A simple null model predicts the island rule

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Abstract

The island rule is a putative pattern in island evolution, where small species become larger on islands and large species become smaller. Despite decades of study, a mechanistic explanation for why some taxonomic groups obey the island rule, while others do not, has yet to be identified. Here, we explore whether the island rule might result from evolutionary drift. We derived a simulation model that predicts evolutionary size changes on islands based on random evolutionary trajectories along bounded trait domains. The model consistently predicted the island rule and could account for its occurrence in plants inhabiting islands in the Southwest Pacific. When support for the island rule was not detected, insular gigantism was often observed, suggesting that natural selection was at work. Overall results indicate that evolutionary drift can provide a parsimonious explanation for the island rule, suggesting future work should focus on circumstances where it does not occur.

KEYWORDS
body size, convergent evolution, dwarfism, evolutionary drift, gigantism, size diversity, trait evolution

INTRODUCTION

Island environments drive predictable trends in the evolution of island organisms (Burns, 2019; Carlquist, 1974). The 'island rule' (Foster, 1964; Lomolino, 1985; Van Valen, 1973) is arguably the most repeatedly documented, yet heavily debated, of these trends. It describes a graded trend in island evolution, whereby small species evolve to become larger, and large species evolve to become smaller, and has found support in vertebrates (Benton et al., 2010; Boback & Guyer, 2003; Bromham & Cardillo, 2007; Clegg & Owens, 2002; Heaney, 1978; Lomolino et al., 2013; Nolfo-Clements et al., 2017), invertebrates (McClain et al., 2006; Palmer, 2002) and plants (Biddick et al., 2019; Burns, 2019). However, many other studies have not found support for the island rule (Lokatis & Jeschke, 2018; Meiri et al., 2008; Meiri et al.,

2006; Meiri et al., 2009). Yet why species obey or disobey the island rule remains an evolutionary mystery.

Many mechanistic hypotheses have been formulated to explain why evolution might favour intermediate body size in island organisms (Case, 1978; Palkovacs, 2003; see discussion in Lomolino et al., 2017). Most invoke natural selection arising from differences in the ecological or environmental conditions of islands relative to continents (e.g. competition, predation or resource availability). For instance, because many predators are absent on isolated islands, release from predation could drive species to converge on their more 'optimal' body size (Lomolino, 1985; Sondaar, 1977). For organisms whose dispersal abilities increase with body size, the filtering effect of colonising isolated islands may naturally select for the largest individuals (immigrant selection, Lomolino, 1984, 1985).

Alternatively, evolutionary size changes in island organisms may not always arise from natural selection. Evolutionary drift, resulting from random mutation, recombination and founder effects, could be an alternative driver of evolutionary change (Jensen et al., 2019; Kimura, 1984). However, the potential effects of drift on patterns in insular size changes such as the island rule have largely been ignored.

Prior explanations for the island rule are deterministic in nature. The role of stochasticity has not been considered in island rule research, even though stochastic processes might generate patterned variation in both the ecology and evolution of island organisms. For example, latitudinal and elevational distributions of species richness often exhibit mid-gradient peaks. These peaks have long been attributed to environmental gradients. However, Colwell and Lees (2000) demonstrate that mid-gradient richness peaks can arise passively due to shared boundaries that constrain the distribution of species' ranges, even when environmental gradients are absent ('mid-domain effect'). Similar boundary effects have been demonstrated in the study of functional trait distributions (Denelle et al., 2019). In particular, Cope (1896) recognised that that evolutionary drift can explain the evolution of increased body size of related species along geologic time scales. 'Cope's Rule', as it has come to be known, can result from evolutionary drift, if the founders of monophyletic linages had relatively small body size and subsequent species randomly drifted away from the lower physiological limit of the lineage (see Gould, 1997).

Islands tend to house fewer species than similar sized sampling areas on the mainland (MacArthur & Wilson, 1967; Rosenzweig, 1995). As a result, the relative importance of species interactions such as competition, predation, parasitism and herbivory, which may select for differences in body size on the mainland, are commonly assumed to be reduced on islands (see Whittaker & Fernández-Palacios, 2007). Once released from these selection pressures, island species may be more heavily influenced by evolutionary drift.

