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

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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.

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 macroevolutionary or biogeographical rule—the 'island rule'[3–5] (Fig. 1). However, previous research has cast doubt on the generality of this pattern[6], suggesting that body size shifts are asymmetrical, with reduced size in some clades (for example, carnivores, heteromyid rodents and artiodactyls) or increased size in others (for example, murid rodents)[7,8]. Even in these cases, the underlying mechanisms driving patterns of insular gigantism and dwarfism remain unclear.

Several mechanisms have been proposed to explain the island rule, including reduced predation, relaxed competition and resource limitation in island environments[9]. In theory, each of these factors may be accentuated in smaller, more isolated islands, where lower levels of interspecific competition and predation could lead to 'ecological release', allowing small-bodied species to increase in body size[5,9]. Conversely, among large-bodied species, 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 because primary productivity and associated resource availability are strongly influenced by climate[9,10]. Although previous studies of body size evolution on islands have tested the effects of these different mechanisms, many have focused on relatively restricted geographic and taxonomic scales and did not directly address the island rule in its broad sense across multiple species within a taxon[10–13], with notable exceptions[9,14–16].

Most work on the island rule has been restricted to mammals (for example, refs. [4,7,14,17]), although the hypothesis has also been tested in amphibians[18], reptiles[19–21], birds[15,22], fish[23], insects[24], molluscs[25] and plants[26]. The highly inconsistent results of these studies (for example, refs. [5,6,27]) 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 sampling variance. Accordingly, a recent systematic review based on a simplified scoring system[27] concluded that empirical support for the island rule is not only potentially biased but also generally low, particularly for non-mammalian taxa. However, scoring approaches provide only limited information, as they do not account for heterogeneity between studies, taxonomic representativeness, sample size or precision in the estimates.

These limitations are best addressed with formal meta-analyses[28,29], hence we tested the island rule hypothesis by applying phylogenetic meta-regressions to a global dataset of 2,479 island–mainland comparisons for 1,166 insular and 886 mainland species of terrestrial vertebrates (Fig. 2 and Supplementary Dataset 1—GitHub link provided in Supplementary Information). Our analytical framework allows us to control for multiple types of variation, including data source, sample size imbalance, intraspecific and intrapopulation variability, and phylogenetic relatedness (see Methods). For each island–mainland comparison, we calculated the log response ratio (lnRR) as the natural logarithm of the ratio between the mean body size of individuals from an insular population M_i and that of mainland relatives M_m ($\mathrm{lnRR} = \log(M_i/M_m)$)[30]. Then, we regressed lnRR against the body mass of the mainland population (M_m; Fig. 1).

This framework provides a clear set of predictions in the context of evolutionary trajectories on islands[4,6,14]. Specifically, as negative values of lnRR indicate dwarfism and positive values indicate

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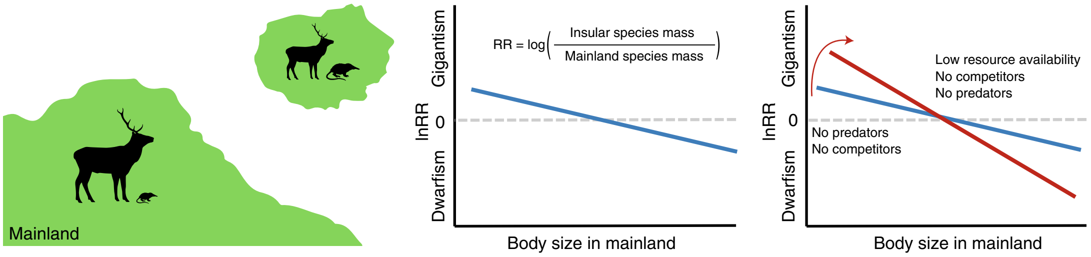

Fig. 1 | Conceptual figure showing body size evolution in island populations. According to the island rule, changes in body size of island populations are dependent on the body mass of mainland relatives, with small species tending to increase in size on islands (gigantism) and large species tending to decrease in size (dwarfism). By plotting the log response ratio (lnRR) between insular mass and mainland mass, against mainland mass, we can test if insular populations adhere to the rule (intercept > 0 and slope < 0; blue line). Mechanisms proposed to drive 'island rule' effects are mainly based on reduced predation, inter- and intraspecific competition, and food availability, suggesting that the relationship will steepen in small, remote islands (red line). Silhouettes extracted from 'phylopic' (www.phylopic.org).

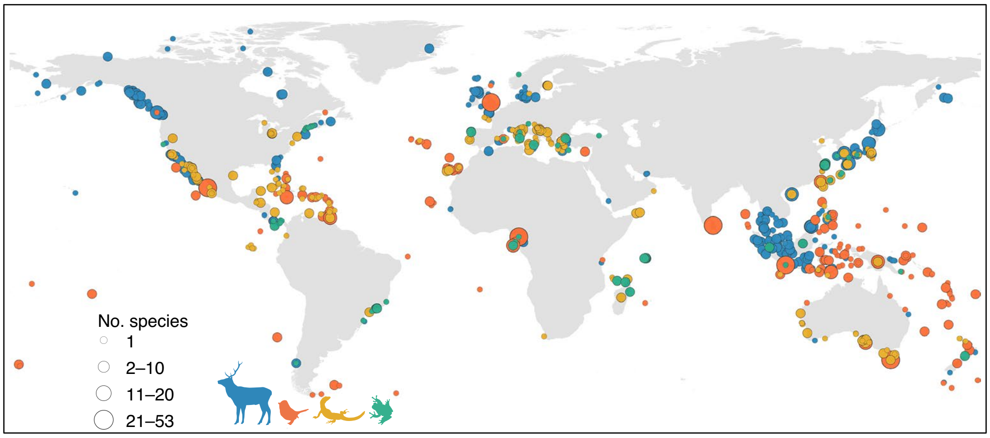

Fig. 2 | Location of island populations included in our analyses for mammals, birds, reptiles and amphibians. Mammals (*N* = 1,058) are shown in blue, birds (*N* = 695) in orange, reptiles (*N* = 547) in yellow and amphibians (*N* = 179) in green. The size of each point indicates the number of species sampled on each island; some points overlap. See Supplementary Fig. 1 for a four-panel figure with the location of insular populations separated for each taxonomic group. ArcMap 10.5. was used to create the map. Silhouettes extracted from 'phylopic' (www.phylopic.org).

gigantism, a positive intercept and negative slope of the lnRR–mainland mass relationship supports the island rule (Fig. 1). Given the contentiousness of the generality in the island rule, we assessed the robustness of our results against potential biases derived of regressing ratios[31,32], using small samples, imputing missing data or the influence of using data from the island rule literature or derived from other studies focused on unrelated questions (that is, publication bias; see Methods). Finally, we use our framework to assess how body size shifts are related to island size, island isolation, island productivity and climate, as well as species diet. The extent to which these different factors explain insular body size shifts allows us to re-evaluate a range of hypotheses for the mechanisms underlying 'island rule' effects on body size, including ecological release[9], immigrant selection[9], resource limitation[9,33,34], thermoregulation[9,15,35], water availability[36,37] and starvation resistance[9,33] (Supplementary Table 1 and Extended Data Fig. 1).

Results

The generality of the island rule. We found that lnRR 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). The relationship was weakly negative but statistically non-significant for amphibians, with a tendency towards gigantism across all body sizes (Fig. 3 and Table 1). We obtained similar results using size ratios corrected for small sample size (lnRR$^{\Delta}$), or by regressing island mass against mainland mass, with support for the island rule across all groups except for amphibians (Supplementary Tables 3 and 4). This indicates that our analyses are robust to small sample size bias[38] or any potential spurious correlation associated to ratio regression models[31,32] (Extended Data Fig. 2). Further, neither imputation nor publication bias influenced our results (Supplementary Tables 5 and 6), with no apparent differences between island–mainland comparisons sampled from studies formally testing the island rule or compiled from unrelated datasets.

