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 develop phylogenetic models 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 mammal 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 ancestors 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.

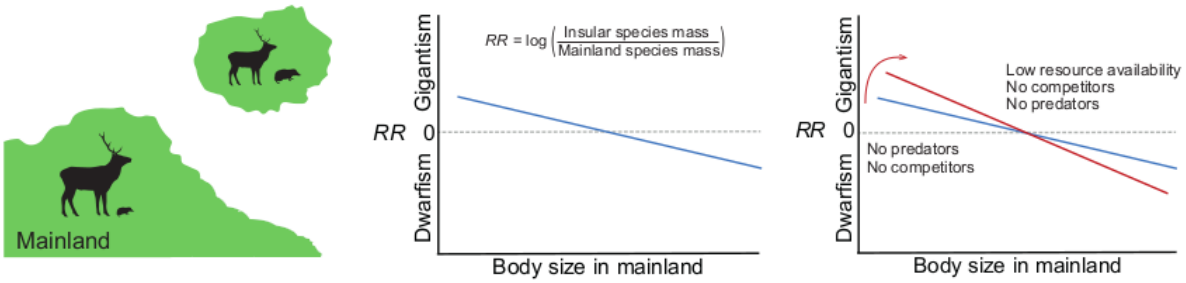

Figure 1. Conceptual figure showing body size evolution in island populations. According to the island rule, changes in body size of island populations is dependent on the body mass of mainland relatives, with small species tending to increase in size on islands (gigantism) and large species tending to decrease in size (dwarfism). By plotting size ratio (*RR*) 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). The mechanisms proposed to drive 'island rule' effects are mainly based on reduced predation, competition, and food availability, suggesting that the relationship will steepen in small, remote islands (red line).

Multiple mechanisms have been proposed to explain the island rule, including reduced predation, relaxed competition and food resource limitation on 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, potentially generating substantial measurement error. Accordingly, a recent systematic review based on a simplified scoring system[24] concluded that differences among studies seem to be partly due to author-related biases and that empirical support for the island rule is generally low, particularly for non-mammalian taxa. However, scoring approaches provide only limited information about the general support for a hypothesis, as they do not account for heterogeneity between studies, taxonomic representativeness, sample size, or precision in the estimates. In contrast, formal meta-analyses are able to systematically test ecological hypotheses, while accounting for the multiple sources of heterogeneity mentioned above[25,26].

To address this issue, we conducted a meta-analysis on a global dataset of 1,986 island-mainland comparisons for 776 species of terrestrial vertebrates, including mammals (724 comparisons, 169 species), birds (633, 466) reptiles (455, 101) and amphibians (174, 40) spread over the globe (Fig. 2). We included species covering a wide range of body masses (0.17–234,315 g) and insular populations inhabiting a diverse array of islands with different sizes (0.04–785,778.2 km^2), spatial isolation (0.03–3835 km from mainland) and different climates. To avoid the widespread author- or publication-biases detected in previous studies[24] we sampled body size measurements from published studies that did not assess the island rule per se, or – in the case of birds – from original morphometric data collected from museum specimens.