Here, we test whether the island rule might arise from evolutionary drift along bounded trait domains. First, we derive a simple null model to predict evolutionary size changes in island organisms based on drift. We then explore how the predictions of this model vary across different timescales by allowing species to drift via incremental steps per generation. Finally, we apply the model to an updated dataset on plants inhabiting small islands in the Southwest Pacific. Results are used to answer three questions: (1) Can simple stochastic processes generate the island rule? (2) Does drift provide a parsimonious explanation for previously reported evidence for the island rule in plants? (3) When the drift model fails, and evidence for the island rule is not observed, is there evidence for convergent, directional size changes?

METHODS

We derived a simple null model to predict how insular size changes might arise from evolutionary drift (Figure 1). The model begins by establishing the range of body sizes displayed by a group of potential island colonists on the mainland (i.e. mainland 'trait space'). The body size of a hypothetical island colonist is then chosen at random from within this trait space, between minimum (*min*) and maximum (*max*) potential body sizes. The island colonist is then allowed to drift evolutionarily to a new, random location in trait space. Under these conditions, the probability of gigantism [$P(G) = (max\text{-}i)max^{-1}$] and the probability of dwarfism [$P(D) = (i)max^{-1}$] sum to unity and vary linearly with a species' original position in trait space (i.e. before it colonised the island from the mainland). When this process is iterated for a suite of related species, in a process akin to 'regression to the mean' (Barnette et al., 2005), the island rule always arises by chance with the probability of dwarfism increasing with initial (mainland) body size, and the probability of gigantism declining with initial size.

The model makes five assumptions in predicting body size evolution on islands (it makes no predictions concerning the evolution of mainland body sizes). First, species drift at the same rate to a new point in trait space following island colonisation. Second, all species have an equivalent amount of time to evolve. Third, there is no gene flow between island and mainland populations following island colonisation. Fourth, island species are bounded by the same range of body sizes as the mainland. Lastly, insular size changes are not under natural selection.

To ensure that the above model is not unrealistic by allowing species to drift to any point along their respective domain, and additionally to explore how predictions vary when drift is allowed to operate for differing amounts of time, we developed a second null model that allowed species to drift via stochastic incremental steps for differing amounts of time (Figure 2). Much like the first, the second simulation begins by establishing a range of body sizes (1–100 arbitrary units) for a group of 100 related species on the mainland. Each species was then allowed to drift via stochastic incremental steps (+1 or −1 per generation) within this bounded domain for a given number of generations. Insular size changes were simulated in this way over 100, 500, 1000 and 5000 generations.

