an insular population M_i and that of mainland relatives M_m, i.e $lnRR =$
92 $\log(M_i/Mm)$[28]. The *lnRR* is therefore an estimate of the effect of island colonization on body size,
93 with negative values ($lnRR < 0$) indicating dwarfism and positive values ($lnRR > 0$) indicating
94 gigantism (Fig. 1). To assess the direction and strength of these relationships, we regressed *lnRR*
95 against the body mass of the mainland population (M_m). Using this framework, a positive

intercept and negative slope intersecting *lnRR* = 0 would provide broad-scale support for the island rule[4,6,11] (Fig. 1, Extended Data Fig. 1).

The main reason to regress ratios against mainland mass is that doing so allows intuitive visualization of the results[5,29] as well as direct comparison with previous studies of the island rule, most of which use the same approach[4-7,11,29,30]. However, since regressing ratios may introduce biases[31,32], we also regressed raw estimates of insular and mainland body size in separate series of phylogenetic meta-regressions, wherein the island rule is supported by intercepts > 0 and slopes < 1. This approach has some limitations in being harder to visualize and less effective in considering intrapopulation variability and measurement error, yet nonetheless provides an alternative approach for assessing the robustness of our results, in line with previous studies[4,5,16,33].

To evaluate the relative role of key mechanisms proposed to influence body size evolution in island fauna (see Supplementary Table 1), we compiled a further range of variables. These included island area (linked to both resource limitation and to ecological release from both predation and competition), spatial isolation (linked to reduced colonisation from mainland populations and immigration selection[34]), seasonality, productivity and species diet (again linked to resource limitation). Because body size evolution is influenced by climate (e.g. Bergmann's rule)[9,35], we also included mean temperature and temperature seasonality (thermoregulation) and, for amphibians, precipitation (water availability). The ecological release and resource limitation hypotheses both predict that insular body-size shifts will be exacerbated in smaller, more isolated islands. If resource availability is a key factor, we also expect large species to undergo dwarfism on islands with high seasonality and low productivity, and for dwarfism to be accentuated in dietary niches with high energy requirements, including carnivory[9]. Finally, mechanisms driven by thermoregulation and water availability predict that body size shifts are associated with temperature and rainfall, respectively (Supplementary Table 1).

Results

The generality of the island rule

We found that *lnRR* (size ratio) and mainland body mass were negatively related for mammals, birds and reptiles, with small species tending to gigantism and large species to dwarfism (Fig. 3).

125 The relationship was weakly negative but statistically non-significant for amphibians, with a
126 tendency towards gigantism across all body sizes (Fig. 3, Table S3). Regressing island mass
127 against mainland mass produced similar results, with support for the island rule across all groups
128 except for amphibians, indicating that our analyses are robust to any potential spurious
129 correlation associated to ratio regression models[31,32] (Extended Data Fig. 2, Table S4). Further,
130 our results were consistent regardless of whether island-mainland comparisons were sampled
131 from studies formally testing the island rule or compiled from unrelated data sets (Table S5).

132 Mainland body mass explained 11.1, 6.7 and 18.5% of the variance in mammals, birds and
133 reptiles, respectively. The amount of further variance explained by phylogeny (0.0–27.6%), data
134 source (1.4–23.5%), and species (27.5–58.2%) fluctuated widely among taxa (Extended Data
135 Fig. 3). Insular body size shifts were largely unrelated to phylogeny in amphibians, slightly
136 related in birds and mammals, and with a stronger phylogenetic signal in reptiles (Extended Data
137 Fig. 3). Thus, the strength of body size changes detected in birds, mammals and amphibians is
138 not driven by large effects in particular clades. Variation between data sources was substantial
139 for mammals and reptiles, but low for amphibians, and birds. Finally, the residual variance was
140 the highest for birds, followed by mammals, amphibians and reptiles (Extended Data Fig. 3),
141 indicating that other factors besides mainland body size may explain insular size shifts.

142 **Ecological mechanisms underlying body size evolution on islands**

143 The pattern of body size evolution in our island-mainland comparisons supported a range of
144 hypotheses. When accounting for body size of the mainland relative, insular shifts in body size
145 of endotherms (mammals and birds) were explained by island area, spatial isolation, and
146 temperature (Fig. 4, Extended Data Fig. 4, 5, Table S6, Supplementary Dataset 4), providing
147 support for hypotheses linked to ecological release from predation and competition, resource
148 limitation, and biased colonization (immigrant selection), as well as suggesting a role for
149 thermoregulation. In turn, for ectotherms (reptiles and amphibians), the main factors were island
150 area and spatial isolation, productivity and seasonality (Fig. 4, Extended Data Fig. 6, 7, Table S6,
151 Supplementary Dataset 4). Again, these results provide support for ecological release, resource
152 limitation, immigrant selection, and starvation resistance hypotheses. We found no effects of diet
153 for any of the four taxa, or precipitation (water availability hypothesis) for amphibians (Extended
154 Data Fig. 4-7). The fact that no single factor explained island effects on body size is not

155 surprising because some hypotheses shared overlapping predictions, making them difficult to
156 disentangle.

157 We found variations in the processes that drove body size evolution in island faunas for the
158 different taxonomic groups. Shifts in body mass of mammals were mostly explained by island
159 size and spatial isolation (Fig. 4), and modulated by climate (mean temperature) (Extended Data
160 Fig. 4), resulting in more pronounced gigantism or dwarfism in small and remote islands (Q_m =
161 11.91, P = 0.003; Fig. 4a, Table S6). In addition, temperature affected mammals similarly across
162 the body mass range, with bodies consistently larger in cool islands and smaller in warm islands.
163 Hence, even those large species that had undergone dwarfism were larger in low temperature
164 than in high temperature insular environments (Q_m = 7.77, P = 0.005, Extended Data Fig. 4e,
165 Table S6).