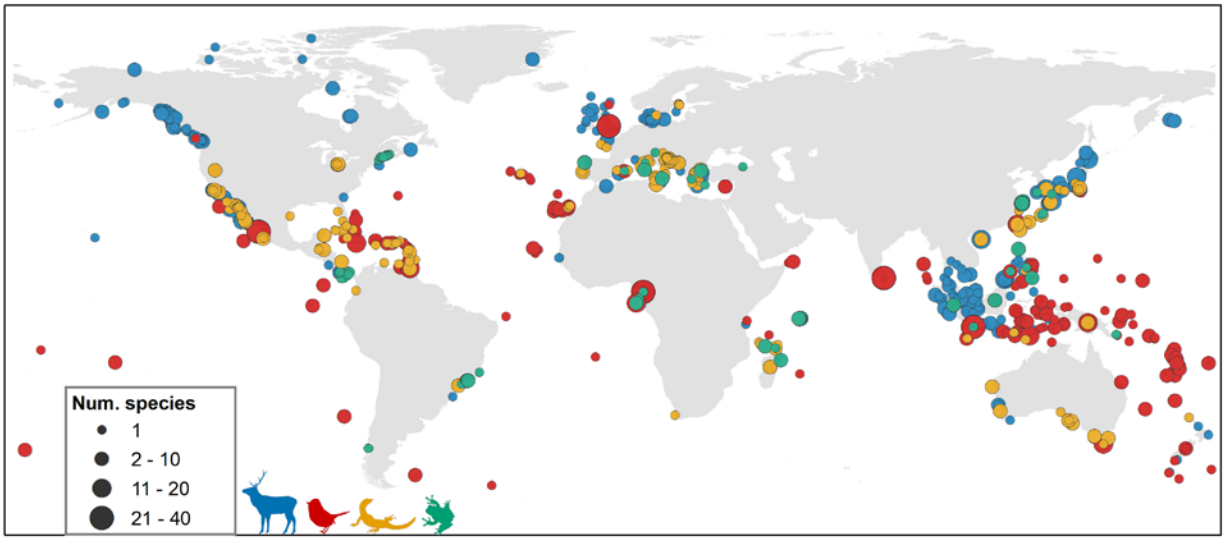

Figure 2. Location of island populations included in our analyses for mammals (N = 712, blue), birds (N = 633, red), reptiles (N = 323, orange), and amphibians (N = 168, green). The size of each point indicates the number of species sampled on each island.

Our analytical framework has the key advantage of allowing us to control for multiple types of variation, including data source, sample size imbalance, intraspecific and intra-population variability, and phylogenetic relatedness. For each island-mainland comparison, we calculated the response ratio (*RR*) as the natural logarithm of the ratio between the mean body size of individuals from an insular population M_i and that of individuals from an ancestral mainland population M_m, i.e $RR = \log(M_i/Mm)$[27]. The *RR* is therefore an estimate of the effect of island colonization on body size, with negative values ($RR < 0$) indicating dwarfism and positive values ($RR > 0$) indicating gigantism (Fig. 1). To assess the direction and strength of these relationships, we regressed *RR* against the body mass of the mainland population (M_m). Using this framework, a positive intercept and negative slope intersecting $RR = 0$ would provide broad-scale support for the island rule[4,6,11] (Fig. 1, Extended Data Fig. 1).

To assess 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 ancestral populations and immigration selection[28]), seasonality, productivity and diet (again linked to resource limitation).

Because body size evolution is influenced by climate (e.g. Bergmann's rule)[9,29], 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 *RR* (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). The relationship was weakly negative but non-significant for amphibians, with a tendency towards gigantism across all body sizes (Fig. 3). When we did not account for sampling variability in our models (which reflects intra-population variability and measurement error in the estimates, see Methods), the patterns across all groups became weaker, with intercept confidence interval (CI) overlapping zero, and flatter or less steep slopes (Extended Data Fig. 2).

Although we found support for the island rule in mammals, birds and reptiles (Fig. 3), with explained variance of mainland body mass equal to 12.2, 6.3 and 21.0%, respectively, there was still a high degree of heterogeneity across effect sizes that was explained by variability within species, phylogeny or between studies (Extended Data Fig. 3). Insular body size shifts were largely unrelated to phylogeny in birds, mammals and amphibians, with a stronger phylogenetic signal in reptiles, yet not enough for the pattern to disappear (Extended Data Fig. 3). Thus, the strength of size-shifts in birds, mammals and amphibians is not clade-specific. Also, there was high variability within species in amphibians, birds and mammals, but less so for reptiles. Specifically, reptilian species predictably had a similar change in body size in islands in comparison with the mainland population. Variation between studies was high for mammals and reptiles, but low for birds, and negligible for amphibians. Finally, residual variance was the

highest for birds, followed by mammals, amphibians and reptiles (Extended Data Fig. 3), indicating that other factors besides mainland body size may explain insular size shifts.