To test whether this null model approach could predict the island rule in plants, we analysed a modified version of our previously published dataset on plants (Biddick et al., 2019). These data come from isolated islands in the Southwest Pacific, whose floras were derived by long-distance dispersal from New Zealand or Australia. To promote conformity to the assumption of no island-mainland gene flow, we removed measurements from Tuhua (Mayor Island) in the updated dataset, which was
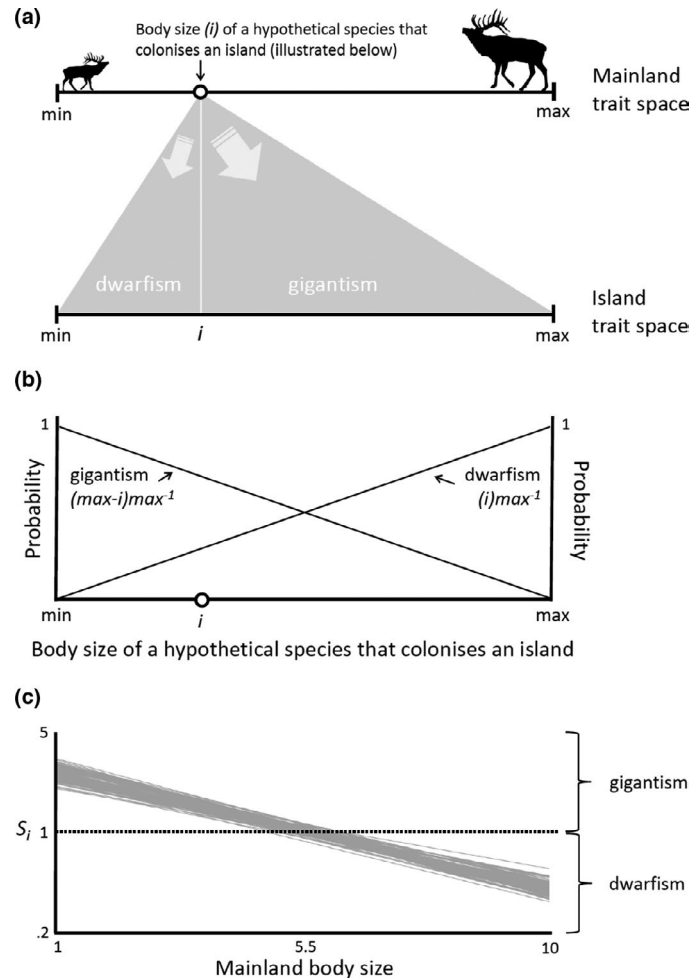
FIGURE 1 A simple simulation model illustrating how the island rule can arise from evolutionary drift. The upper horizontal line in (a) represents the range of body sizes for a given group of organisms on the mainland (i.e. 'trait space'). This might represent body mass, carapace length, plant stature or any other trait. The point labelled (*i*) represents the hypothetical body size of a species that colonises an island from the mainland. Assuming that island trait space is equal to that of the mainland, yielding the lower horizontal line in (a), the relative area of each grey triangle represents the relative probabilities of becoming smaller or larger on the island via evolutionary drift. (b) illustrates the probabilities of insular gigantism and insular dwarfism given different initial (mainland) body sizes. (c) illustrates the results of simulated relationships between evolutionary size changes (*y-axis*) and mainland body sizes (*x-axis*) for a group of related species. During each simulation replicate, initial body sizes for 100 species were drawn at random from the mainland trait space. Each species was then allowed to drift to a new location randomly, and the corresponding line of best fit between insular size changes (S_i, island body size ÷mainland body size) and mainland body size was then plotted as a grey line. This procedure was iterated 100 times, each resulting in a negative relationship between insular size changes and mainland body sizes (i.e. the 'island rule')

the least isolated island in the dataset (30 km from the North Island of New Zealand).

Data were split into two lifeform categories (woody & herbaceous [i.e. 'forbs', excluding graminoids]), and three trait categories (stature [$n = 85$], leaf area [$n = 118$] & seed size [$n = 85$]) and were each analysed separately ($n = 6$ life form x trait groupings). We then tested for evidence of island rule by regressing insular size changes (S_i, island size estimate ÷mainland size estimate) against mainland values (*M*), following Lomolino et al., (2013). Alternative statistical tests for evidence of the island rule are available and may be more appropriate under certain circumstances (see Welch, 2009), but we chose this method because we later use our drift model to predict insular size changes, regardless of whether S_i values

decline with *M* values. Both variables were logarithm transformed prior to analysis.