166 Similarly, in birds, we found that body size was smaller in warmer insular environments and
167 larger in low temperature islands (Q_m = 14.57, P = 0.001, Extended Data Fig. 5e, Table S6).
168 Contrary to the resource limitation hypothesis, small-sized birds did not become larger in highly
169 seasonal islands, but large-sized birds had reduced dwarfism on islands with high seasonality in
170 temperatures (Q_m = 10.03, P = 0.002, Extended Data Fig. 5f, Table S6).

171 In reptiles, the combination of island area and spatial isolation were the most important factors
172 explaining variation in body size (Q_m = 12.63, P = 0.002, Fig. 4c, Table S6), with productivity
173 and seasonality being also supported but with weaker effects (Extended Data Fig. 6g, h, Table
174 S6). Similar to mammals, the tendency towards dwarfism or gigantism in large-bodied or small-
175 bodied reptiles was more apparent in isolated small-sized islands (Fig 4c), with stronger effects
176 of area than isolation (Extended Data Fig. 6a, b, Table S6). The effects of productivity and
177 seasonality were only partially in line with predictions, as small-sized species were larger on
178 islands with high seasonality, but smaller on islands with high productivity (Fig 5b, Extended
179 Data Fig. 6e, f). In turn, large-bodied reptiles were smaller on islands with low productivity and
180 high seasonality.

181 Finally, the relationship between size ratio and mainland mass in amphibians was slightly steeper
182 in small and remote islands (Fig. 4d), with island area being marginally more important than
183 spatial isolation (Table S6, Extended Data Fig. 7a,b). The effect of seasonality was clearer, with
184 amphibian species inhabiting islands with high seasonality (unpredictable environments) tending

toward gigantism, whereas those from islands with low seasonality (predictable environments) being similar in size to mainland counterparts (Q_m = 10.18, P = 0.001, Extended Data Fig. 7h, Table S6).

Discussion

Based on comprehensive morphometric data from a worldwide sample of island fauna, we show consistent patterns of body size evolution across terrestrial vertebrates in accordance with predictions of the island rule. This finding was robust to alternative modelling approaches, measurement error and publication bias. Moreover, we have demonstrated that insular size shifts are contextual and depend not only on the body size of mainland relatives (island rule *sensu stricto*) but also on species ecology, and the physiographic and climatic characteristics of particular island environments[9].

Repeated evolutionary trajectories on islands

Overall, we found a clear negative relationship between insular body size variation and the body mass of mainland individuals for three of the four groups (mammals, birds, and reptiles). Nevertheless, although insular populations exhibit a strong signal of island rule effects, there remains substantial, unexplained variation about the trend line. Mainland body mass explains between 6.7 and 18.3% of the variation in insular size in these three taxonomic groups, which is similar to that reported in other studies (<30% in studies that did not correct for phylogenetic relatedness, intrapopulation or intraspecific variability[5,11,12,29,36]). We also conducted the first multispecies test of island rule effects in amphibians, showing that the relationship goes in the expected direction but with a weak effect (2 %), possibly because the body mass range in amphibians is narrower and thus most amphibians tend to gigantism on islands with reduced risk of predation.

Our findings contrast with the recent review rejecting the island rule in mammals, birds and reptiles[24] and other taxon-specific studies focused on lizards[16,33] and turtles[17], yet corroborate the patterns reported in snakes[15], mammals[4,9] and birds[5,12]. Further, we have demonstrated that the island rule is not a clade-specific pattern in mammals[6], birds and amphibians. We conclude that the contradictory results of previous studies may have related to sampling bias, heterogeneity and phylogenetic relatedness (i.e. statistical non-independence), and that by accounting for these

214 effects in our global models we are able to demonstrate that vertebrate animals evolve in largely
215 consistent ways on islands.

216 A corollary that emerges from the island rule is that body size converges on islands. Specifically,
217 if insular environments select for intermediate body sizes, closer to the optimal size of the focal
218 clade, then the size spectrum of organisms found on islands should be narrower compared to the
219 mainland[37,38]. Theoretically, the optimal body size towards which small and large species may
220 converge in low-diversity systems such as islands should correspond to the point where the trend
221 intersects the horizontal dashed line ($lnRR = 0$) in the relationship between size ratio and
222 mainland mass, at which point fitness is maximized[37] (but see[39]). Interestingly, the shift between
223 dwarfism and gigantism in our models occurred at approximately 100-250 g in endotherms,
224 slightly larger than the 100 g adult body mass proposed by Brown et al[37] for mammals (but see
225 Damuth et al[38]), and to the mode of the global body size distribution of birds used to separate
226 between small- and large-bodied birds (60 g)[18,40,41]. In addition, our analyses suggest that the
227 optimal body size for island reptiles should be ca. 20-30 g, which is marginally higher than the
228 modal body size of Lepidosaurs (14.1 g)[42]. Whether there is an optimal body size in island biotas
229 has been the subject of much debate[39], but overall we expect that phenotypic variability in
230 morphometric traits will be substantially narrowed if directional selection is operating in island
231 assemblages, a feature that warrants further investigation. Additionally, optimal phenotypes
232 should vary with the environmental characteristics of islands, in particular their area and
233 isolation, climate, productivity and seasonality. For example, in mammals, our results suggest
234 that the optimum would be ca. 100 g in warm islands and ca. 900 g in cold insular environments
235 (Extended Data Fig. 4f).