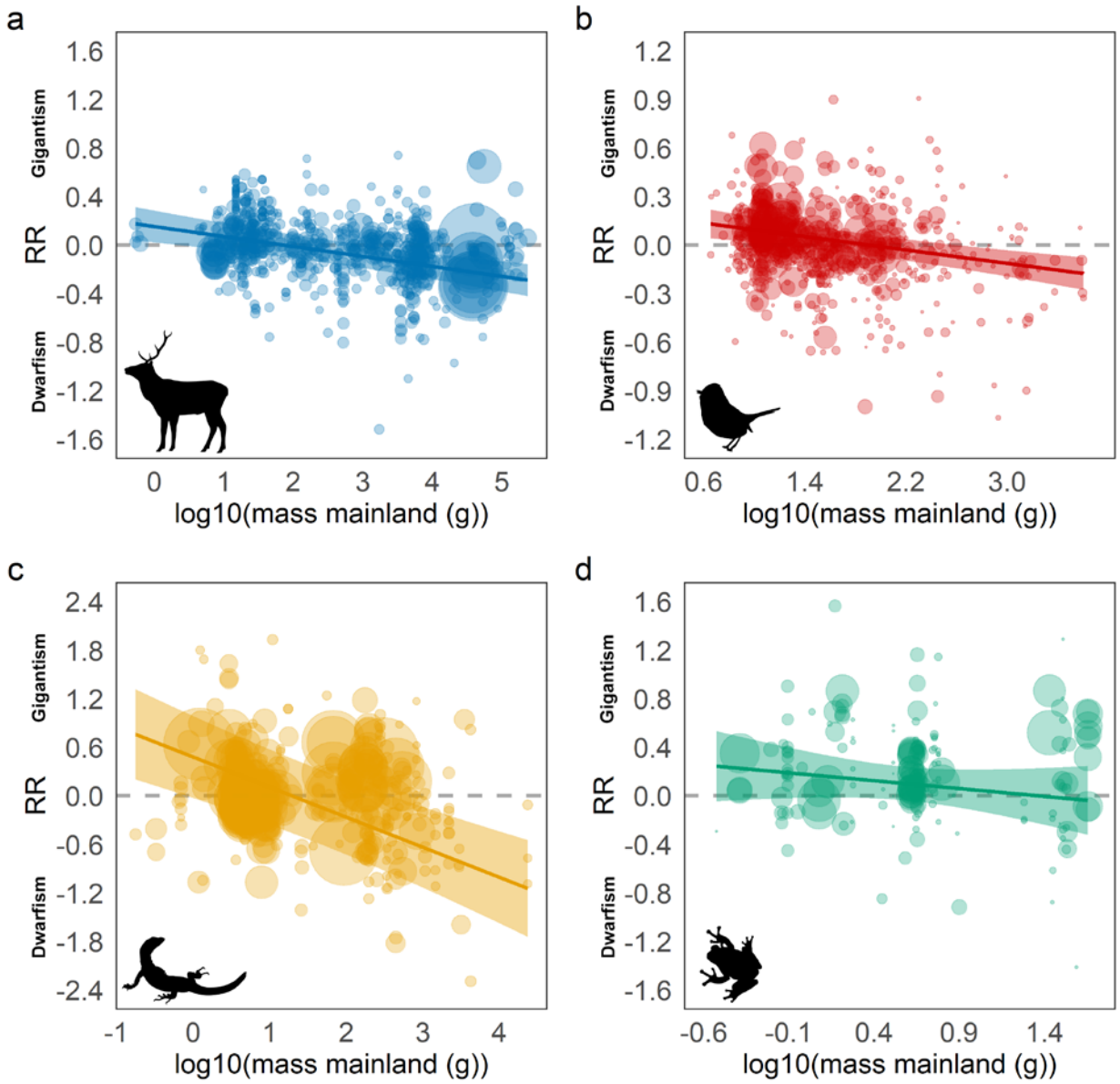

Figure 3. Relationship between RR (log-ratio between island mass and mainland body mass) and body mass in the mainland for (a) mammals, (b) birds, (c) reptiles and (d) amphibians. Models were fitted using multi-level, mixed-effects models with mainland body mass as moderator, and observation-level ID, study ID, species ID and phylogeny as random effects. RR > 0 indicates gigantism; RR < 0 indicates dwarfism; and RR = 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. Note that y-axes have different scales.