We then generated expected island size changes under evolutionary drift as described in Figure 1. However, rather than selecting mainland values from a uniform random distribution, simulations began with empirical estimates of mainland body sizes, which were assumed to reflect ancestral states (see Welch, 2009). To conform to the assumption of equivalent trait domains between islands and the mainland, we subsequently selected island trait values from a probability density function fit to observed frequency distributions of mainland trait values. For each analysis, mainland domains were bound by the minimum and maximum observed values in the dataset, regardless of geographical origin [e.g. we did
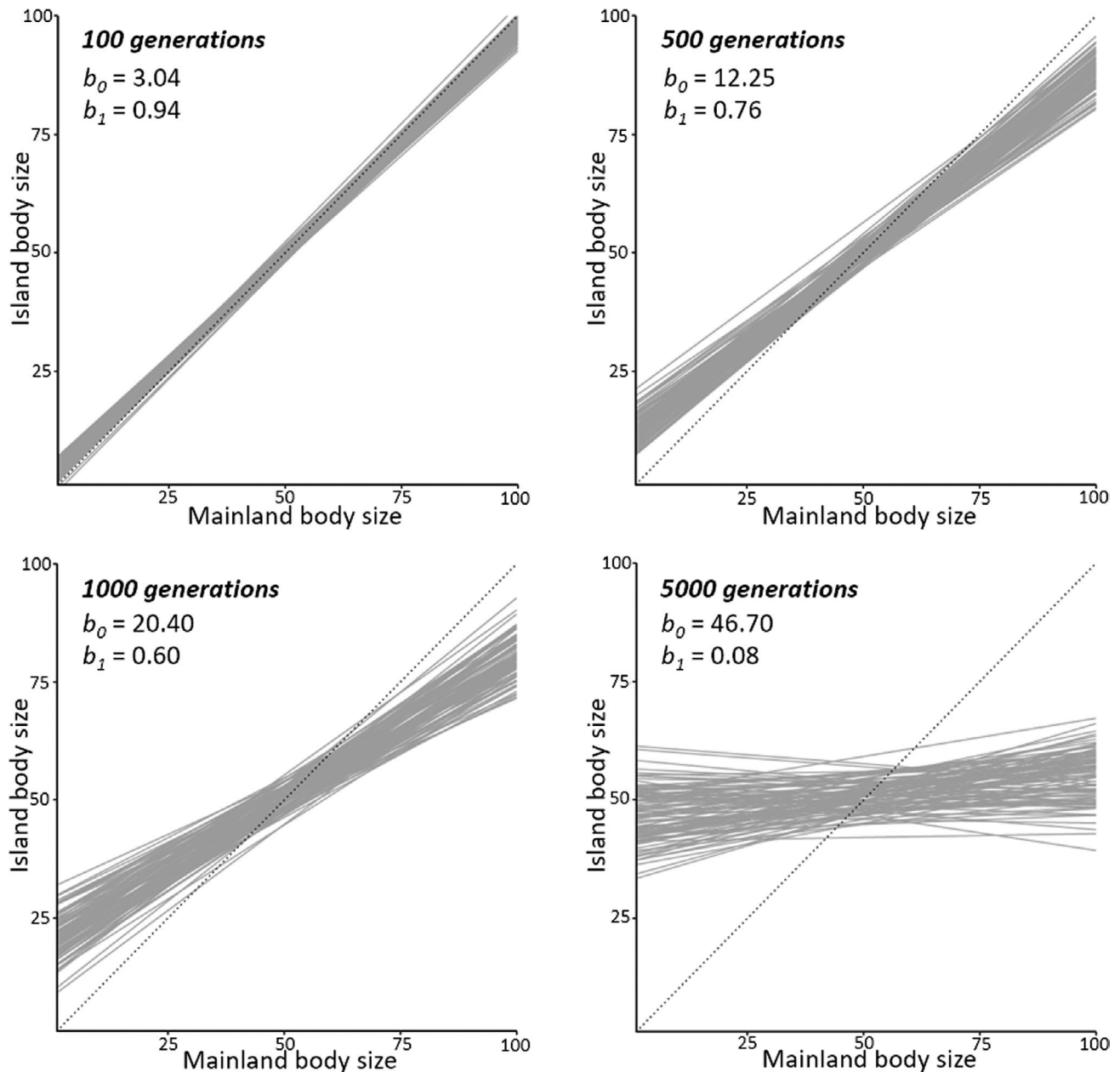
FIGURE 2 Simulated relationships between island (*y-axis*) and mainland body size (*x-axis*) in a group of 100 related species. Initial body sizes were chosen randomly from a domain bounded between 1 and 100 (units arbitrary). Each species was then allowed to drift via single incremental steps (+1 or −1 per generation) for a given number of generations, and the corresponding best fit between island and mainland body size was then plotted as a grey line. This procedure was iterated 100 times at 100, 500, 1000 and 5000 generations. The mean slope (b_1) and intercept (b_0) are denoted in each panel. Black, dashed lines denote isometry

not fit separate density functions for New Zealand and Australia]. Probability density functions were derived using the kernel density function in the *msm* package in *R* (Jackson, 2011; R Core Team, 2018). Observed S_i values were then regressed against expected S_i values using simple linear models. This process was then iterated 1000 times to obtain average p and r^2 values for the six trait x life form groupings, as well as for each trait across all life forms. All variables were logarithm-transformed prior to analyses.