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

Ecological mechanisms underlying body size evolution on islands. The pattern of body size evolution in our island–mainland comparisons provides some insight into the likely mechanisms

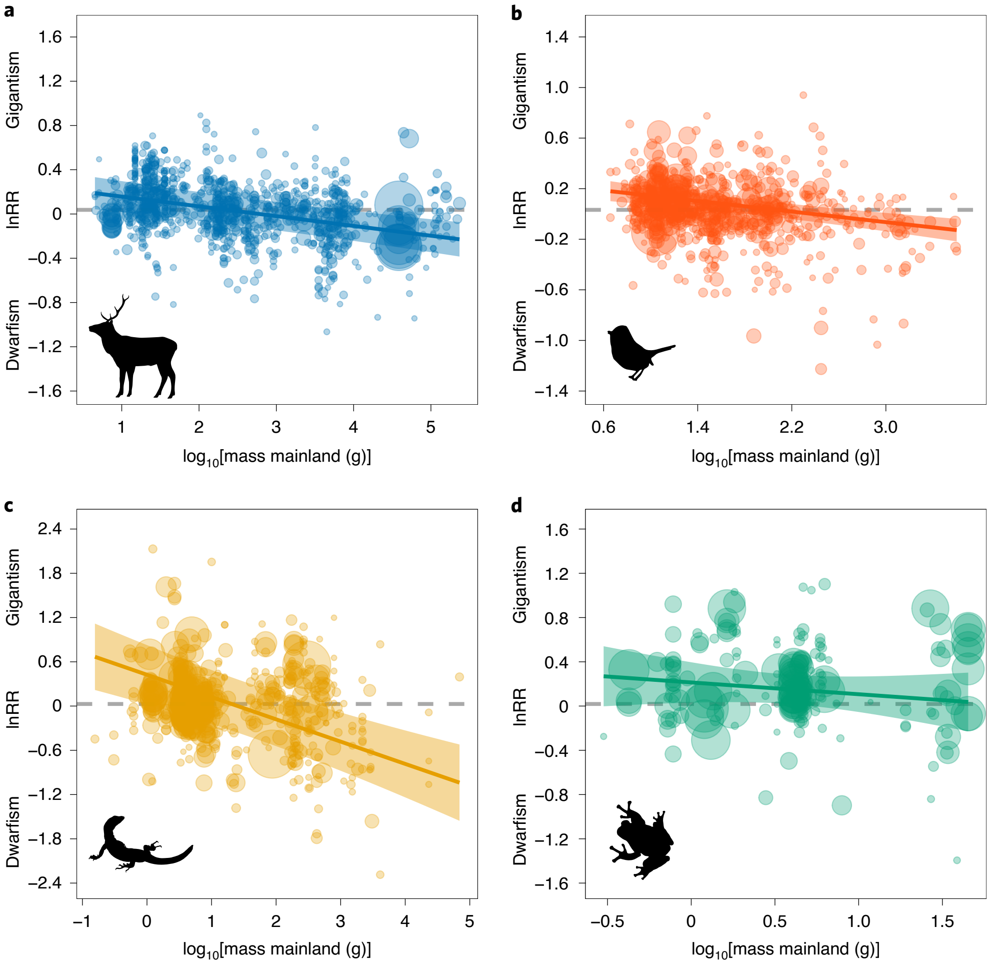

Fig. 3 | 'Island rule' effects in terrestrial vertebrates. a–d, Relationship between lnRR (log response ratio between island mass and mainland body mass) and body mass in the mainland for mammals ($N = 1,058$; **a**), birds ($N = 695$; **b**), reptiles ($N = 547$; **c**) and amphibians ($N = 179$; **d**). Models were fitted using phylogenetic multi-level meta-regression models with mainland body mass as moderator, and observation-level ID, source 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 points represents the inverse of the sampling variance for each paired island–mainland response ratio in the model. Shaded areas represent 95% confidence intervals. Note that *y* axes have different scales. Silhouettes extracted from 'phylopic' (www.phylopic.org).

driving 'island rule' effects (Extended Data Figs. 5–8, Supplementary Table 7 and Supplementary Dataset 2—GitHub link provided in Supplementary Information). Overall, insular size shifts arise through some combination of ecological release from predation and competition, resource limitation, biased colonization (that is, immigrant selection) and starvation resistance. The fact that no single factor explained island effects on body size is not surprising because some hypotheses shared overlapping predictions, making them difficult to disentangle.

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

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

Finally, the relationship between size ratio and mainland mass in amphibians was slightly steeper in small and remote islands (Fig. 4d), with island area being marginally more important than spatial isolation (Extended Data Fig. 8). The effect of seasonality was clearer, with amphibian species inhabiting islands with high seasonality (unpredictable environments) tending towards gigantism, whereas those from islands with low seasonality (predictable environments) being similar in size to mainland counterparts

(Extended Data Fig. 8). We found no effects of diet for any of the four taxa, or precipitation for amphibians, contrary to the water availability hypothesis.

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 (island mass versus mainland mass regressions), small sample bias, data imputation 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 the physiographic and climatic characteristics of particular island environments[9].

Repeated evolutionary trajectories on islands. We found a clear negative relationship between insular body size variation and the body mass of mainland individuals in mammals, birds and reptiles. Mainland body mass explains between 7.0 and 17.6% of the variation in insular size divergence in these three taxonomic groups, which is similar to that reported in smaller-scale studies of bats (15%), birds (13%), snakes (42%), non-volant and terrestrial mammals (11–21%) and turtles (8%)[5,14,15,39,40]. Contrary to these earlier studies, our analyses are corrected not only for phylogenetic relatedness, but also for variability between species and intrapopulation variability, thereby strengthening the evidence for predictable evolutionary trajectories on islands. Nevertheless, the island rule provides only a partial explanation for these trajectories because substantial variation around the trend line remains unexplained. 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 (1.4%), possibly because the body mass range in amphibians is narrower and limited to small sizes (~0.5–50 g) and thus most amphibians tend to gigantism on islands with reduced predation risk.

Our findings are in contrast with a number of studies rejecting the island rule, including a recent review of evidence from across mammals, birds and reptiles[27], as well as other taxon-specific studies focused on lizards[20,41] and turtles[21]. On the other hand, the patterns we detect are consistent with analyses supporting the island rule in snakes[19], mammals[4,9] and birds[5,15] We conclude that the contradictory results of previous studies may have been related to sampling bias, heterogeneity between sources and species, and phylogenetic relatedness (that is, statistical non-independence). By accounting for these effects in our global models we are able to demonstrate that vertebrate animals evolve in largely consistent ways on islands. Further, we have shown that the island rule is not clade-specific and instead applies to numerous clades within major taxonomic groups, particularly in mammals and birds.

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

Table 1 | Parameter estimates for the phylogenetic meta-regression models testing the generality of the island rule in terrestrial vertebrates

Class	*k*	Intercept (CI)	Slope (CI)	QM (*P* value)	R^2_m	R^2_c
Mammals	1,058	0.208 (0.052, 0.365)	−0.088 (−0.122, −0.055)	27.30 ($P<0.001$)	11.4	67.8
Birds	695	0.216 (0.117, 0.315)	−0.104 (−0.145, −0.064)	25.40 ($P<0.001$)	7.0	50.4
Reptiles	547	0.410 (0.006, 0.814)	−0.305 (−0.419, −0.190)	27.21 ($P<0.001$)	17.6	84.2
Amphibians	179	0.195 (0.012, 0.377)	−0.107 (−0.320, 0.107)	0.96 ($P=0.328$)	1.4	68.5

k, number of island–mainland comparisons (lnRR); CI, confidence interval; QM, test of moderators ($\log_{10}$(mainland mass)); R^2_m, marginal R^2, estimated percentage of heterogeneity explained by the moderator (fixed effects); R^2_c, conditional R^2, percentage of heterogeneity attributable to fixed and random effects.

Ecological mechanisms influencing body size variation. Because body size is intimately linked to many physiological and ecological characteristics of vertebrates, it may be associated with a variety of environmental factors. As a consequence, the body size of colonizing species may predictably evolve as the result of selective pressures associated with insular environments (for example, low food resources, few competitors, no predators) and others that act across larger geographic scales (for example, climate). For mammals and reptiles, our results suggest that insular body size shifts are indeed governed by spatial isolation and island size, with individuals becoming dwarfs or giants in remote islands of limited size. Furthermore, the slope of the relationship between size ratio and mainland mass was slightly steeper for birds and amphibians in small remote islands than in large islands near continental land masses (Fig. 4). This points to a combination of resource limitation (with small islands having fewer resources to maintain large-sized organisms[48,49]) along with release from interspecific competition and predation pressure in small, species-poor islands. The pattern is also consistent with biased colonization favouring larger individuals with higher dispersal abilities (immigration selection[50]). Conversely, our results showed that body size divergence on islands close to the mainland was minimal, reflecting two non-mutually exclusive processes. First, many of these islands have been connected to the continent by land bridges so recently that phenotypic differences have not had time to accumulate. Second, regular dispersal between mainland and island populations promotes gene flow, with introgression counteracting divergent selection[51,52].