Ecological mechanisms underlying body size evolution in islands

The pattern of body size evolution in our island-mainland comparisons supported a range of hypotheses. When accounting for body size of the mainland ancestor, insular shifts in body size of endotherms (mammals and birds) was explained by island area, spatial isolation, and temperature (Fig. 4, Extended Data Fig. 4, 5), providing support for hypotheses linked to ecological release from predation and competition, resource limitation, and biased colonization (immigrant selection), as well as suggesting a role for thermoregulation. In turn, for ectotherms (reptiles and amphibians), the main factors were island area and spatial isolation, productivity and seasonality (Fig. 4, Extended Data Fig. 6, 7). Again, these results provide support for ecological release, resource limitation, immigrant selection, and starvation resistance hypotheses. We found no effects of diet for any of the four taxa, or precipitation (water availability hypothesis) for amphibians (Extended Data Fig. 4-7). 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.

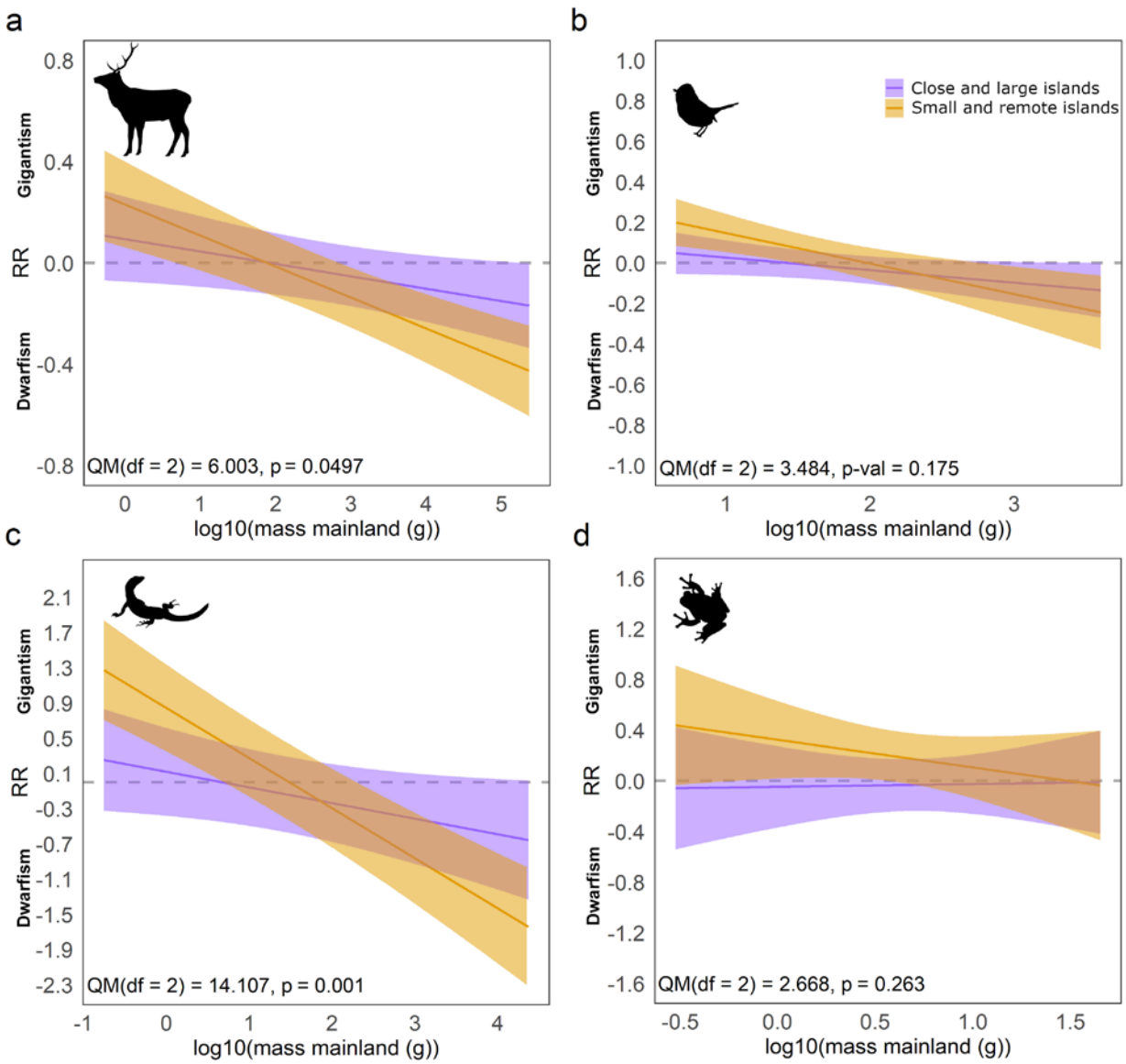

Figure 4. The effect of island area and spatial isolation on insular size shifts in terrestrial vertebrates for (a) mammals, (b) birds, (c) reptiles and (d) amphibians. Continuous variables are represented at the 10% and 90% quantile for each extreme (close vs remote islands; small vs large islands). *RR* > 0 indicates gigantism; *RR* < 0 indicates dwarfism; and *RR* = 0 indicates stasis (no shift in body size from mainland to island populations). Shaded areas represent 95% confidence intervals. QM indicates the explained heterogeneity (variance) by the interaction between each explanatory factor and body mass for the model *RR* ~ mass:area + mass:distance.

We found variations in the processes that drove body size evolution in islands for the different taxonomic groups. Shifts in body mass of mammals were mostly explained by island size and spatial isolation, and modulated by climate (mean temperature) (Fig. 4), resulting in more

pronounced gigantism or dwarfism in small and remote islands ($Q_{m\ (slope)}$ = 6.00, P = 0.05, Fig. 4a). In addition, temperature affected mammals similarly across the body mass range, with bodies consistently larger in cool islands and smaller in warm islands. Hence, even those large species that had undergone dwarfism were larger in low temperature than in high temperature insular environments ($Q_{m\ (slope)}$ = 7.60, P = < 0.01, Extended Data Fig. 4e).