Lastly, we tested for convergent patterns in gigantism or dwarfism in all nine trait x life form categories described above. Island and mainland trait values were compared using unequal variance paired t-tests (i.e. Welch's *t*-tests). All analyses were conducted in the R environment (R Core Team, 2013). The *dplyr* package (Wickham et al., 2015) was used for data manipulation, *ggplot2* (Wickham, 2016) for data visualisation and *purr* (Henry & Wickham, 2019) for modelling across nested datasets.

RESULTS

Our simple null model consistently predicted the island rule. When a suite of hypothetical species were allowed to drift to a random point within their respective domain, hypoallometric relationships between island and mainland body sizes were observed (i.e. slopes less than one, Figure 1c). When species were instead allowed to drift via incremental steps over varying generation times, mean best fit curves with slopes less than one were similarly observed. Under these conditions, the island rule pattern became more evident when species had drifted over greater numbers of generations (Figure 2).

Analogous results were obtained using empirical data. In all nine trait x lifeform categories, our null model predicted negative relationships between insular size changes and mainland trait values (depicted as grey lines in Figure 3). Most trait x life form categories (all three stature comparisons and two leaf area categories) showed empirical support for the island rule (Table 1, Figure 3). In each of these cases, insular size changes were predicted statistically by the drift model (Table 1). The four remaining categories showed no support for the

island rule (all seed size categories and leaf area in forbs), and the null model failed to predict insular size changes.

Three of the four trait x life form categories that did not show support for the island rule (all but seed size in forbs) showed a different evolutionary trend – convergent insular gigantism (Table 1). One final category, seed sizes in forbs, showed no patterned differentiation in insular size changes. It showed no evidence for the island rule, the drift model failed to predict size changes on islands, and no support for convergent patterns in either gigantism or dwarfism was observed.

DISCUSSION

Previous work has typically evoked natural selection to account for the island rule (e.g. Sondaar, 1977; Heaney, 1978; Lomolino, 1985). For example, larger size in small-bodied organisms may enhance resource acquisition, if larger size enables the capture of larger food items. On the other hand, because resources tend to be more limited on islands, smaller size in large-bodied organisms may evolve to reduce their energetic requirements (McClain
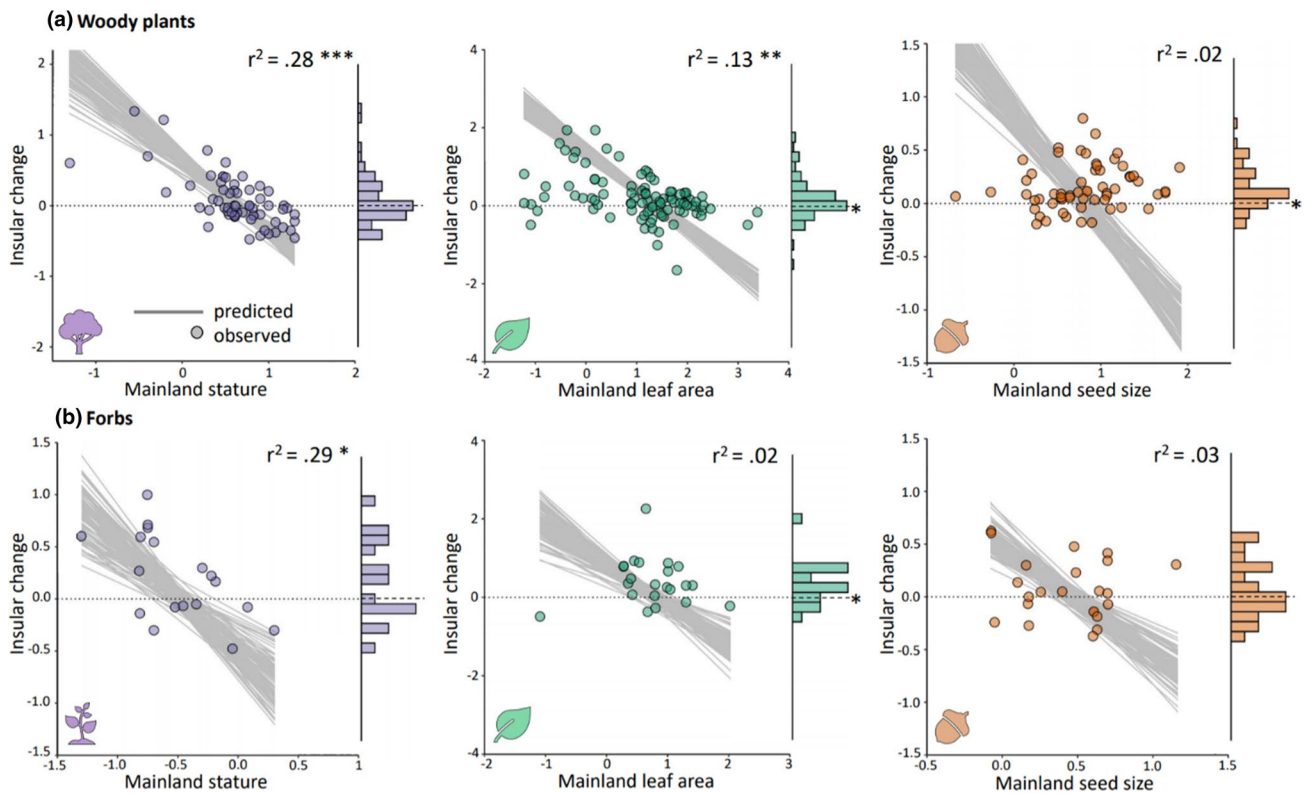