236 **Ecological mechanisms influencing body size variation**

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

244 the slope of the relationship between size ratio and mainland mass was slightly steeper for birds
245 and amphibians in small remote islands than in large islands near continental land masses (Fig.
246 4). This points to a combination of resource limitation (with small islands having fewer resources
247 to maintain large-sized organisms[43,44]) along with release from interspecific competition and
248 predation pressure in small, species-poor islands. The pattern is also consistent with biased
249 colonization favouring larger individuals with higher dispersal abilities (immigration selection[34]).
250 Conversely, our results showed that body size divergence on islands close to the mainland was
251 minimal, reflecting two non-mutually exclusive processes. First, many of these islands were
252 connected to the continent by land bridges so recently that phenotypic differences have not had
253 time to accumulate. Second, regular dispersal between mainland and island populations promotes
254 gene flow, with introgression counteracting divergent selection[45,46].

255 Besides island physiographic characteristics (area and isolation), other relevant factors were
256 temperature conditions in endotherms and resource availability and seasonality in ectothermic
257 organisms. Mammals and birds both responded to island temperature in line with the heat
258 conservation hypothesis, with small- and large-sized species exhibiting exacerbated gigantism
259 and diminished dwarfism, presumably to conserve heat in colder, harsher insular environments.
260 Additionally, temperature seasonality was an important determinant of the size of large-bodied
261 birds, with populations on highly seasonal islands being similar in size to mainland populations.
262 One possibility is that larger size in these cases may help to maintain energy reserves during
263 periods with low food availability, allowing them to thrive in otherwise hostile environments.
264 Another possibility is that bird populations on highly seasonal islands – which tend to be situated
265 at relatively high latitudes – are more often seasonally mobile or even migratory, potentially
266 increasing gene flow with mainland populations or weakening adaptation to the local
267 environment[47]. These findings add new insights to previous results regarding the role of thermal
268 and feeding ecology on morphological divergence in island birds[48,49]. Traditionally, changes in
269 feeding ecology were thought to be the prime force in driving morphological divergence in
270 island birds[48,49]. Yet, our results imply that physiological mechanisms related to heat
271 conservation ('thermoregulation hypothesis') and energy constraints ('starvation resistance
272 hypothesis') may also shape body size evolution in island birds.

273 Our results suggest that resource availability and seasonality are important factors explaining
274 body size evolution in reptiles, with some deviations from the patterns predicted. As
275 hypothesized, large species were much smaller on islands with low resource availability, and
276 small species were larger on islands with high seasonality (Extended Data Fig. 6g, h). Yet,
277 unexpectedly, small species became larger on islands with low productivity, perhaps because
278 increased intraspecific competition favors large individuals under the high population densities
279 that reptiles often attain on islands[50,51].

280 Overall, most amphibians tended to gigantism, presumably as a result of increased growth rate
281 or lower mortality due to reduced predation pressure on islands[52]. Additionally, we found that
282 body size of amphibians consistently increased on islands where resources were highly seasonal
283 and unpredictable, perhaps to maximize energy reserves and withstand long periods without
284 food, for example during aestivation or hibernation[53] (i.e., "starvation resistance hypothesis"). In
285 turn, we did not find a clear relationship between precipitation and body size (i.e. "water
286 availability hypothesis"). It appears that gigantism in island amphibians is mostly driven by
287 physiological mechanisms that maximize growth rate, particularly in smaller, more isolated
288 islands (Fig. 4d). These findings should be further explored when more data on island-mainland
289 pairwise populations of amphibians become available.

290 **Body size evolution in extinct species**

291 Our analyses focused solely on extant species for which we could gather data on measurement
292 error and sample size (essential for meta-analyses). The widespread extinction of large species
293 on islands, including dwarf morphotypes of large species such as insular elephants in Sicily and
294 the Aegean islands[54,55], may have masked the historical pattern of phenotypic variation on
295 islands[56]. Giant insular birds[48,57], primates[58,59], and lizards[60], along with large insular turtle
296 species, went extinct during the Holocene and late Pleistocene[61], most likely because of
297 overhunting by humans and the introduction of invasive species[62,63]. Overall, it is estimated that
298 human colonization of oceanic islands was followed by the extinction of 27% of insular endemic
299 mammals[64], as well as over 2000 bird species in the Pacific region alone[66], with these losses
300 biased towards large-bodied, flightless, ground-nesting species[62]. Extinct species may shed light
301 on the patterns and processes of size evolution in insular vertebrates because species extinctions
302 have substantially altered the biogeography of body size in island faunas. Indeed, present-day

303 body size may reflect the selective pressure on larger individuals, leading to downsized insular
304 communities[65,66]. For example, the predominance in our dataset of smaller-bodied organisms
305 could reflect the extinction of large species on islands[62], or the fact that few islands support large
306 species in any case. Either way, analyses based on present-day patterns may bias our perception
307 of the rule and scaling coefficients, hence including extinct species may strengthen the signal
308 that we report for extant species[29].

309 We foresee that, under global change, the extinction of insular species and the introduction of
310 novel (invasive) species may trigger new equilibria, with concomitant shifts in the composition
311 of insular communities and the opening of novel niches to which species may respond via
312 genetic adaptations and phenotypic plasticity. Recent evidence indicates that even introduced
313 species on islands, which were not included in our analysis, predictably evolve towards dwarfism
314 or gigantism[67-69]. In theory, as the Anthropocene gathers pace, further extinctions will drive a
315 decline in the mean body size of the overall island community, pushing optimal body sizes
316 towards the lower end of body size ranges in the different vertebrate groups.