Similarly, in birds, we found that body size was smaller in warmer insular environments and larger in low temperature islands ($Q_{m\ (slope)}$ = 8.48, P < 0.01, Extended Data Fig. 5e). Contrary to the resource limitation hypothesis, small-sized birds did not become larger in highly seasonal islands, but large-sized birds had reduced dwarfism in islands with high seasonality in temperatures ($Q_{m\ (slope)}$ = 9.73, P = <0.01, Extended Data Fig. 5f, Supplementary Table 1).

In reptiles, the combination of island area and spatial isolation were the most important factors explaining variation in body size ($Q_{m\ (slope)}$ = 14.10, P = <0.01, Fig. 4c), with productivity and seasonality being also supported but with weaker effects (Extended Data Fig. 6g, h). Similar to mammals, the tendency towards dwarfism or gigantism in large-bodied or small-bodied reptiles was more apparent in isolated small-sized islands (Fig 4c), with stronger effects of area than isolation (Extended Data Fig. 6a, b). The effects of productivity and seasonality were only partially in line with predictions, as small-sized species were larger in islands with high seasonality, but smaller in islands with high productivity (Fig 5b, Extended Data Fig. 6e, f). In turn, large-bodied reptiles were smaller in islands with low productivity and high seasonality.

Finally, the relationship between size ratio – mainland mass in amphibians was slightly steeper in small and remote islands (Fig. 4d), with island area being more important than spatial isolation ($Q_{m\ (slope)}$ = 3.21, P = 0.07, Extended Data Fig. 7a). The effect of seasonality was clearer, with 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 ($Q_{m\ (slope)}$ = 5.55, P = 0.02, Extended Data Fig. 7h).

Discussion

Based on worldwide sampling of island faunas, we show evidence that the island rule explains patterns of body size evolution across terrestrial vertebrates. Moreover, we have demonstrated

that insular size shifts are contextual and depend not only on the ancestor's body size (island rule *sensu stricto*) but also on physiographic, ecological and climatic characteristics[9].

The generality of the island rule

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 island-rule signal, there remains substantial, unexplained variation about the trend line. Mainland body mass explains between 6.3 and 21% 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[5,11,12,30,31]). 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 in 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[16,32] 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, and that by accounting for these effects in our global models we are able to demonstrate that vertebrate animals evolve in largely consistent ways on islands.