Besides island physiography (area and isolation), other relevant factors were temperature conditions in endotherms and resource availability and seasonality in ectothermic organisms. Mammals

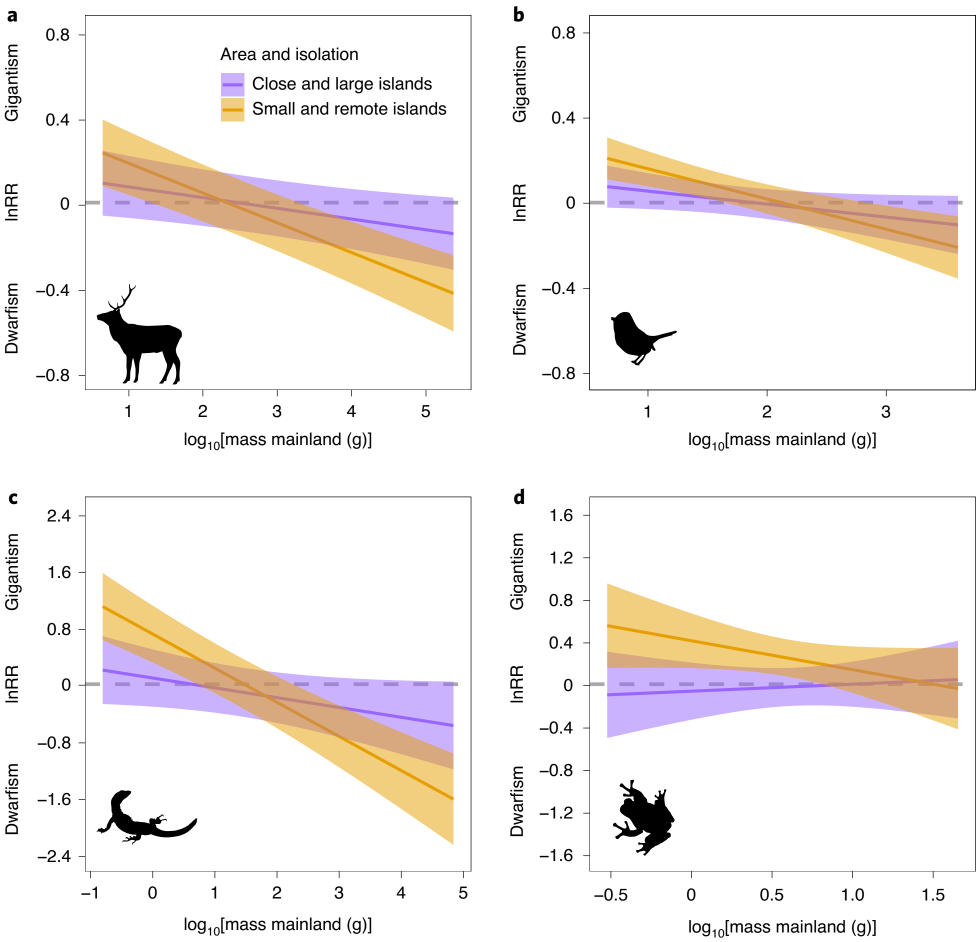

Fig. 4 | The effect of island area and spatial isolation on insular size shifts in terrestrial vertebrates. a–d, The lnRR–mainland mass relationships for small and remote islands, and for close and large islands are shown for mammals (N = 1,058; **a**), birds (N = 695; **b**), reptiles (N = 547; **c**) and amphibians (N = 179; **d**). Continuous variables are represented at the 10% and 90% quantile for each extreme (close versus remote islands; small versus large islands). lnRR > 0 indicates gigantism, lnRR < 0 indicates dwarfism and lnRR = 0 indicates stasis (no shift in body size from mainland to island populations). Shaded areas represent 95% confidence intervals. Silhouettes extracted from 'phylopic' (www.phylopic.org).

and birds both responded to island temperature in line with the heat conservation hypothesis, with small- and large-sized species exhibiting exacerbated gigantism and diminished dwarfism, presumably to conserve heat in colder, harsher insular environments. Additionally, temperature seasonality was an important determinant of the size of large-bodied birds, with populations on highly seasonal islands being similar in size to mainland populations. One possibility is that larger size in these cases may help maintain energy reserves during periods of low food availability, allowing them to thrive in otherwise hostile environments. Another possibility is that bird populations on highly seasonal islands—which tend to be situated at relatively high latitudes—are more often seasonally mobile or even migratory, potentially increasing gene flow with mainland populations or weakening adaptation to the local environment[53]. These findings add new insights to previous results regarding the role of thermal and feeding ecology on morphological divergence in island birds[54,55]. Traditionally, changes in feeding ecology were thought to be the prime force in driving morphological divergence in island birds[54,55]. Yet, our results imply that physiological mechanisms related to heat conservation ('thermoregulation hypothesis') and energy constraints ('starvation resistance hypothesis') may also shape body size evolution in island birds.

In reptiles, we find some evidence that resource availability and seasonality are important factors explaining body size evolution, with some deviations from the patterns predicted. As hypothesized, large species are much smaller on islands with low resource availability, and small species are larger on islands with high seasonality. Yet, unexpectedly, small species are larger on islands with low productivity, perhaps because increased intraspecific competition favours large individuals under the high population densities that reptiles often attain on islands[56,57].

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

Body size evolution in extinct species. Our analyses focused on extant species for which we could gather information on the variation around the morphometric estimates, along with sample size (essential for meta-analyses). The widespread extinction of large species on islands, including dwarf morphotypes of large species such as insular elephants in Sicily and the Aegean islands[60,61], may have masked the historical pattern of phenotypic variation on islands[62]. Giant insular birds[54,63], primates[64,65] and lizards[66], along with large insular turtle species, went extinct during the Holocene and late Pleistocene[67], most likely because of overhunting and the introduction of invasive species[68,69]. Overall, it is estimated that human colonization of oceanic islands was followed by the extinction of 27% of insular endemic mammals[70], as well as over 2,000 bird species in the Pacific region alone[71], with these losses biased towards large-bodied, flightless, ground-nesting species[68]. Extinct species may shed new light on size evolution in insular vertebrates because species extinctions have substantially altered the biogeography of body size in island faunas, potentially leading to downsized insular communities[72,73]. For example, the predominance in our dataset of smaller-bodied organisms could reflect the extinction of large species on islands[68], or simply the fact that few islands support large species. Either way, further studies should include data from extinct species as this may alter or strengthen the signal that we report for extant species[39].

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

Conclusions

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

Methods

Data collection. We collected baseline morphometric data from articles included in a recent assessment of the island rule[27], as well as other compilations assembled to test the hypothesis in reptiles[20], mammals[6] and birds[15]. To expand this sample, we then performed a literature search (February 2020) in the Web of Science Core Collection 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*) (Appendix 1). Because this search was complementary to the data we had gathered from previous compilations[6,15,20,27], we downloaded only the first 500 hits out of a total of 33,431 hits ordered by relevance, and removed duplicates already included in our dataset. We reviewed every island–mainland comparison reported in published studies and traced primary source data when possible to extract original measurements. We also extracted data from all studies containing morphometric measurements for insular populations when these could be matched with equivalent data published elsewhere for relevant mainland taxa. We excluded problematic data, such as comparisons that were not supported by taxonomic or phylogenetic evidence, or that reported morphometric data restricted to single specimens or without sample size. In addition, we excluded comparisons based on extinct taxa as they are often known from very few or incomplete specimens (Supplementary Dataset 3—GitHub link provided in Supplementary Information).

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[41]. 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 the Web of Science Core Collection and Google Scholar. We also compiled morphometric data for 442 insular and 407 mainland bird species from an independent global dataset of avian functional traits[79].

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

Our final dataset contained 529 data sources and 2,479 island–mainland comparisons[7,10,17,36,58,79–601]. In total, we collated morphometric measurements for 63,561 insular and 154,875 mainland specimens representing mammals (1,058 island–mainland comparisons), birds (695 comparisons), reptiles (547 comparisons) and amphibians (179 comparisons) from across the globe (Fig. 2). A total of 2,068 island–mainland comparisons (83.4%) were within-species (for example, subspecies) comparisons and 411 (16.6%) were between-species comparisons. Insular populations were sampled from an array of islands varying widely in size (0.0009–785,753 km^2), climate and level of spatial isolation (0.03–3,835 km from mainland). To explore the drivers of body size shifts in insular populations, we also sampled species with a wide range of average body masses (0.18–234,335 g). We collated data on body size indices (body mass, body length, cranial and dental measurements) of different taxa in island and mainland populations following strict morphological, phylogenetic and biogeographic criteria. Specifically, we always compared the same body size index for island and mainland populations. For within-species comparisons, we compared island and mainland populations based on the information given by the authors of the relevant study (for example, taking note of which mainland source populations are likely to inhabit a particular island because of colonization history or isolation via rising sea levels[89,101,240,385,547]). When we matched comparisons independently, we used information published in the study reporting the insular form, selecting the geographically closest mainland population whenever possible. In addition, we prioritized latitudinal alignment of mainland and island populations to avoid confounding effects of latitudinal variation in body size. In the case of island endemics, we compared island populations with their closest mainland relative whenever these were identifiable by phylogenetic data or other information reported in each particular study. This usually meant selecting their sister species or the geographically closest representative of a sister clade or polytomy (Supplementary Dataset 1—GitHub link provided in Supplementary Information). If we could not reliably establish the closest mainland relative, we discarded the data (Supplementary Dataset 3—GitHub link provided in Supplementary Information).