317 **Conclusions**

318 Of the many evolutionary implications of living on islands – together referred to as the 'island
319 syndrome'[2] – the effects on body size are the most widely known and controversial. We have
320 shown that these 'island rule' effects are widespread in vertebrate animals, although the evidence
321 for amphibians is inconclusive. Morphological changes were directional for species at the
322 extremes of the body size range in mammals, birds and reptiles, following the predicted pattern
323 of convergence towards intermediate "optimum" body sizes, in line with optimal body size
324 theory[37,38,40]. Although this convergence towards morphological optima may result from natural
325 selection or phenotypic plasticity, the exact mechanism producing these changes on islands is
326 still not well understood. Nonetheless, we found that consistent transitions towards intermediate
327 body sizes were associated with a combination of factors, indicating a range of different
328 ecological mechanisms. Our results highlight the contextual nature of insular size shifts, where
329 island physiographic, climatic and ecological characteristics play a fundamental role in shaping
330 body size evolution, reinforcing the idea that large-scale macroevolutionary patterns do not arise
331 from single mechanisms but are often the result of multiple processes acting together[70,71].

Methods

Data collection

As a starting point, we collected morphometric data from articles included in a recent assessment of the island rule[24], as well as other compilations assembled to test the hypothesis in reptiles[16], mammals[6], and birds[12]. We reviewed every island-mainland comparison reported in previous studies and traced primary source data when possible to extract original measurements. In many cases, we excluded problematic data, including comparisons that were not supported by taxonomic or phylogenetic evidence, or which were based on reported morphometric data for single specimens, or did not report sample size, or reported extinct taxa for which data quality is lower than for extant taxa (Supplementary Dataset 3). To expand our sample, we then performed a literature search (February 2020) in Web Of Science (WOS) using the following search string: ("island rule" OR "island effect" OR "island syndrome" OR island*) AND (gigantism OR dwarfism OR "body size" OR weight OR SVL OR snout-vent length OR length OR size) AND (mammal* OR bird* OR avian OR amphibia* OR reptile*). We downloaded the first 500 hits from this search, removing duplicates already included in our data set. We extracted data from all studies containing relevant morphometric measurements for insular populations or, where possible, both insular and adjacent mainland populations.

It has been argued that research on the island rule might be prone to ascertainment bias, where researchers are more likely to notice and measure animals of extreme body size when conducting research on islands[33]. To help overcome this problem, we collected body size data not only from studies testing the island rule, or reporting dwarfism and gigantism in island fauna, but also from studies that did not specifically test hypotheses related to the island rule. We matched unpaired insular populations with independent data from mainland populations by performing species-specific searches in WOS and Google Scholar. We also compiled morphometric data for 442 insular and 407 mainland bird species measured from live individuals and museum specimens for analyses unrelated to the island rule[27].

Large islands may be more 'mainland like' in relation to factors that are thought to affect body size (i.e. competition, resource availability and predation[5]). Thus, when major islands were at least 10 times larger than a nearby island, we treated the large island as the mainland comparison, following previous studies testing the island rule[4,5,16]. Consequently, a single mid-

362 sized island can simultaneously be treated as the continent in comparisons with smaller islands,
363 and the island in comparisons with larger continents. When authors reported data referring to an
364 entire archipelago instead of a specific island (3% of cases), we used the size of the largest island
365 as island area.

366 Our final dataset contained 2,478 island-mainland comparisons, 2,023 (81.6%) of which were
367 within-species (e.g. subspecies) and 455 (18.4%) of which were between-species comparisons.
368 We collated data on body size indices (body mass, body length, cranial and dental
369 measurements) of different taxa in island and mainland populations following strict
370 morphological, phylogenetic and biogeographic criteria. Specifically, we always compared the
371 same body size index for island and mainland populations. For within-species comparisons, we
372 compared island and mainland populations based on the information given by the authors of the
373 relevant study (e.g. taking note of which mainland source populations are likely to inhabit a
374 particular island because of colonization history or isolation via rising sea levels[72-76]). When we
375 matched comparisons independently, we used information published in the study reporting the
376 insular form, selecting the geographically closest mainland population whenever possible. In
377 addition, we prioritized latitudinal alignment of mainland and island populations to avoid
378 confounding effects of latitudinal variation in body size. In the case of island endemics, we
379 compared island populations to their closest mainland relative whenever these were identifiable
380 by phylogenetic data or other information reported in each particular study. This usually meant
381 selecting their sister species or the geographically closest representative of a sister clade or
382 polytomy (Supplementary Dataset 2). If we could not reliably establish the closest mainland
383 relative, we discarded the data (see Supplementary Dataset 3).

384 When more than one body size index was reported in published studies, we chose only one index
385 by giving priority to different indices for different taxonomic groups, prioritizing those which
386 had a tighter relationship with body mass (Table S2). For mammals, we selected indices in this
387 order of preference: body mass, body length, cranial length (skull length or condylobasal length),
388 and dentition (e.g. canine length)[5]. For birds, preferred indices were body mass, wing length,
389 tarsus length and bill length. Finally, for amphibians and reptiles, size was reported as body
390 mass, snout-vent-length (SVL), carapace length (CL, for turtles) and total length (TL, including
391 SVL and tail length). To avoid size biases attributable to sexual size dimorphism, we calculated

392 the pooled mean and the combined SD using standard formulae for combining groups[77].
393 Alternatively, we compared size of mainland and island populations for males or females only if
394 information for the other sex was not available. We included measurements for adults only. Data
395 from zoos or studies that could not be georeferenced were discarded. As different authors
396 reported size using different indices, to allow cross-taxa and cross-study comparisons we
397 converted island and mainland size to body mass equivalents using published allometric
398 relationships (see Supplementary Table 2). If allometric relationships were not available, we
399 derived them based on published datasets or data extracted from the literature[42,78-84]. Calculated
400 allometric relationships were derived using OLS (Ordinary Least Square) or PGLS (Phylogenetic
401 Generalized Least Square) models of the $\log^{10}$ transformed body mass against the $\log^{10}$
402 transformed body size index (e.g. condylobasal length, data available at
403 https://github.com/anabenlop/Island_Rule).

