The island rule: an assessment of biases and research trends

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The island rule: an assessment of biases and research trends

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Running header: Island rule

Abstract

Aim The island rule has been widely applied to a range of taxonomic groups, with some studies reporting supporting evidence but others questioning this hypothesis. To bring more clarity to this debate, we conducted a comparative analysis of the available literature, focussing on potential biases.

Location Worldwide

Methods We performed a systematic review to identify studies testing the island rule and translated these studies' outcomes, so that they follow a consistent approach. The studies were assessed for differences in their analysis of the island rule. We created an authorship network showing who published studies with whom on the topic and weighted the data based on co-authorship and number of publications.

Results We identified 143 relevant studies, finding a significantly lower frequency of supporting studies according to our consistent approach (50%) than the authors' own statements (59%). Two core-author groups could be identified with a strong publication record on the island rule. The first group has predominately published studies supporting the rule, whereas the other group has mainly published studies questioning it. According to a subsequent analysis excluding studies with a high risk of HARKing (hypothesizing after the results are known), the frequency of studies supporting the rule further dropped to 42%.

Main conclusions Empirical support for the island rule is low, especially for non-mammalian taxa and when using a consistent evaluation approach. Differences among studies in supporting versus questioning this hypothesis seem to be partly due to author-related biases. Methods to address potential biases in studying ecological hypotheses are urgently needed. We offer such a method here.

Keywords: author biases, author groups, hierarchy of hypotheses, island biogeography, island dwarfism, island gigantism, island rule

Introduction

The observation that species on islands are smaller or larger than their mainland counterparts has led to the formulation of the island rule which describes *"the tendency for a graded series of changes in the size of island vertebrate species in relation to mainland congeners, such that small-bodied species tend to get larger, and vice versa"* – definition from a standard textbook on Island Biogeography (Whittaker and Fernández-Palacios 2007, p. 346). The island rule was first formulated by Leigh van Valen (1973) who stated that *"the regular evolution of mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals"* (p. 35). These findings were based on a study by Foster (1964), who had described the tendency of several mammalian orders to be either larger (Rodentia) or smaller (Carnivora, Artiodactyla, Lagomorpha) when isolated on marine islands compared to related mainland populations. The island rule was fundamentally reshaped by Lomolino in 1985 (see also Heaney 1978), who had reviewed a similar but much larger dataset than Foster. He stated that *"[...] rather than describing characteristic differences among mammalian orders, the island rule should account for the graded trend from gigantism in the smaller species of insular mammals to dwarfism in the larger species"* (p. 4 in Lomolino 1985).

The definition of the island rule by Mark Lomolino (1985, 2005) has dominated research on this hypothesis. However, it has recently been challenged by Shai Meiri et al. (2004, 2008) who, consistently with Foster's (1964) original study on body-size evolution of islands, underline the importance of phyletic constraints. In turn, the number of publications on the island rule has increased rapidly, with over half of all studies published after 2005.

The island rule – a universal pattern across taxa?

Apart from studies on the island rule that focus on mammals (e.g. Meiri et al. 2006; Bromham and Cardillo 2007; Palombo 2009; Lyras et al. 2010; Rozzi and Palombo 2014), researchers have also applied and tested this general hypothesis for a number of other taxonomic groups, including amphibians (Montesinos et al. 2012), birds (e.g. Clegg and Owens 2002; Boyer and Jetz 2010), dinosaurs (Benton et al. 2010), fish (Herczeg et al. 2009), insects (e.g. Palmer 2002), molluscs (Welch 2010; McClain et al. 2006), reptiles (e.g. Boback and Montgomery 2003; Meiri 2007, 2008) and even plants (Burns et al. 2012). While it has been supported for enigmatic taxa such as spring tails (Ulrich and Fiera 2010) or cave-dwelling plant hoppers (Hoch et al. 2014), several studies have questioned the rule's validity, e.g. for lizards (Meiri 2007; Itescu et al. 2014; Runemark et al. 2015).