When more than one body size index was reported in published studies, we prioritized those indices related most closely to body mass (Supplementary Table 2). For mammals, we selected indices in the following order of preference: body mass, body length, cranial length (greatest skull length or condylobasal length) and dentition (for example, canine length)[5]. For birds, preferred indices were body mass, wing length, tarsus length and bill length. Finally, for amphibians and reptiles, size was reported as body mass, snout–vent length, carapace length (for turtles) and total length (including snout–vent length and tail length). In all cases, we included measurements only for adults. To avoid size biases attributable to sexual size dimorphism, we calculated the pooled mean for both sexes and the combined standard deviation using standard formulae for combining groups[602]. When information was available for only one sex (male or female), we restricted our size comparisons to the sex for which we had morphometric data in both mainland and island populations. Data from zoos or studies that could not be georeferenced were discarded.

To overcome the problem that different authors report size using different indices, we used allometric relationships to convert island and mainland size to body mass equivalents, thereby enabling cross-taxa and cross-study comparisons. Although this conversion is imprecise, morphological indices and body mass are nonetheless highly correlated across the global scale and wide range of body sizes within our samples (providing more accurate predictions than simply assuming an exponent ~3, as in previous studies testing the island rule[5,9]). We used published allometric relationships where available (Supplementary Table 2), or derived them based on published datasets[47,179,603–608] and other data sources (Supplementary Dataset 4—GitHub link provided in Supplementary Information). To calculate allometric relationships, we used ordinary least square models of the $\log_{10}$-transformed body mass against the $\log_{10}$-transformed body size index (for example, condylobasal length; Supplementary Table 2 and Dataset 4).

For birds, we complemented published data with standardized morphometric measurements from 3,618 museum specimens and live individuals of 436 insular and 404 mainland bird species (see ref. [79]). We used wing length in the main analyses instead of tarsus length because the former is a better predictor of body mass in our dataset ($R^2_{\mathrm{wing}} = 0.89$ versus $R^2_{\mathrm{tarsus}} = 0.69$; Supplementary Table 2; see also ref. [609]). Although wing length may change during moult or thereafter because of wear, these effects are negligible in relation to interspecific differences[79], and minimized by calculating averages across multiple individuals. Further, interobserver differences between measurements may explain some variation in wing length estimates, but again this bias was shown to have negligible effects in our dataset by comparing repeated measures from different observers (see ref. [79]). To assess the consistency in our results, we repeated analyses using tarsus length, another popular proxy of overall body size in birds[610]. Our results were unchanged (Supplementary Fig. 2).

To select suitable comparisons for museum specimens, we first classified species as either insular or continental by overlapping International Union for Conservation of Nature range polygons with a geographic information system land layer including continental land masses. For each insular species we then identified continental sister species from avian phylogenies[611], using the method described above. We excluded bird species that are highly pelagic or aerial (for example, swifts) and fully migratory species, because in these groups it is unclear whether insular and mainland forms experience different environments[15]. Further, we also excluded flightless bird species, because morphological changes may be owing to flightlessness rather than island dwelling per se[15].

We calculated the response ratio (lnRR; equation (1)) as effect size in our meta-regressions, where we divided the mean body mass of individuals from an insular population, $\bar{M}_{\mathrm{i}}$, by that of the nearest mainland relative, $\bar{M}_{\mathrm{m}}$, and then applied the natural logarithm. Unlike unlogged ratios, the sampling distribution of lnRR is normal, particularly for small samples[30], and thus less prone to statistical artefacts associated with ratio-based regressions.

$$\mathrm{lnRR} = \ln\left(\frac{\bar{M}_{\mathrm{i}}}{\bar{M}_{\mathrm{m}}}\right) \tag{1}$$

Response ratios >0 indicate a shift towards larger sizes (gigantism) whereas ratios <0 indicate shifts towards smaller sizes (dwarfism). Besides mean measurements, we recorded measures of variation, that is, standard deviation, standard error or coefficient of variation, and sample sizes of the body size indices in island and mainland organisms. Standard deviation and sample sizes were used to calculate sampling variances (equation (2)), which were then used to weight each response ratio (coupled with the amount of heterogeneity, that is, the variance in the underlying effects)[30].

$$\hat{\sigma}^2\,(\mathrm{lnRR}) = \frac{\mathrm{SD}^2_{\mathrm{i}}}{N_{\mathrm{i}}\bar{M}^2_{\mathrm{i}}} + \frac{\mathrm{SD}^2_{\mathrm{m}}}{N_{\mathrm{m}}\bar{M}^2_{\mathrm{m}}}; \tag{2}$$

where $\mathrm{SD_i}$ and $\mathrm{SD_m}$ are the standard deviation of the mean body size in the insular and the mainland population, respectively, and N_{i} and N_{m} the sample sizes. Standard deviations (SD) were extracted from raw data when possible. If ranges were provided instead of standard deviation (or standard error or coefficient of variation), we calculated standard deviation following ref. [612]. If neither ranges nor measures of variation were reported, but the reported sample size was >1, we imputed standard deviation based on the coefficient of variation from all complete cases ('Bracken approach'[613]). Imputation was done for 22% of all cases in mammals, 1.1% in birds, 11% in reptiles and 7.3% in amphibians, all within the upper limit of imputations (<30% of all cases per group) advised in previous studies[90].

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, in kilometres) and the island area (in square kilometres). We completed missing data on island characteristics using the United Nations Environment Programme island database (http://islands.unep.ch/) and the Threatened Island Biodiversity Database (http://tib.islandconservation.org/). Missing information was calculated using Google Earth. Additionally, we extracted the normalized difference vegetation index (NDVI) as a proxy for resource availability on islands[614]. We also calculated the standard deviation of the NDVI to assess seasonality in leaf or vegetation cover, as an index of seasonality in available resources. The NDVI was downloaded from the NASA Ames Ecological Forecasting Lab (https://lpdaacsvc.cr.usgs.gov/appeears/task/area).

As 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 version 2.0 (http://worldclim.org[615]). Specifically, we used variables that are more closely associated with the proposed underlying mechanisms of Bergmann's rule (that is, thermoregulation and starvation resistance): mean annual temperature, annual precipitation, and seasonality of temperature and precipitation[616]. We assumed that the time period for these bioclimatic variables (1970–2000), although not necessarily matching the actual time period of body size evolution in the insular populations, roughly represents the climatic conditions in the Holocene, a period relatively climatically stable where most of our populations became isolated (that is, after the Last Glacial Maximum; see also ref. [9]). Because climatic variability across cells substantially exceeds variation within cells in the Holocene, current layers are considered adequate for geographic comparisons. All spatial variables were downloaded at 0.1 degree resolution, and we averaged all cells per island to obtain a mean value of each environmental variable (for example, temperature, NDVI, precipitation and so on). Finally, for each species included in our dataset, we collated diet information from EltonTraits for birds and mammals[617], and from other sources for reptiles[607,618], and classified species as carnivores (>50% diet consisting of vertebrates) or non-carnivores (<50% diet consisting of vertebrates), following previous studies[79,619]. As all amphibians in our dataset are carnivores[620], we did not record their diet.

Data analyses. To test the island rule hypothesis, we used phylogenetic meta-regressions between lnRR and body mass of mainland relatives, following most previous studies of the island rule (for example, refs. [4,5,76,621,622]). A negative slope for this relationship would support the island rule (Fig. 1).

The use of multiple populations of the same species can overestimate the actual number of degrees of freedom, generating type 1 errors. We controlled for this by adding 'Species' as a random effect intercept in our analyses. Additionally, body size evolution in insular vertebrates is heavily influenced by phylogenetic effects, with species within entire clades seemingly showing either dwarfism or gigantism[6]. Thus, we accounted for phylogeny by including the phylogenetic relatedness correlation matrix as a random effect. The species term captures the similarities of effect sizes within the same species, while the phylogenetic term represents the similarity due to relatedness[623]. We also added 'Source' as a random effect intercept to account for between-source variability and the fact that we had multiple response ratios per study. In some cases, 'Source' represented the combination of two sources of data, one for the island size and one for the 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[29]. Total heterogeneity and heterogeneity due to phylogeny, source and species identity were computed following ref. [29].

We tested the robustness of our results against several potential limitations. As multiple island populations were often compared with a single mainland population, we accounted for these repeated measures in a variance–covariance matrix where the diagonal includes the sampling variances and the off-diagonals of the matrix represent the shared variance (covariance) among the response ratios due to the common mainland population[624]. Further, we compared our main results with models fitted with lnRR and sampling variances corrected for small sample size[38]. Another potential problem is that regressions using ratios may lead to spurious correlations[31,32]. Thus, we conducted an additional analysis testing the statistical significance of body size trends by regressing island mass against mainland mass, following previous studies[4,5,20,41]. Phylogenetic meta-regressions were run using island mass as the response variable and mainland mass as the predictor (both transformed with natural log), with random effects as specified above, and sampling variance $\mathrm{SD}^2_{\mathrm{i}}/\bar{M}^2_{\mathrm{i}} \times N_{\mathrm{i}}$. This approach has some limitations in being harder to visualize and less effective in considering the sampling variance of measurements (representing intrapopulation variability), yet nonetheless provides an alternative approach for assessing the robustness of our results, in line with previous studies[4,5,20,41]. 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. To evaluate the relative roles of key mechanisms proposed to influence body size evolution in island fauna, we compiled a further range of variables (Supplementary Table 1 and Extended Data Fig. 1). These included island area (linked to both resource limitation and to ecological release from both predation and competition) and spatial isolation (linked to reduced colonization from mainland populations for smaller taxa, that is, immigration selection[50]). In addition, we included climatic and resource seasonality, which are linked to the starvation resistance hypothesis, and productivity and species diet, each of which are linked to resource limitation. Because body size evolution may be influenced by climate (for example, Bergmann's rule)[9,621], we also included mean temperature, which is linked to body size adaptations for enhancing heat conservation or dissipation (thermoregulation hypothesis). For amphibians, we included precipitation as a proxy for water supply linked to aquatic habitats, moisture and humidity (water availability hypothesis).