FIGURE 3 Relationships between insular size changes (island size estimates ÷mainland size estimates) and mainland sizes of plants inhabiting islands in the Southwest Pacific. Plant stature (m) is depicted in purple (left), leaf area (cm^2) is depicted in green (middle) and seed size (mm^2) is depicted in orange (right). Woody plants are shown above ('a') and herbaceous species are shown below ('b'). Grey curves represent expected relationships between insular size changes and mainland size estimates generated by the drift model ($n = 100$ replicates). Coloured circles illustrate empirical values. Dashed horizontal lines represent isometric relationships between island and mainland taxa. Vertical histograms are frequency distributions of Si values. Those with asterisks denote cases illustrating evidence of gigantism. All axes are logarithm$_{10}$-transformed

TABLE 1 Statistical analyses of insular size changes in plants inhabiting islands in the Southwest Pacific

Plant functional trait (n)	Support for island rule? Linear regression: $Log_{10}(S_i) \sim Log_{10}(M)$		Support for drift? Linear regression: $Log_{10}(S_{i\,observed}) \sim Log_{10}(S_{i\,predicted})$		Support for convergence? Paired t-test: $H_0: \bar{x}_I = \bar{x}_M$	
	b_I	p	r^2	p	t	p
Stature – All (84)	−0.319	< 0.001*	0.17	0.040*	0.036	0.971
Stature – Woody (66)	−0.530	< 0.001*	0.24	< 0.001*	1.442	0.154
Stature – Forbs (19)	−0.637	< 0.001*	0.37	0.007*	2.033	0.058
Leaf area – All (118)	−0.236	< 0.001*	0.15	< 0.001*	4.314	< 0.001*
Leaf area – Woody (95)	−0.247	< 0.001*	0.18	< 0.001*	3.33	0.001*
Leaf area – Forbs (23)	−0.001	0.994	0.03	0.459	2.986	0.007*
Seed size – All (85)	0.052	0.333	0.01	0.359	5.251	< 0.001*
Seed size – Woody (61)	0.057	0.260	0.02	0.257	5.625	< 0.001*
Seed size – Forbs (24)	−0.139	0.431	0.03	0.469	1.490	0.150

Categories of plant functional traits are shown in the first column along with sample sizes. Tests for evidence of the island rule, linear regression of insular size changes (S_i) against mainland values (M), are shown in the second set of columns. Tests for congruency between observed insular size changes ($S_{i\,observed}$) and predicted insular size changes by a simple drift model ($S_{i\,predicted}$) are shown in the third set of columns. Tests for unidirectional insular size changes (evidence for gigantism) is shown in the fourth set of columns. The drift model successfully predicted insular size changes when support for the island rule was observed, and it failed to predict insular size changes when it did not occur. Under these circumstances, convergent patterns of insular gigantism were often observed.