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 to the mainland[33,34]. Theoretically, the optimal body size towards which small and large species may converge on in low-diversity systems such as islands, should correspond to the point where the trend intersects the horizontal dashed line ($RR = 0$) in the size ratio – mainland mass relationship, at which point fitness is maximized[33] (but see[35]). Interestingly, the shift between dwarfism and gigantism in our models occurred at approximately 70-80 g in endotherms, similar to the 100 g adult body mass proposed by Brown et al[33] for mammals, and to the mode of the global body size distribution of birds used to separate between small- and large-bodied birds (60 g)[18,36,37]. In

addition, our analyses suggest that the optimal body size for island reptiles should be ca. 20-30 g, which is slightly larger than the modal body size of Lepidosaurs (14.1 g)[38]. Whether there is an optimal body size in islands has been fiercely debated[35], but overall we should expect that phenotypic variability in morphometric traits will be substantially narrowed if directional selection is operating in islands, a feature that warrants further investigation. Additionally, that optimum should vary with the environmental characteristics of the islands, in particular area and isolation, climate, productivity and seasonality. For example, in mammals, the optimum would be ca. 25 g in warm islands and ca. 400 g in cold insular environments (Extended Data Fig. 4f).

Ecological mechanisms influencing body size variation

Because body size is intimately linked with many physiological and ecological characteristics of vertebrates, it may be associated with a variety of environmental factors. For instance, the body size of colonizing species may predictably evolve as the result of selective pressures associated with insular environments (low food resources, no predators, isolation) and others that act across larger geographic scales (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 size ratio – mainland mass relationship 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[39,40]) 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[28]).

Besides island physiographic characteristics (area and isolation), other relevant factors were temperature conditions in endotherms and resource availability and seasonality in ectothermic organisms. Mammals 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 to maintain energy reserves during

periods with 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[41]. These findings add new insights to previous results regarding the role of thermal and feeding ecology on morphological divergence in island birds[42,43]. Traditionally, changes in feeding ecology were thought to be the prime force in driving morphological divergence in island birds[42,43]. 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 birds in islands.

Resource availability and seasonality were important factors explaining body size evolution in reptiles, with some deviations from the patterns predicted. As hypothesized, large species were much smaller on islands with low resource availability, and small species were larger on islands with high seasonality (Extended Data Fig. 6g, h). Yet, unexpectedly, small species became larger in islands with low productivity, perhaps because increased intraspecific competition favors large individuals under the high population densities that reptiles often attain on islands[44,45].

Overall, most amphibians tended to gigantism, which may be the result of either an increased growth rate or a lower mortality[46] due reduced predation pressure in islands. Interestingly, we found that the 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 (e.g., during aestivation or hibernation[47], i.e., "starvation resistance hypothesis"). In turn, we did not find a clear relationship between precipitation and body size (i.e. "water availability hypothesis"). It seems thus that amphibian gigantism in islands is mostly driven by physiological mechanisms that maximize growth rate, and that this could be exacerbated in smaller, isolated islands (Fig. 4d). 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 solely on extant species for which we could gather data on measurement error and sample size (essential for meta-analyses). The widespread extinction of large species in islands, including dwarf morphotypes of large species such as insular elephants in Sicily and the

Aegean islands[48,49], may have masked the pattern, making it harder to detect a signal[50]. Giant insular birds[42,51], primates[52,53], lizards[54], and large insular turtle species went extinct during the Holocene and late Pleistocene[55], most likely because of overhunting by humans and the introduction of invasive species[56,57]. Overall, it is estimated that 27% of insular endemic mammals have gone extinct since human colonization of oceanic islands[58], and that the loss of birdlife in the Pacific islands may exceed 2000 species[59], mostly large-bodied, flightless, ground-nesting birds[56]. Extinct species may shed more light on the patterns and processes of size evolution in insular vertebrates because species extinctions have substantially altered the biogeography of body size in island faunas. Indeed, present-day body size may reflect the selective pressure on larger individuals, leading to downsized insular communities[60,61]. For example, the bias of our dataset towards smaller-bodied organisms could reflect the extinction of large species on islands[56], or the fact that few islands support large species in any case. Altogether, this suggests that analyses based on present-day patterns may somewhat bias our perception of the rule and scaling coefficients, and that including extinct species would strengthen the signal that we already report for extant species[30].

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 novel 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[62,63]. In theory, as the Anthropocene gathers pace, further extinctions will drive a decline in the 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 referred to 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[33,34,36]. 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[64,65].