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. In line with the ecological release and resource limitation hypotheses, we expected the slope of the lnRR–mainland mass relationship to be steeper in smaller islands, isolated from the mainland and with fewer or no predators (Fig. 1). Further, if resource availability is a key factor, we also expected large species to undergo dwarfism on islands with low productivity[48,49], and for dwarfism to be accentuated in dietary niches with high energy requirements, including carnivory[9]. In addition, high seasonality in resources and in temperature was expected to result in increased gigantism in small-sized species, because energy reserves increase faster than energy depletion as body size increases (starvation resistance hypothesis)[9,625]. We hypothesized that smaller species would benefit comparatively more by increasing in size than larger species. As amphibians are generally small sized, we also fitted a model for this group with only additive terms (mainland mass + sdNDVI) where seasonality in resources (sdNDVI) would result in larger body sizes for all species. Finally, mechanisms driven by thermoregulation and water availability predict that body size shifts are associated with temperature and rainfall, respectively. Mean temperature was expected to predominantly affect endotherms and small ectotherms with good thermoregulating abilities (reptiles and anurans) living on cold islands that, compared with similar-sized species on islands with a mild climate, would exhibit more pronounced gigantism to enhance heat conservation. We fitted the effect of mean temperature (T_{mean}) as an interactive (mainland mass × T_{mean}) or additive term (mainland mass + T_{mean}) to assess whether only small species or all species would increase in size in low temperature islands (Supplementary Tables 1 and 7, and Extended Data Fig. 1).

Prior to modelling, 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 did not cross zero. We assessed the explained heterogeneity using QM and the percentage of variance explained by the moderators using R^2 marginal[626]. 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 version 3.5.3[627] using the packages metafor v2.0[628] and metagear v0.4[629] for the meta-regression models and data imputation, metaDigitise v1.0[630] for data extraction from plots, ape v5.2[631] for estimating branch lengths and resolving polytomies, rotl v3.0.4[632] for building the phylogenies for our species by searching the Open Tree Taxonomy[633] and retrieving the phylogenetic relationships from the Open Tree of Life[634], sf v0.7-3[635] and raster v2.7-15[636] for spatial analyses, dplyr v0.8.0.1[637] and reshape2 v1.4.3[638] for data manipulation and ggplot2 v3.3.0.9000[639] and ggpubr v0.1.8[640] for data visualization. ArcMap 10.5 was used for Fig. 2. Silhouettes in figures were extracted from 'phylopic' (www.phylopic.org). The PRISMA checklist for systematic reviews is available in Appendix 3.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data are available at https://github.com/anabenlop/Island_Rule and https://figshare.com/projects/Body_size_evolution_in_insular_vertebrates/89102.

Code availability

The code to conduct the analyses is available at https://github.com/anabenlop/Island_Rule.

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Author contributions

A.B.-L. conceived and coordinated the research, led the analyses and wrote the first draft; A.B.-L., L.S., J.G.-Z., M.A.J.H. and J.A.T. helped to develop the conceptual framework; L.S. compiled the environmental rasters; J.A.T., P.W. and B.M. provided morphometric data. All authors contributed to the data collection from the literature and to the writing of the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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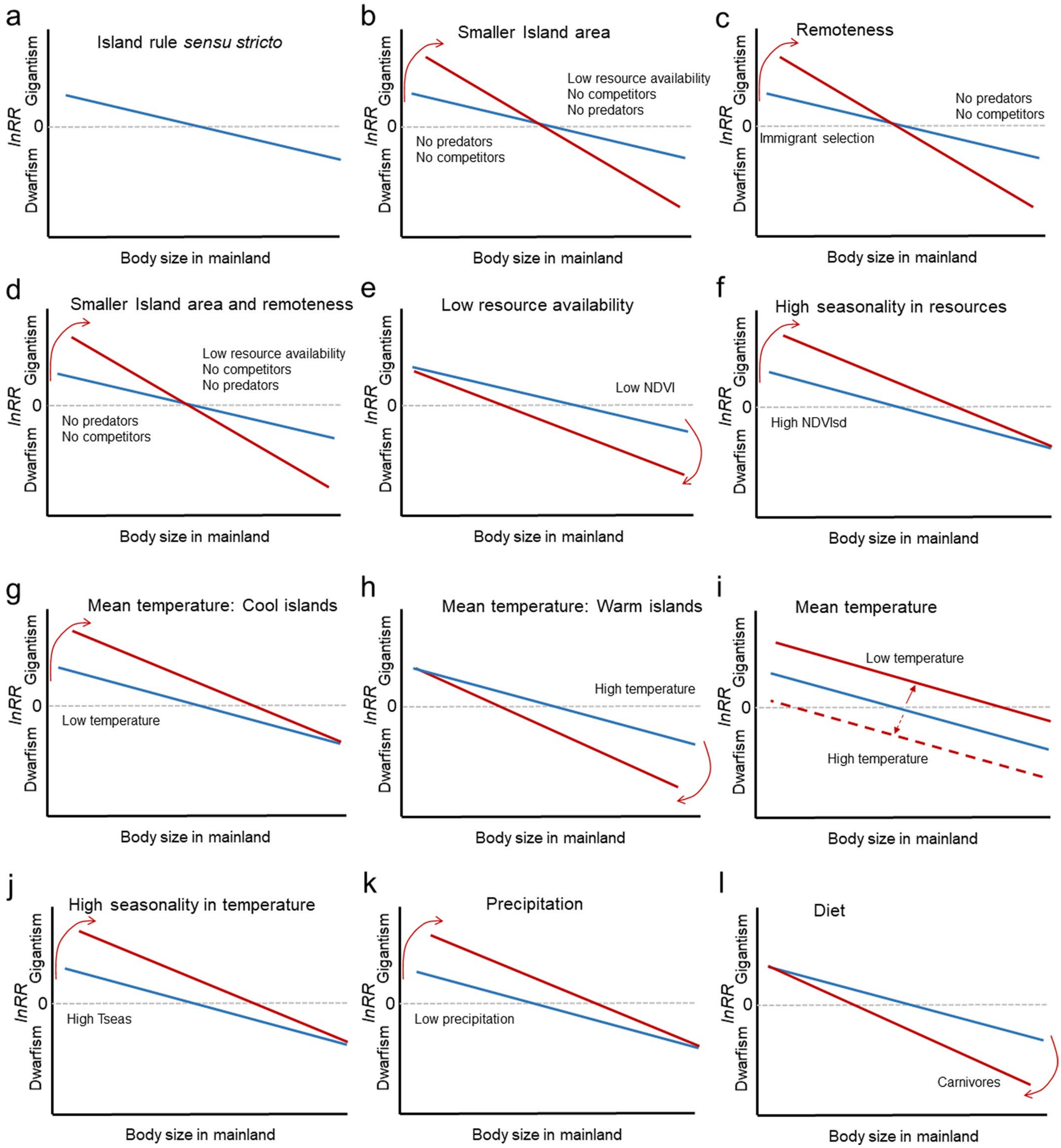
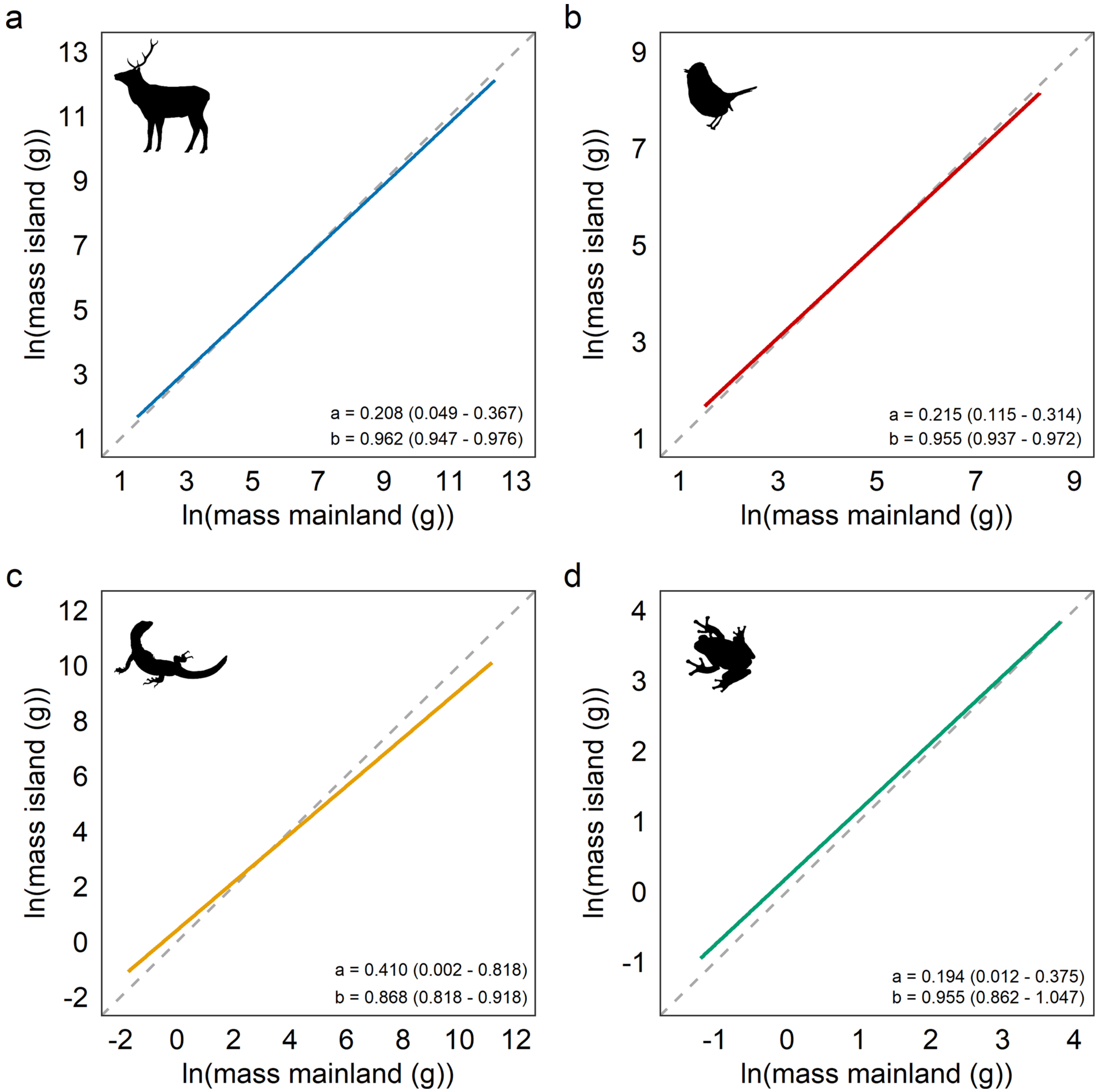
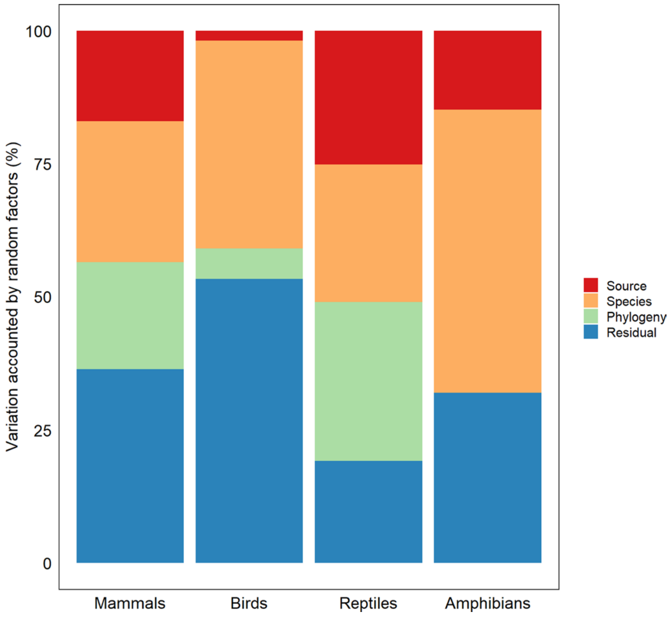