404 For birds, we complemented measurements from literature with standardized wing-length
405 measurements from 3,641 museum specimens and live individuals of 442 insular and 407
406 mainland bird species (see[27]). We used wing length instead of tarsus length, which is often used
407 as single proxy of overall body size[85], because the former is a better predictor of body mass
408 (R^2_{wing} = 0.89 vs R^2_{tarsus} = 0.69, Table S2) (see also[86]). Using tarsus instead of wing length did not
409 change our results (Fig. S2). To select suitable comparisons for museum specimens, we first
410 classified species as either insular or continental by overlapping IUCN range polygons with a
411 GIS land layer including continental land masses. For each insular species we then identified
412 continental sister species from avian phylogenies[87], using the method described above. We
413 excluded pelagic, highly aerial birds (e.g. swifts) and fully migratory species because in these
414 groups it is unclear whether insular and mainland forms experience different environments[12].
415 Further, we also excluded flightless bird species, because morphological changes may be due to
416 flightlessness rather than island dwelling per se[12].

417 We calculated the response ratio (*lnRR,* eq. 1) as effect size in our meta-regressions, where we
418 divided the mean body mass of individuals from an insular population $\overline{M}_i$ by that of the nearest
419 mainland relative, $\overline{M}_m$, and then applied the natural logarithm. Unlike unlogged ratios, the
420 sampling distribution of *lnRR* is normal, particularly for small samples[28], and thus less prone to
421 statistical artefacts associated with ratio-based regressions.

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

Response ratios greater than zero indicate a shift towards larger sizes (gigantism) whereas ratios less than zero indicate shifts towards smaller sizes (dwarfism). Besides mean measurements, we recorded measures of variation, i.e. standard deviation (SD), standard error (SE) or coefficient of variation (CV), and sample sizes of the body size indices in island and mainland organisms. SD and sample sizes were used to weight each response ratio by the inverse of the sampling variance (Eq. 2).

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

SDs were extracted from raw data when possible. If ranges were provided instead of SD (or SE or CV), we calculated SD following[88]. If neither ranges nor measures of variation were reported, we imputed SD based on the coefficient of variation from all complete cases ("Bracken approach"[89]). Imputation was done for < 30% of all cases per group[90], 22% of all cases in mammals, 1.1% in birds, 11% in reptiles and 7.3% in amphibians.

For each study and island-mainland comparison, we compiled the mainland and island names, the study reference, the body size index used , the geographic coordinates, the distance to the closest mainland (spatial isolation, km) and the island area (km^2). We completed missing data on island characteristics using the UNEP island database (http://islands.unep.ch/) and the Threatened Island Biodiversity Database (TIB, http://tib.islandconservation.org/). Missing information was calculated using calculated using Google Earth. Additionally, we extracted the Normalized Difference Vegetation Index (NDVI) as a proxy for resource availability on islands[91]. We also calculated the standard deviation of NDVI to assess seasonality in leaf or vegetation cover, as an index of seasonality in available resources. NDVI was downloaded from NASA Ames Ecological Forecasting Lab (https://lpdaacsvc.cr.usgs.gov/appeears/task/area).

Because climate influences both resource requirements and primary productivity, body size evolution should also be influenced by climatic conditions on islands. We thus extracted island climatic conditions from WorldClim v. 2.0 (http://worldclim.org[92]). Specifically, we used variables that are more closely associated with the proposed underlying mechanisms of

451 Bergmann's rule (i.e. thermoregulation and starvation resistance): mean annual temperature,
452 annual precipitation, and seasonality of temperature and precipitation[93]. We assumed that the
453 time period for these bioclimatic variables (1970–2000), although not necessarily matching the
454 actual time period of body size evolution in the insular populations, roughly represents the
455 climatic conditions in the Holocene, a period relatively climatically stable where most of our
456 populations became isolated (i.e., after the last glacial maximum; see also[9]). Because climatic
457 variability across cells substantially exceeds variation within cells in the Holocene, current layers
458 are considered adequate for geographic comparisons. All spatial variables were downloaded at
459 0.1-degree resolution, and we averaged all cells per island to obtain a mean value of each
460 environmental variable (e.g., temperature, NDVI, precipitation, etc). Finally, for each species
461 included in our dataset, we collated diet information from EltonTraits for birds and mammals,
462 and from other sources for reptiles[83,94], and classified species as carnivores (> 50% diet
463 consisting of vertebrates) or non-carnivores (< 50% diet consisting of vertebrates), following
464 previous studies[27,95]. As all amphibians in our dataset are carnivores[96], we did not record their
465 diet.

466 **Data analyses**

467 To test the island rule hypothesis, we used phylogenetic meta-regressions between *lnRR* and
468 body mass of mainland relatives, following most previous studies of the island rule (e.g. [4,5,7
469 6,30,97]). A negative slope for this relationship would support the island rule (Fig. 1).

470 Use of multiple populations of the same species can overestimate the actual number of degrees
471 of freedom, generating type-1 errors. We controlled for this by adding 'Species' as a random
472 effect intercept in our analyses. Additionally, body size evolution in insular vertebrates is heavily
473 influenced by phylogenetic effects, with species within entire clades seemingly showing either
474 dwarfism or gigantism[6]. Thus, we accounted for phylogeny by including the phylogenetic
475 relatedness correlation matrix as a random effect. The species term captures the similarities of
476 effect sizes within the same species, while the phylogenetic term represents the similarity due to
477 relatedness[98]. We also added 'Source' as a random effect intercept to account for between-source
478 variability and the fact that we had multiple response ratios per study. In some cases, 'Source'
479 represented the combination of two sources of data, one for the island size and one for the
480 mainland size. Finally, we included an observation level random effect, which represents the

residual variance that needs to be explicitly modelled in a meta-analysis[26]. Total heterogeneity, and heterogeneity due to phylogeny, study and species identity were computed following Nakagawa & Santos (2012)[26]. Because multiple island populations were often compared with a single mainland population, we accounted for these repeated measures in a variance-covariance matrix[99]. Another potential problem is that regressions using ratios may potentially lead to spurious correlations[31,32]. Thus, we conducted an additional analysis testing the statistical significance of body size trends by regressing raw island mass against mainland mass, following previous studies[4,5,16,33]. Phylogenetic meta-regressions were run using log-transformed island mass as the response variable, and log-transformed mainland mass as the predictor, with random effects as specified above, and sampling variance $sd_i^2/mass_i^2*N_i$. The island rule predicts an intercept > 0 and slope < 1. Finally, we assessed publication bias by testing the influence of data source on the relationship between size ratio and mainland mass. This involved comparing whether patterns differed in island-mainland pairs extracted from studies testing the island rule (38.6% of cases) versus pairs extracted from studies not testing the island rule (61.4% of cases).