*Denotes statistically significant results.

et al., 2006). Islands also lack many types of predators that are common on the mainland, and reduced predation pressure may enable smaller bodied prey to evolve larger size. On the other hand, larger bodied prey may no longer benefit from their large size to fend off predators (Sondaar, 1977; although see discussion in Lomolino, 1985).

The island rule has only recently been explored in plants (Biddick et al., 2019). However, trends in plant evolution on islands have intrigued biologists for centuries. Darwin (1959) noticed that many trees endemic to oceanic islands evolved from herbaceous ancestors on continents. He reasoned that 'weedy' species are the first to colonize young oceanic islands and subsequently evolve into trees (the 'weeds-to-trees' phenomenon) due to competition for light (Darwin, 1959), or selection for increased longevity (Wallace, 1902), or shifts in preferred habitats (Carlquist, 1974). Darwin's hypothesis has since found support in several archipelagos (Baldwin, 2007; Böhle et al., 1996; Lens et al., 2013; Wagstaff et al., 2011). However, the 'weeds-to-trees' phenomenon cannot not explain why plants sometimes dwarf on islands. It also fails to explain why some plant traits conform to the island rule, but others do not (Biddick et al., 2019; Burns, 2016).

Results from this study suggest a parsimonious explanation for the island rule in plants. Although we only sampled a subset of total island floras, approximately half of our empirical analyses showed evidence for the island rule, which typifies previous work on the subject in animals. In all of these cases, our simple null model predicted a significant amount of variation in observed evolutionary size changes, indicating that simple evolutionary drift can provide a parsimonious explanation for insular size changes. However, correlation between empirical data and model predictions does not demonstrate causation and other explanations are possible.

Lomolino (2005) provides a similar, although slightly less parsimonious, explanation for the evolution of intermediate body size on islands. He argued that under reduced selective pressures promoting phenotypic divergence on the mainland (e.g. competition & predation), selection will favour the convergent evolution of 'fundamental' or 'optimal' body size on islands.

We intentionally made our null model as simple as possible, as a starting point to better understand how drift might promote patterns in the evolution of island organisms. Consequently, it makes a number of simplifying assumptions, which when violated are likely to compromise its predictions. First, our simple null model assumes that species evolve at similar rates. Adaptive radiations, which refer to the rapid evolution of closely related species, are common on isolated islands (Marques et al., 2019). Paradoxically, oceanic islands are also storehouses for relictual species (Roubik & de Camargo, 2012), some of which have remained unchanged for millennia.

This suggests that the assumption of similar rates of evolution may be frequently violated, thereby diminishing the drift model's capacity to predict insular size changes.

Second, it assumes that all island species have an equivalent amount of time to evolve, or in other words, species colonise islands at the same time. Because recent colonists have comparatively little time to evolve on islands relative to earlier colonists, differences in the time since colonisation is likely to generate heterogeneity in insular size changes in suites of similar species, even when they are evolving along the same trajectories. Cox and Burns (2017) show that time since divergence explains a small but significant amount of variation in insular size changes in the Chatham Island flora, providing direct evidence that this assumption can be unrealistic. Nevertheless, the null model still predicted a significant amount of variation in insular size changes in cases where evidence for the island rule was observed. Violations of this assumption may explain why it tended to predict less variable, steeper relationships between S_i and M was observed. Future work using dated phylogenies is needed to better understand how differences in the time since divergence among island species might affect patterns in insular size changes.

Our simple drift model also assumes no gene flow between islands and the mainland. Gene flow is likely to slow the divergence of insular species and could also influence the evolution of mainland taxa (Welch, 2009). Unlike the previous two assumptions, this assumption is unlikely to be seriously violated in our study. Our dataset was intentionally restricted to islands that are oceanic in origin and distantly located from the mainland, providing a severe impediment to pollen and seed dispersal. The assumption of equivalent trait domains between islands also seems realistic, although we lack evidence to demonstrate it directly.