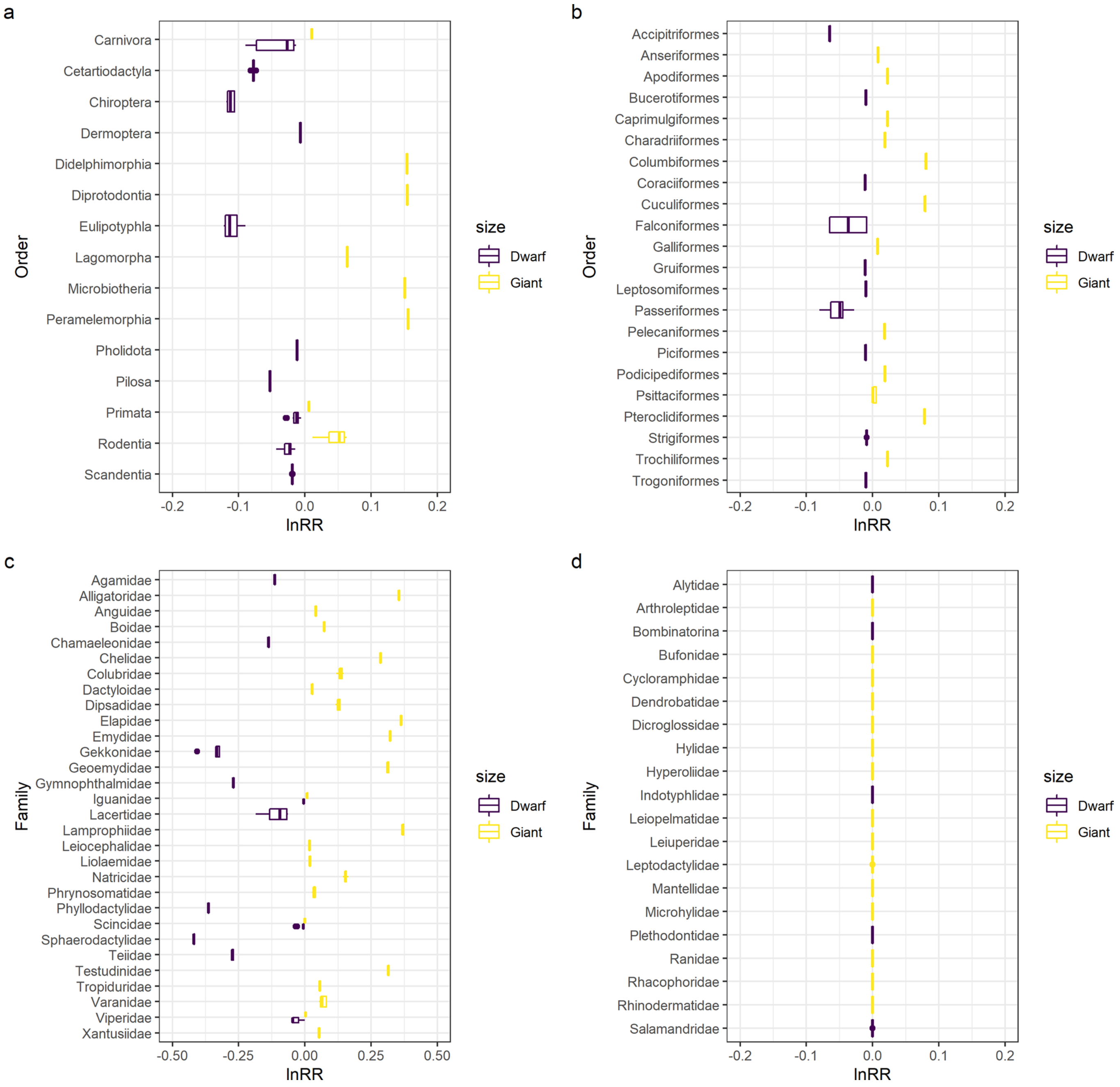
Extended Data Fig. 1 | Conceptual models depicting the different hypotheses tested to explain insular size shifts in vertebrates. Expected insular size shifts are depicted as a result of (**a**) Island rule effects; (**b**) island area; (**c**) spatial isolation (distance to mainland); (**d**) a combination of island area and distance to mainland; (**e**) primary productivity, (**f**) seasonality in resources; (**g**) mean temperature affecting mostly small species in cool islands; (**h**) mean temperature affecting mostly small species in warm islands; (**i**) mean temperature affecting all species; (**j**) seasonality in temperature; (**k**) precipitation; (**l**) species dietary preferences (carnivores vs non carnivores). Detailed information on the different hypotheses can be found in Supplementary Table 1.