Methods

Data collection

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[32]. In this sense, the general application of the island rule to a wide range of taxonomic groups would be problematic. We have overcome this problem by going back to the original sources, with measurements taken and reported in the period 1895-2019, many years before the island rule hypothesis was even postulated in 1964[1]. Specifically, we collected data from articles included in the recent assessment of the island rule[24], tracing original data sources when possible to extract original measurement data. We also reviewed the literature included in previous studies of reptiles[16], mammals[6], and birds[12], and excluded comparisons that were not supported by taxonomic or phylogenetic evidence and added others that were omitted. Additionally, we performed a literature search 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*). The first 300 hits (ordered by relevance) were checked and included if they contained relevant measurement data (i.e. for insular populations or, preferably, for both insular and mainland populations). Unpaired insular populations were matched when possible by performing species-specific searches of adjacent mainland populations in WOS and Google Scholar. Any study reporting morphometric measurements in insular populations was included regardless of whether it tested the island rule

or not, thereby avoiding comparisons that were based on species with well-known extreme body sizes only. We also included museum and live specimens that were for the first time measured and used to test the validity of the island rule in this study.

We collated published data on body size (body mass, body length and cranial and dental measurements) of different taxa in island and mainland populations following morphological (same body size index for island and mainland populations), phylogenetic and geographic criteria. When more than one body size index was reported in published studies, we gave priority to different indices for different taxonomic groups. For mammals, we selected indices in this order of preference: body mass, body length, cranial length (skull length or condylobasal length), and dentition (e.g. 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 (SVL), carapace length (CL, for turtles) and total length (TL, including SVL and tail length). To avoid size biases attributable to sexual size dimorphism, we calculated the population mean body size by averaging male and female means. Alternatively, we compared size of mainland and island populations for males or females only if information for the other sex was not available. We included measurements for adults only. As different authors reported size using different indices, island and mainland size were converted to body mass equivalents using published allometric relationships (see Supplementary Table 2). If allometric relationships were not available, we derived them based on published datasets or data extracted from the literature[38,66-72]. Calculated allometric relationships were derived using OLS or PGLS of the $\log^{10}$ transformed body mass against the $\log^{10}$ transformed body size index (e.g. condylobasal length, data available at https://github.com/anabenlop/Island_Rule).

Island populations were compared to conspecifics from adjacent mainland populations. In the case of island endemics, we compared island populations to their closest mainland relative (i.e., sister species) whenever these were identifiable by phylogenetic data or other information reported in each particular study. 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 (see[6,7]). 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.

We complemented measurements from literature for birds with standardized wing-length measurements from 3,229 museum specimens and 462 live specimens of 448 insular and 413 mainland bird species (see[73,74]). We used wing length instead of tarsus length, which is often used as single proxy of overall body size[75], because the former is a better predictor of body mass (R^2_{wing} = 0.89 vs R^2_{tarsus} = 0.69, Table S2) (see also[76]). Using tarsus instead of wing length did not change our results (Fig. S1). To select suitable comparisons for museum specimens, we first classified species as either insular or continental by overlapping IUCN range polygons with a GIS land layer including continental land masses. For each insular species we then identified continental sister species from avian phylogenies, choosing the geographically closest species in the case of polytomies. We excluded pelagic and highly aerial birds (e.g. swifts) because in these groups it is unclear whether insular and mainland forms experience different environments[12]. Further, we also excluded flightless bird species, because morphological changes may be due to flightlessness rather than island dwelling per se[12].

We calculated the response ratio (*RR*, eq. 1) as effect size in our meta-analysis, where we divided the mean body mass of individuals from an insular population $\bar{M}_i$ by that of individuals from an ancestral mainland population, $\bar{M}_m$, and then applied the natural logarithm. Unlike unlogged ratios, the sampling distribution of *RR* is normal, particularly for small samples[27], thus avoiding possible statistical problems and artefacts associated with regressions using ratios.

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

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. Means were calculated as pooled means of adult male and female mean body sizes. Data from

zoos or studies that could not be georeferenced were discarded. SD and sample sizes were used to weight each response ratio by the inverse of the sampling variance (Eq. 2).

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

SDs were extracted from raw data when possible. If ranges were provided instead of SD (or SE or CV), we calculated SD following[77]. If neither ranges nor measures of variation were reported, we imputed SD based on the coefficient of variation from all complete cases ("Bracken approach"[78]). Imputation was done for 26% of all cases in mammals, 1.2% in birds, 14.3% in reptiles and 7.7% in amphibians, thus for < 30% in all cases[79]. We excluded all cases when only one individual was measured in either mainland or island and thus the SD was zero.