Dwarf or giant – size is in the eye of the beholder

An aspect that has led to confusion in studies testing the island rule is that the terms "large" and "small" in relation to body size of animals are often not explicitly defined (Meiri et al. 2005). A possibility to overcome this problem is to perform cladewide analyses comprising data of species that represent a large fraction of the size spectrum of the studied group: the strength and significance of correlations between the body sizes of the mainland populations and body-size ratios of island/mainland pairs (or alternatively the corresponding island population) can be analysed. This has been the method of choice when testing the general validity of the island rule for selected groups (Lomolino 1985; McClain et al. 2006; Meiri 2007; Meiri et al. 2008; Welch 2009; Itescu et al. 2014). Many studies, however, report changes in body size for single species or populations and then relate their observations to the island rule. Examples are found across taxa: insects (Pizzo et al. 2011; Hoch et al. 2014), fishes (Herczeg et al. 2009), amphibians (Montesinos et al. 2012), dinosaurs (e.g. Benton et al. 2010), birds (Mathys and Lockwood 2009), and a number of mammalian species including mice (Michaux et al. 2002), deer (Simard et al. 2008) and marten (López-Martín et al. 2006). When categorizing a species as “small” or “large”, many researchers rely on some sort of clade-specific and predefined reference point.

The agreement on a "threshold" beyond which species are either large (and predicted to decrease in size in insular environments) or small (and predicted to increase in size) is closely connected to the discussion about optimal body sizes and size-area relationships. This is because – in accordance with the island rule – insular environments select for body sizes closer to the optimal size of the focal clade, narrowing the size spectrum found on islands compared to the mainland (Brown et al. 1993; Damuth 1993; Fig. S1). The optimal body size is the size at which organisms of a given clade maximize their reproductive power (i.e. *"instantaneous rate of conversion of energy into offspring in a mature organism"*, Brown et al. 1993; see also Case 1978). Optimal body-size theory implies that large clades such as mammals have a fundamental size at which fitness is maximized (Raia et al. 2010). These fundamental sizes are the thresholds that define whether a species is small or large. Unfortunately, there is much disagreement about where to locate the optimal body size. For birds, the threshold is thought to lie between 70 and 120 g for adults (Clegg and Owens 2002), and Boback and Guyer 2003 found a body-length threshold of 1m for snakes. Most studies concerning this matter have focused on mammals: Brown et al. (1993) and Marquet and Taper (1998) estimated 100 g adult body mass, while the value is closer to 1 kg according to Damuth (1993) and the threshold for carnivores in Lomolino (1985) is about 2.5 kg. To avoid problems with unclear body-mass thresholds, Meiri (2008) performed tests for five different thresholds in mammals, ranging from 100 g to 10 kg. For a comprehensive review and critique of optimal body size theory see Raia et al. (2010).

HARKing: *Hypothesizing After the Results are Known*

When interpreting data and results, *HARKing* (Kerr 1998; Neuroskeptic 2012; Munafò et al. 2017) is a frequent phenomenon, i.e. researchers use observations as confirmation of hypotheses that were only formulated or thought of *after* evaluating the data. This approach is not necessarily problematic, as it can yield valuable and creative ideas and explanations. However, such post-hoc explanations need to be clearly labelled as such, as they otherwise lead to biases in the perceived overall support of a given hypothesis in synthesis studies. When researchers perform a study on body-size evolution but have not originally planned to test the island rule, they will probably not present their research results in the context of the island rule if the results are not in line with the rule (they might not even think about the rule). However, if in analysing their data, the authors realize that these are supporting a general hypothesis such as the island rule, they might include the island rule as an explanation for their results, and they might even present their whole study as if it had been planned as a test of the island rule from the beginning.