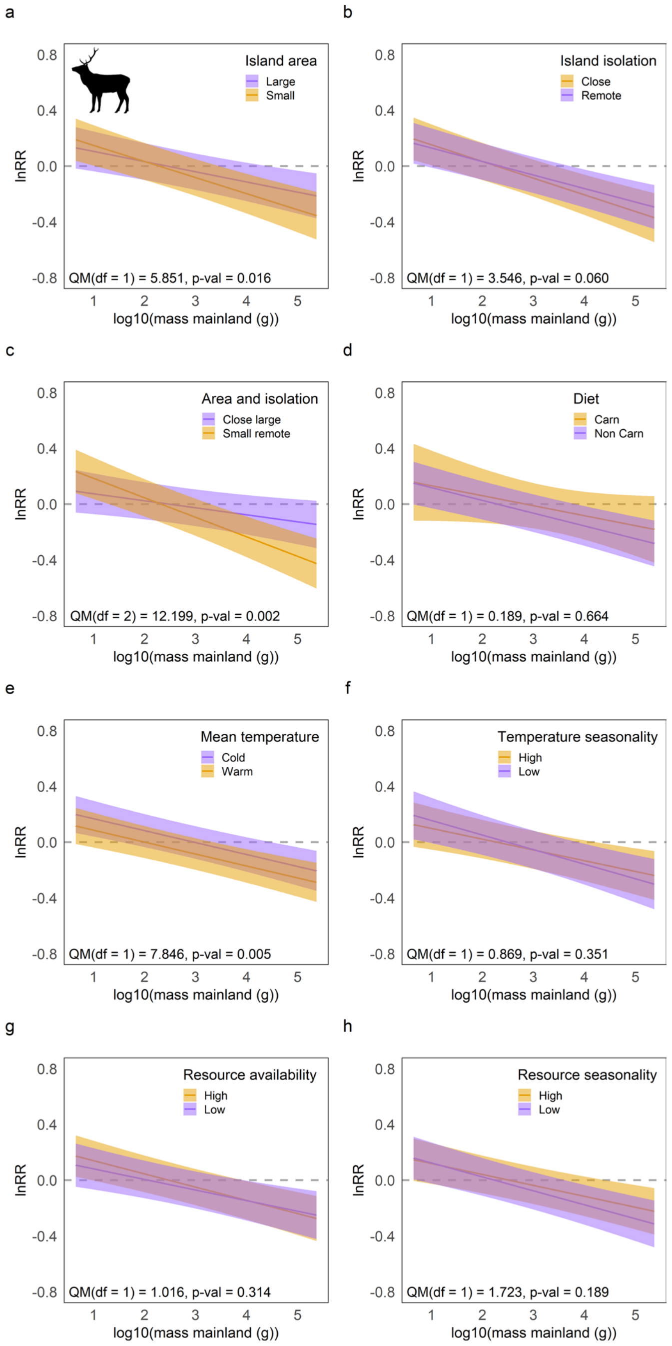
Extended Data Fig. 2 | Phylogenetic meta-regression models of island body size versus mainland body size. Mean body size (ln-transformed mass, in g) on islands versus mainland is shown for (**a**) mammals, (**b**) birds, (**c**) reptiles and (**d**) amphibians. The dashed line has a slope of 1 and an intercept of 0. The solid lines represent the phylogenetic meta-regression slope estimate. The intercept a and slope b are presented in each plot along with CI. The island rule holds if the intercept is > 0 and the slope < 1.



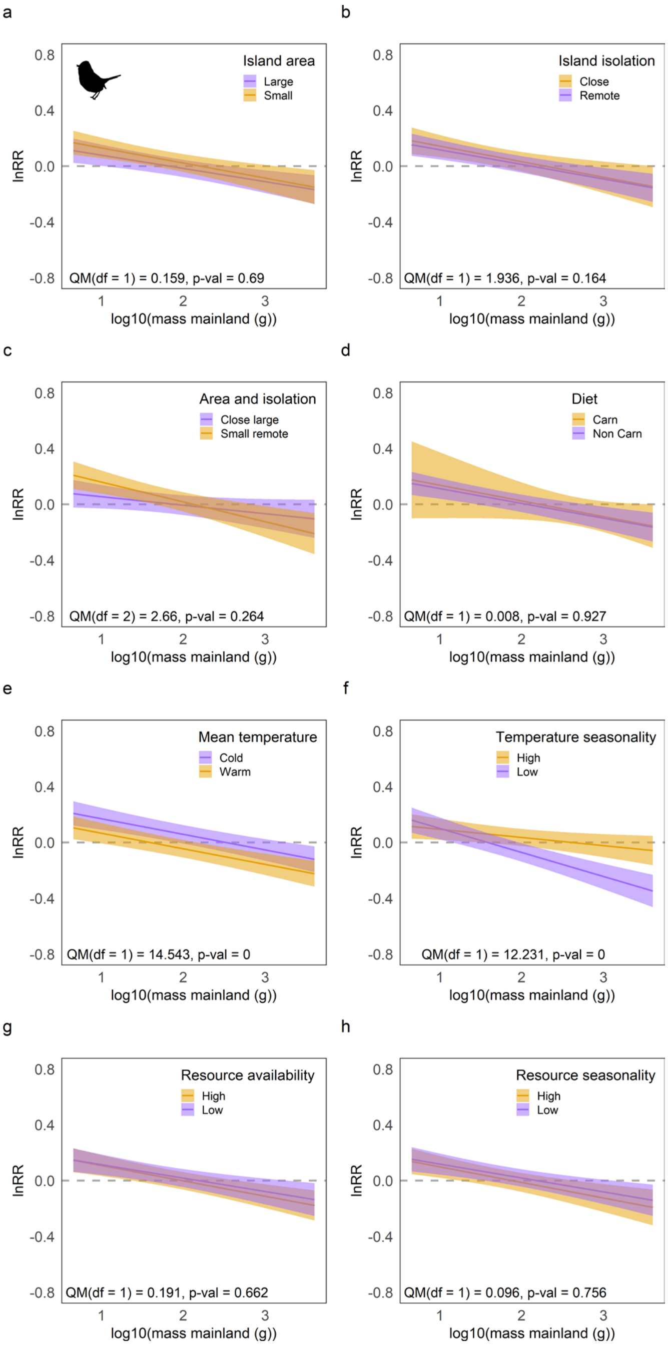
Extended Data Fig. 3 | Variation accounted for by random factors (Source, Species and Phylogeny) and residual variation. The amount of variance accounted for by phylogeny was the largest for reptiles and mammals, and low for birds. The extent of variance explained by data sources was larger for mammals and reptiles, and low for amphibians and birds. The residual variance was highest for birds, followed by mammals, amphibians and reptiles, indicating that other factors besides mainland body size may help to explain insular size shifts (see Extended Data Fig. 5–8).



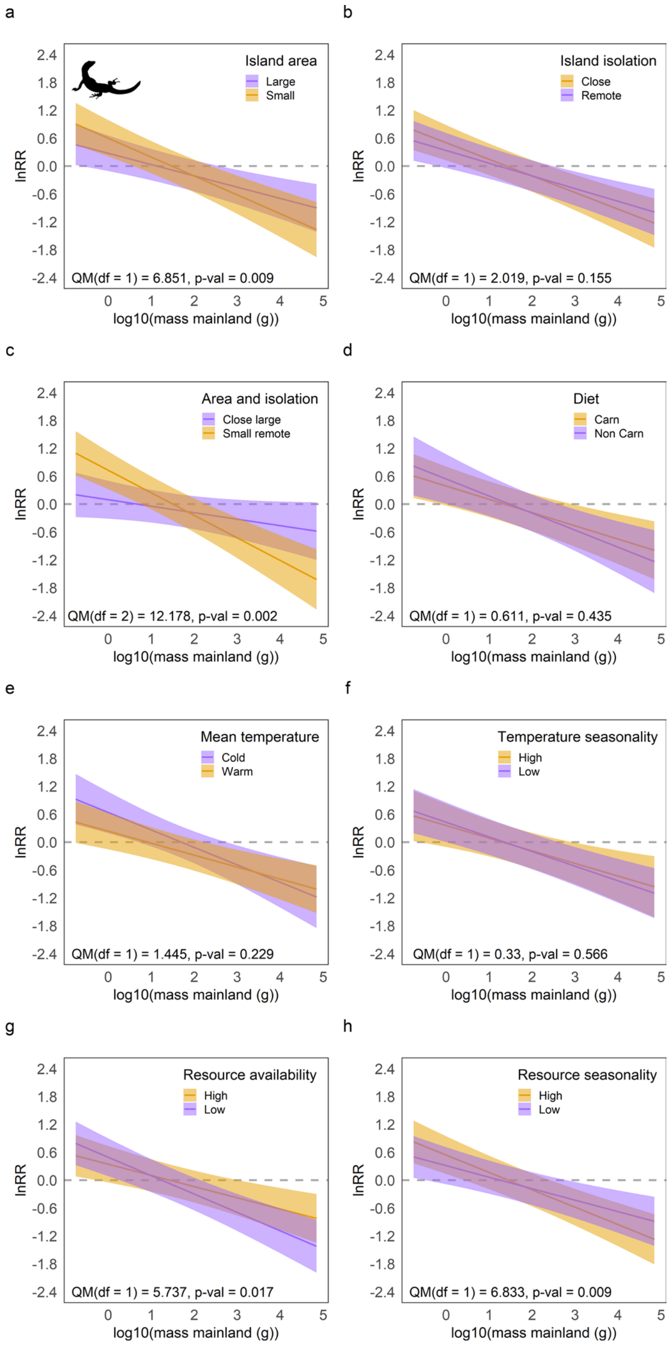
Extended Data Fig. 4 | Phylogenetic random effects across taxonomic orders. Boxplots of the variation in phylogenetic random effects across orders are shown for (**a**) mammals and (**b**) birds; and across families for (**c**) reptiles and (**d**) amphibians. Positive values indicate a tendency towards gigantism, whereas negative values indicate dwarfism.