Testing ecological hypotheses explaining insular size shifts

We evaluated well-established ecological hypotheses that may explain insular size shifts. Specifically, we examined whether size shifts could be explained by the ecological release[9], immigrant selection [9], resource limitation[9,100,101], thermoregulation[9,12,102], water availability[103,104] or starvation resistance[9,100] hypotheses using indices of these effects, namely island size, island isolation, island productivity and climate, and species diet (see details in Supplementary Table 1). We modelled interactions between body size and each of the explanatory variables because we expected these factors to differentially affect species of different sizes, thus producing different effects in small, medium-sized and large species. We expected the slope of the relationship to be steeper in smaller islands, isolated from the mainland and with fewer or no predators (Fig. 1). We also expected a differential response of large species to low resource availability compared to small species, as the former had higher energetic requirements, leading to increased dwarfism on islands but no extreme gigantism in small species. High seasonality in resources and in temperature was expected to result in increased gigantism in smaller species, because energy reserves increase faster than energy depletion as body size increases. We hypothesized that smaller species would benefit comparatively more by increasing in size than larger species. Because amphibians are generally small-sized, we also fitted a model with only

additive terms (mainland mass + sdNDVI) where seasonality in resources would result in larger body sizes for all species. Finally, mean temperature was expected to predominantly affect small species living on cold islands which, compared to similar-sized species on islands with a mild climate, would exhibit more pronounced gigantism to enhance heat conservation. We fitted the effect of temperature as an interactive (mainland mass x Tmean) or additive term (mainland mass + Tmean) to assess whether only small species or all species would increase in size in low temperature islands (see details in Extended Data Fig 1, Table S6).

Prior to modeling, all the moderators (explanatory variables) were inspected and $\log_{10}$-transformed if necessary to meet normality assumptions in model errors. We considered a result to be significant when the 95% confidence interval (CI) did not cross zero. We assessed the explained heterogeneity using Omnibus test for moderators (Q_m) and the percentage of variance explained by the moderators using R^2 marginal[105]. All figures show the relationship between size response ratio and body mass, and how this might be altered by the mechanisms explained above.

All analyses were performed in R 3.5.3[106] using the packages *metafor v2.0*[107] and *metagear v0.4*[90] for the meta-regression models and data imputation, *ape v5.2*[108] for estimating branch lengths and resolving polytomies, *rotl v3.0.4*[109] for building the phylogenies for our species by searching the Open Tree Taxonomy[110] and retrieving the phylogenetic relationships from the Open Tree of Life[111], *sf v0.7-3* [112] and *raster v2.7-15*[113] for spatial analyses, *dplyr v0.8.0.1*[114] and *reshape2 v1.4.3*[115] for data manipulation and *ggplot2 v 3.3.0.9000*[116] and *ggpubr v0.1.8* [117] for data visualization. ArcMap 10.5 was used for Figure 2. Silhouettes in figures were extracted from 'phylopic' (https.phylopic.org).

Data and Code availability

All data and code are available at https://github.com/anabenlop/Island_Rule and https://figshare.com/account/home#/projects/89102.

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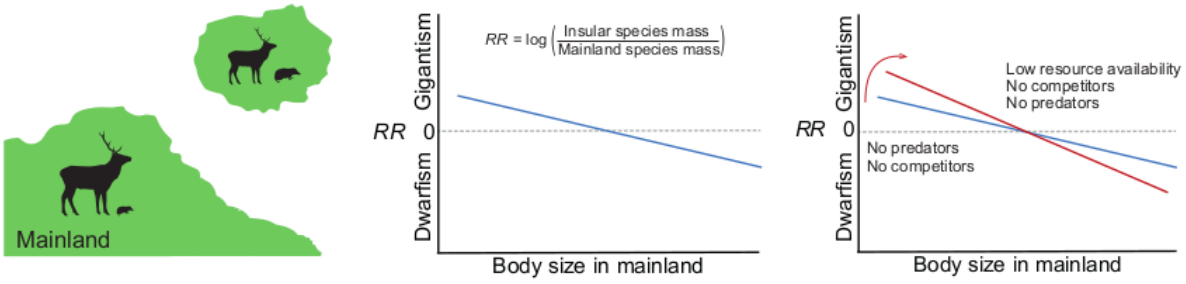
Author Contributions

ABL conceived and coordinated the research, led the analyses and wrote the first draft; ABL, LS, JGZ, MH and JAT helped to develop the conceptual framework; LS compiled the environmental

803 rasters; JAT, PW and BM provided morphometric data. All authors contributed to the data
804 collection from the literature and to the writing of the final manuscript.

805

806 **Figure 1.**



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809 **Figure 1.** Conceptual figure showing body size evolution in island populations. According to the
810 island rule, changes in body size of island populations are dependent on the body mass of
811 mainland relatives, with small species tending to increase in size on islands (gigantism) and large
812 species tending to decrease in size (dwarfism). By plotting size ratio (*RR*) between insular mass
813 and mainland mass, against mainland mass, we can test if insular populations adhere to the rule
814 (intercept > 0 and slope < 0) (blue line). The mechanisms proposed to drive 'island rule' effects
815 are mainly based on reduced predation, inter- and intra-specific competition, and food
816 availability, suggesting that the relationship will steepen in small, remote islands (red line).