Lastly, the model assumes that island traits are not under selection. Yet our analyses do not imply that selection is unimportant in island evolution. Critically, our null model is based on the premise that body size distributions are shaped by selection on the mainland. Species interactions, such as competition and predation, are likely to be more prevalent on the mainland, because mainland environments regularly support greater numbers of species (MacArthur & Wilson, 1967), and greater species diversity likely selects for greater heterogeny in body size distributions (see Lomolino, 2005). These selection pressures are relaxed on islands, because of their reduced species richness, opening the door for a stronger influence of evolutionary drift.

Few, if any, previously derived null models are entirely stochastic. For example, null model analyses of character displacement typically hold the smallest and largest species in constant (i.e. equal to empirical estimates) to ensure randomisation intervals are always equal to that observed (e.g. Marchinko et al., 2004). However, the sizes of the largest and smallest species in co-occurring assemblages are unlikely to be free from selection. Similarly, null model analyses of island co-occurrence patterns typically constrain row and column totals (i.e. species richness on islands and archipelago-wide occurrence patterns in species), which are likely to be shaped by deterministic processes such as competition, predation or trait mediated selection (see Gotelli & Graves, 1996). Our analytical procedure contains a similar amount of determinism, which arises from fixed maximum and minimum body sizes, which could be under selection. Trait boundaries are fundamental to our model and the island rule pattern would not emerge via drift without them. While it is possible to imagine a scenario in which trait domains are unbounded and body size is permitted to evolve freely without limitation, such a scenario would ignore the physiological limitations of biology.

Directional size changes in several plant traits also indicate that the assumption of no selection was often violated. While plant stature consistently obeyed the island rule and showed no evidence for a tendency towards gigantism, results for leaf area and seed size were different. Forbs consistently produced larger leaves on islands, regardless of their mainland (ancestral) size. Leaf area was also higher in woody plant species. However, in this growth form, increases in leaf size were higher in small-leaved species than they were for large-leaved species. These results suggest that selection can override the importance of drift in determining leaf size evolution on islands. Selection may favour increased leaf size for a variety of reasons, including differences in the climatic conditions on islands or changes in herbivore communities (see Burns, 2019). However, insular leaf gigantism remains an unsolved evolutionary riddle that awaits future study.

The size and shape of plants are known to vary strongly with environmental conditions. Light, water and nutrients can generate marked differences in leaf size and stature of genotypically similar plants. Using common plants grown in common gardens, Burns et al., (2012) found that patterns in insular size changes were not biased by environmental effects. However, this study was based on a small subset of the species considered here and future work would benefit from addressing how environmental conditions affect island–mainland comparisons of plant morphology.

Seed sizes were also generally larger on islands. However, seed gigantism was more pronounced in woody species than herbaceous species. Although they were unable to determine exactly why large seeds are advantageous on islands, Kavanagh and Burns (2014) show that differences in seed gigantism between growth forms are linked to dispersal mode. Forbs tend to be wind dispersed, which is likely to limit the evolution of larger, heavier seeds that constrain their dispersal potential. On the other hand, fleshy-fruited species that are dispersed by frugivorous animals are

freed from this constraint, allowing for greater evolutionary change in seed size. Fleshy-fruitedness is more common in woody plant species, providing an explanation for why seed gigantism is more pronounced in this growth form (see Burns, 2019).

Overall results from this study showed that a simple null model mimicking evolutionary drift across bounded trait domains consistently predicts the island rule in plants. Evolutionary drift might therefore provide a parsimonious explanation for the island rule in general. However, analyses also revealed a strong signature of selection in most plant traits that did not show evidence of the island rule. Under these circumstances, convergent patterns of trait gigantism occurred for reasons that await additional study.

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AUTHOR CONTRIBUTIONS
M.B & K.C.B conceived the idea. M.B. curated the data, wrote the code, and made the resulting figures. M.B & K.C.B. wrote and prepared the manuscript together.

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DATA ACCESSIBILITY
No new data were used.

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