We additionally extracted per study and island-mainland comparison the mainland and island names, the study identity, the type of size measurement, 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/), the Threatened Island Biodiversity Database (TIB, http://tib.islandconservation.org/) or were calculated using Google Earth. Additionally, we extracted the Normalized Difference Vegetation Index (NDVI) as a proxy for resource availability in islands[80]. We also calculated the standard deviation of NDVI to assess the 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[81]). Specifically, we used variables that are more closely associated with the proposed underlying mechanisms of Bergmann's rule (i.e. thermoregulation and starvation resistance): mean annual temperature, annual precipitation, and seasonality of temperature and precipitation[82]. 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 (i.e., after the last glacial maximum; see also[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 (e.g., temperature, NDVI, precipitation, etc). Finally, for each species included in our database, we collated diet information for each species from EltonTraits for birds and mammals, and from other sources for reptiles[71,83], and classified species as carnivores (> 50% diet consisting of vertebrates) or non-carnivores. As amphibians are mostly carnivores[84], we did not record their diet.

Data analyses

We used phylogenetic meta-regressions between *RR* and body mass of the mainland population (common ancestor) to test the island rule hypothesis. If the island rule holds, we would expect the slope of the relationship to be negative (Fig. 1). Body mass was used as predictor in these analyses to allow cross-taxa and cross-study comparisons.

Use of multiple populations of the same species can overestimate the actual number of degrees of freedom, enhancing 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 implemented phylogeny as a correlation matrix derived from an ultrametric phylogenetic tree and assuming the Brownian model of evolution. The species term captures the similarities of effect sizes within the same species, while the phylogenetic term represents the similarity due to common ancestors[85]. We also added ‘Study’ as a random effect intercept to account for between-study variability and the fact that we had multiple response ratios per study. In some cases, ‘Study’ 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-analytic model[26]. We partitioned the variance among the random factors by calculating the amount of heterogeneity explained by each factor relative to the total heterogeneity I^2 that is not attributed to sampling error[86]. Because we had multiple comparisons between island populations and one mainland population (common comparison) that might inflate precision in the estimates,

we modelled such dependencies by computing a variance-covariance matrix[87]. For comparison we ran models excluding sampling variance, assuming equal precision in body size measurements and report the results in SI.

Testing ecological hypotheses explaining insular size shifts

We evaluated different well-established ecological hypotheses that may explain insular size shifts. Specifically, we tested the ecological release hypothesis (island size, which act as a proxy for number of predators and competitors), the immigrant selection hypothesis (island isolation), the resource limitation hypothesis (productivity and diet), and the thermoregulation, water availability and starvation resistance hypotheses (climatic variables) (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, producing different patterns for small, medium-sized and large species. Specifically, we expected the slope of the relationship to be steeper in smaller islands, isolated from the mainland and with 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 in 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 dwarf species. Because amphibians are generally small-sized, we also fitted an additive model where seasonality in resources would result in larger body sizes for all species. Finally, mean temperature was expected to affect differentially small species in cold islands which, compared to similar-sized species in islands with a mild climate, would exhibit more pronounced gigantism to enhance heat conservation. Similarly, large-bodied species would become smaller in warm islands than in cooler islands. We also tested if species across the whole body mass range would respond similarly to temperature by using temperature as an additive term where the slope of the relationship does not change but the intercept does.

Prior to the modeling, all the predictors 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[88]. We present all figures displaying the size response ratio – mass relationship, and how this might be altered by the mechanisms explained above.

All analyses were performed in R 3.5.3[89] using the packages *metafor*[90] and *metagear*[79] for the meta-regression models and data imputation, *ape*[91] for estimating branch lengths and resolving polytomies, *rotl*[92] for building the phylogenies for our species by searching the Open Tree Taxonomy[93] and retrieving the phylogenetic relationships from the Open Tree of Life[94], *sf* [95] and *raster*[96] for spatial analyses, *dplyr*[97] for data manipulation and *ggplot2*[98] for data visualization. ArcMap 10.5 was used for Figure 2. All data and code are available at https://github.com/anabenlop/Island_Rule. Silhouettes in figures were extracted from 'phylopic' (https.phylopic.org).

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