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Figure 2.

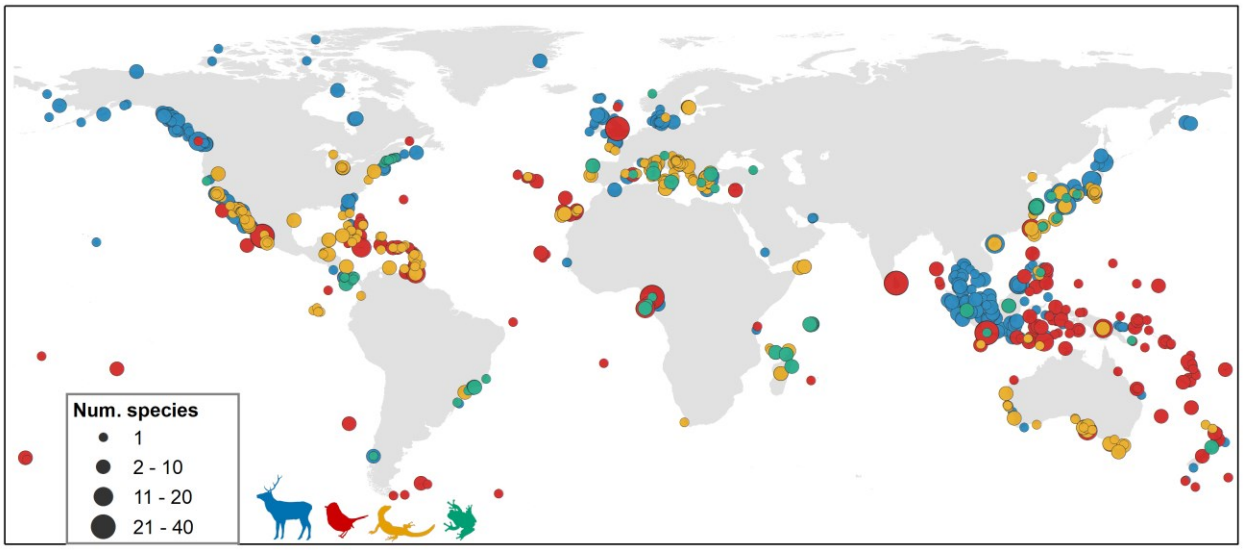


Figure 2. Location of island populations included in our analyses for mammals (N = 1046, blue), birds (N = 706, red), reptiles (N = 548, orange), and amphibians (N = 178, green). The size of each point indicates the number of species sampled on each island. Note that some points overlap others. The reader is advised to see Fig. S1 for a clearer representation of the insular populations for each taxa.

Figure 3.