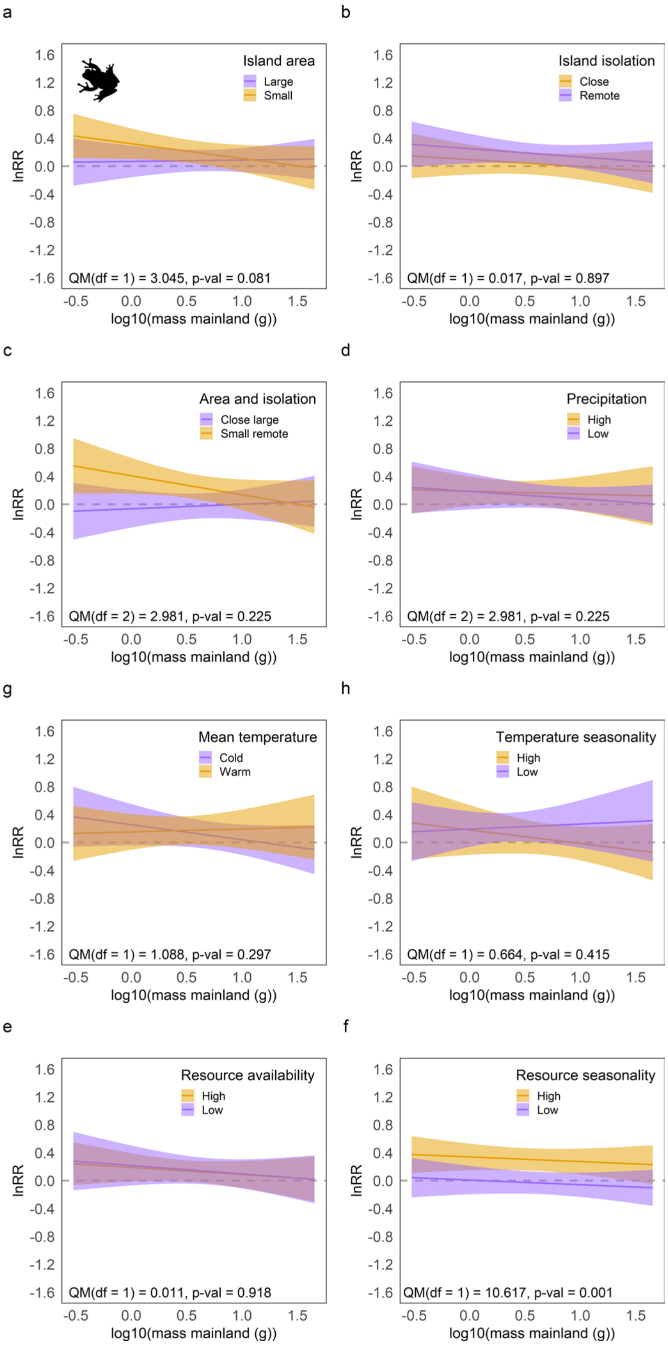
Extended Data Fig. 5 | Ecological factors explaining insular size shifts in mammals. Only 1-2 variables are displayed per plot, while keeping the other predictors at median values. Continuous variables are represented at the 10% and 90% quantile for each extreme (close vs remote or small vs large, and low vs high). lnRR > 0 indicates gigantism, lnRR < 0 indicates dwarfism, and lnRR = 0 indicates no shift in body size in islands compared to mainland populations. Shaded areas represent 95% CI. QM indicates the explained heterogeneity (variance) by the interaction between each explanatory factor and body mass (for example mass:area in panel a), or the explanatory factor only in case of intercept-only models (for example temperature in this case). See Supplementary Table 7 for details.



Extended Data Fig. 6 | Ecological factors explaining insular size shifts in birds. Only 1-2 variables are displayed per plot, while keeping the other predictors at median values. Continuous variables are represented at the 10% and 90% quantile for each extreme (close vs remote or small vs large, and low vs high). lnRR > 0 indicates gigantism, lnRR < 0 indicates dwarfism, and lnRR = 0 indicates no shift in body size in islands compared to mainland populations. Shaded areas represent 95% CI. QM indicates the explained heterogeneity (variance) by the interaction between each explanatory factor and body mass (for example mass:area in panel a), or the explanatory factor only in case of intercept-only models (for example temperature in this case). See Supplementary Table 7 for details.



Extended Data Fig. 7 | Ecological factors explaining insular size shifts in reptiles. Only 1-2 variables are displayed per plot, while keeping the other predictors at median values. Continuous variables are represented at the 10% and 90% quantile for each extreme (close vs remote or small vs large, and low vs high). lnRR > 0 indicates gigantism, lnRR < 0 indicates dwarfism, and lnRR = 0 indicates no shift in body size in islands compared to mainland populations. Shaded areas represent 95% CI. QM indicates the explained heterogeneity (variance) by the interaction between each explanatory factor and body mass (for example mass:area in panel a), or the explanatory factor only in case of intercept-only models (for example temperature in this case). See Supplementary Table 7 for details.



Extended Data Fig. 8 | Ecological factors explaining insular size shifts in amphibians. Only 1-2 variables are displayed per plot, while keeping the other predictors at median values. Continuous variables are represented at the 10% and 90% quantile for each extreme (close vs remote or small vs large, and low vs high). lnRR > 0 indicates gigantism, lnRR < 0 indicates dwarfism, and lnRR = 0 indicates no shift in body size in islands compared to mainland populations. Shaded areas represent 95% CI. QM indicates the explained heterogeneity (variance) by the interaction between each explanatory factor and body mass (for example mass:area in panel a), or the explanatory factor only in case of intercept-only models (for example seasonality in resources – sdNDVI in this case). See Supplementary Table 7 for details.

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Policy information about availability of computer code

Data collection	Data from figures was extracted with the package metaDigitise v1.0 in R 3.5.3
Data analysis	Data was analysed using: 'R' v 3.5.3 and 'ArcMap' v 10.5

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Phylogenetic meta-analysis of the generality of the island rule in vertebrates and potential mechanisms underlying insular size shifts. and
Research sample	We assembled a global dataset of 2,479 island-mainland comparisons for 1,166 insular and 886 mainland species of terrestrial vertebrates, including mammals (1,058 island-mainland comparisons), birds (695 comparisons) reptiles (547 comparisons) and amphibians (179 comparisons) spread over the globe. In total we included morphometric measurements of 154,875 mainland and 63,561 insular specimens from species covering a wide range of average body masses (0.18–234,335 g)
Sampling strategy	We collected data from articles included in a recent assessment of the island rule and previous compilations included in previous studies of reptiles, mammals, and birds, tracing original data sources when possible to extract original measurement data. We additionally sampled body size measurements from published studies that did not assess the island rule per se, or – in the case of birds – also from original morphometric data collected from museum and live specimens. Overall, we included information retrieved from peer-reviewed articles, live and museum specimens, and expedition reports.
Data collection	Morphological data obtained from the literature and from measurements of live caught individuals and preserved museum skins. Ecological data obtained from the literature. Environmental data was obtained from publically available spatially-explicit rasters.
Timing and spatial scale	Data collection started in February 2018 and continued up to November 2020, with major gaps in between due to focus on other projects. Note that all data come from literature except for data on museum specimens, which was collected for another study (Pigot et al. 2020. NEE 4, 230-239.
Data exclusions	We excluded problematic data, such as comparisons that were not supported by taxonomic or phylogenetic evidence, or which reported morphometric data restricted to single specimens or without sample size. In addition, we excluded comparisons based on extinct taxa since they are often known from very few or incomplete specimens. Excluded studies and reasons for exclusion are specified in Supplementary Dataset 3.
Reproducibility	No experiments were undertaken. All data and codes necessary to reproduce the findings of this study are available at https://github.com/anabenlop/Island_Rule
Randomization	Our sampled belonged to either island populations, or mainland populations of the same or closely related species. No randomization was required or applied.
Blinding	NA

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

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☐	☒	Animals and other organisms
☒	☐	Human research participants
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Methods

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☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	No laboratory animals were used.
Wild animals	A significant proportion of the avian data are from museum specimens. Some data are included from wild-caught birds that were not harmed during data collection and subsequently released into the wild. In all cases, birds were caught by mist-netting, a passive, non-invasive technique which does not harm the individual birds.
Field-collected samples	No samples were taken from the field
Ethics oversight	Natural Environment Research Council

Note that full information on the approval of the study protocol must also be provided in the manuscript.