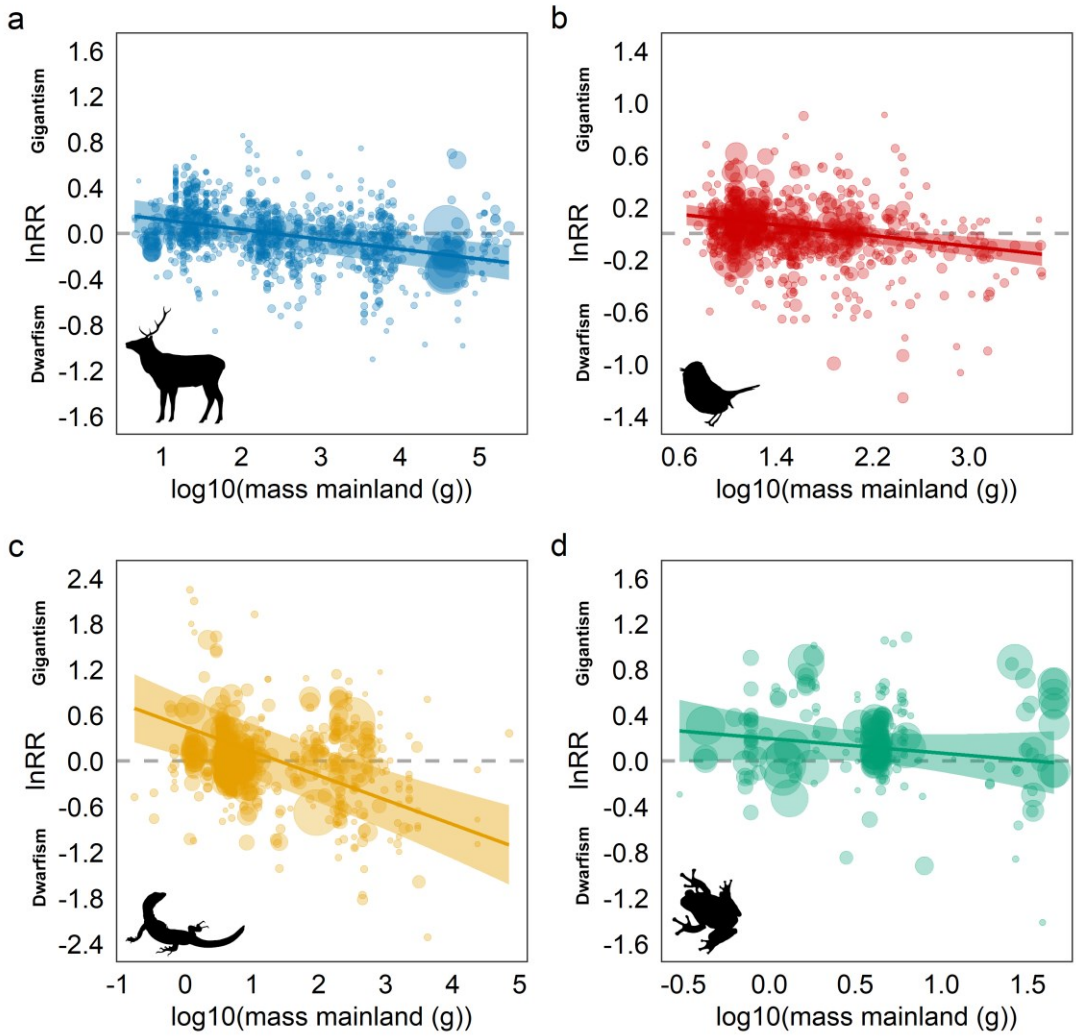
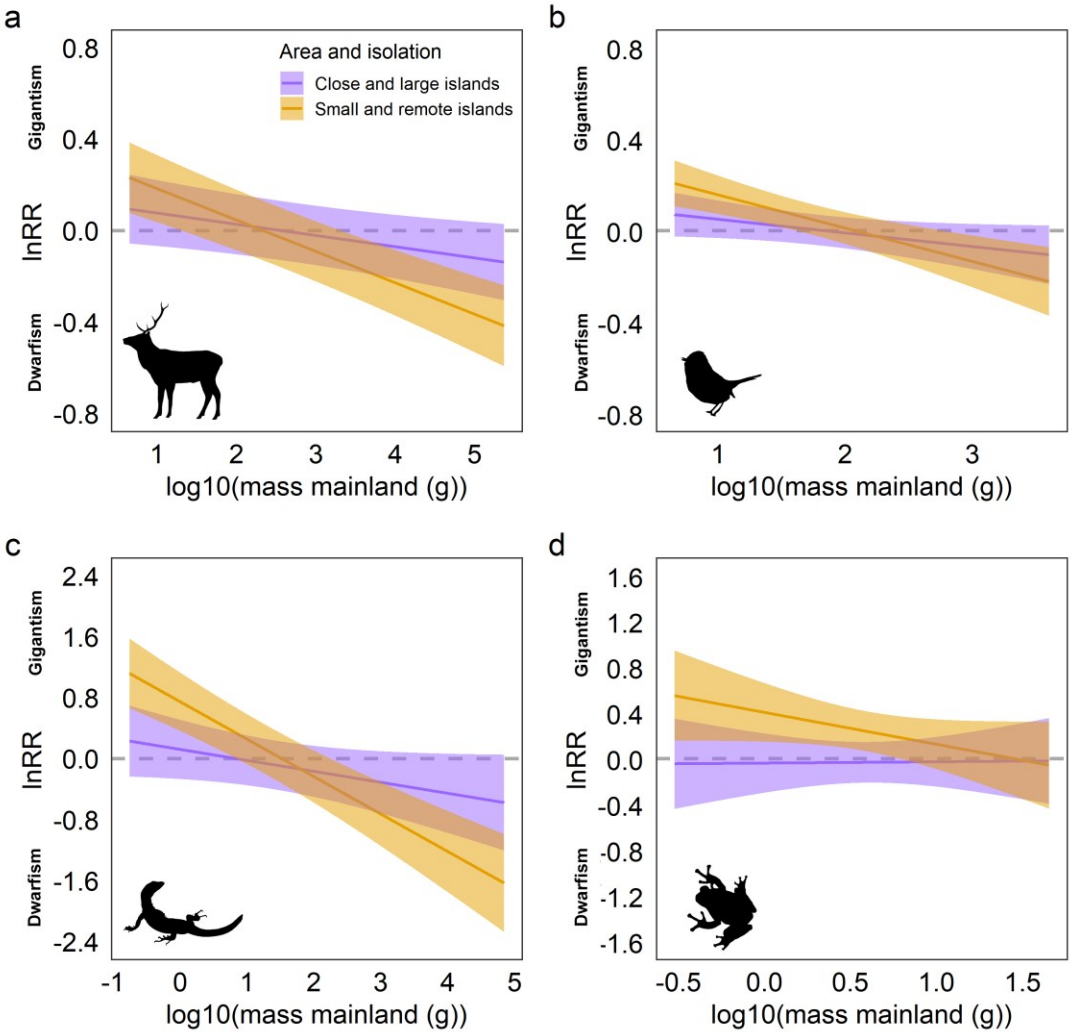


Figure 3. Relationship between *lnRR* (log-ratio between island mass and mainland body mass) and body mass in the mainland for (a) mammals (N = 1046), (b) birds (N = 706), (c) reptiles (N = 548) and (d) amphibians (N = 178) . Models were fitted using phylogenetic multi-level meta-regression models with mainland body mass as moderator, and observation-level ID, study ID, species ID and phylogeny as random effects. *lnRR* > 0 indicates gigantism; *lnRR* < 0 indicates dwarfism; and *lnRR* = 0 indicates stasis (no shift in body size from mainland to island populations). The size of the points represents the weight of each paired island-mainland ratio in the model according to sampling error. Shaded areas represent 95% confidence intervals. Note that y-axes have different scales.

850 **Figure 4.**



851

852 **Figure 4.** The effect of island area and spatial isolation on insular size shifts in terrestrial
853 vertebrates for (a) mammals (N = 1046), (b) birds (N = 706), (c) reptiles (N = 548) and (d)
854 amphibians (N = 178). Continuous variables are represented at the 10% and 90% quantile for
855 each extreme (close vs remote islands; small vs large islands). *lnRR* > 0 indicates gigantism;
856 *lnRR* < 0 indicates dwarfism; and *lnRR* = 0 indicates stasis (no shift in body size from mainland
857 to island populations). Shaded areas represent 95% confidence intervals.

858