Goals of this study

Based on a systematic search of the existing literature, we identify relevant studies on the island rule. In addition to extracting the amount of support reported by the authors of the included studies, we apply a consistent evaluation method in order to compare the results across studies, even if they differ in their application of the island rule. The island rule has originally been formulated to describe mammalian patterns of body-size evolution on islands, but it has later been extended to a number of other taxa (see above). We therefore compared the amount of support for the island rule in different taxa. We further created an authorship network showing who published studies with whom on the topic and weighted the results based on co-authorship and number of publications, in order to reduce author-related biases and account for HARKing.

Methods

Literature search

A dataset of articles studying changes in body size on islands was created based on a systematic search in the Web of Science. This query was conducted on 27 August 2015 and yielded 1093 articles. The search term consisted of key words related to (1) the focal hypothesis (island rule) and two related phenomena (island effect and island syndrome) that in some cases include observations of size change comparable to the island rule and (2) islands and island-analogous places such as lakes or isolated valleys: "island rule" OR "island effect" OR "island syndrome" OR ((island* OR lake* OR oasis OR oases OR isolated valley*) AND (gigantism OR dwarfism)). The workflow of the dataset construction followed the recommendations of the PRISMA statement (Moher et al. 2009). Most of the non-relevant articles focused either on the so-called "small island effect" that addresses the relationship between area and biodiversity, or urban "heat islands". The remaining 376 articles were complemented by 11 studies identified by a reverse literature search using van Valen (1973) as a key reference, this time in Google Scholar.

We read these 387 articles to identify those that we considered to be relevant tests of the island rule. A study had to address changes in body size either on marine islands (n=112), marine paleo-islands (n=7), freshwater islands (n=4) or on island-like systems such as lakes, isolated mountains/habitats or caves (n=17). For the assessment of the island rule, the direction and magnitude in body-size change (or of a feature that permitted inference to changes in body size) had to be specified and the body-size distribution of the studied clade had to be accessible; this also included articles that did not explicitly refer to the island rule. Information on eco-evolutionary explanations for the observed changes in body size were included if available. A total of 143 articles fulfilled these criteria and were included in the dataset which is available as an online supplement to this article. A list of all articles that were analysed is found in Appendix 1.

Assessment of island rule support

Island rule support was extracted from the publications following the assessment of the original authors. In addition, an independent assessment of island rule support was carried out that was based on the mode of the body size distribution of the focal taxonomic group. We decided to use this approach for our independent assessment because it is the one that allows to include the main fraction of available studies (not because it would be a preferable approach). For this assessment, all studied species were grouped into their respective taxonomic group: mammals, birds, dinosaurs, reptiles, amphibians or arthropods. For each taxon, a value was set that defined if the body size of an animal, population or species was considered "small" or "large". This calibration value was equal to the mode in a body-size distribution of the respective taxon. "Small" animals were defined as those that are distinctly smaller than the calibration value, and "large" animals were defined as those that are distinctly larger (i.e. no overlap of the calibration value with the measured variance in body size of the focal population of a species). In this way, a consistent prediction of body-size change could be made. If the prediction matched the actually observed body-size change, the island rule was considered supported; if the observed body-size change differed from the prediction, the island rule was considered questioned; and if the results were ambiguous, that is if the results were partly supporting (e.g. for some of the islands, populations or species studied) and partly questioning the island rule, the study was categorized as undecided. Please note that this scoring approach differs from vote counting which is only based on significance values and has key weaknesses (Koricheva et al. 2013). A similar approach was applied by Jeschke et al. (2012) and Heger and Jeschke (2014).

Selected calibration values follow the grouping and size distribution published in O'Gorman and Hone (2012): extant mammals 100g, extant birds 30g, extinct dinosaurs 1000kg, squamate reptiles 10g (snakes 1m, following Boback and Guyer 2003 because the body size of snakes is usually measured as body length rather than body mass) and amphibians 1g.

As the island rule is only rarely tested in its entirety but typically applied for a one-sided change of body size, we discriminated several sub-hypotheses of the island rule according to the predicted direction of body-size change (dwarfism, gigantism, mixed). Also, not all studies were convertible to the mode-based assessment with calibration values for different taxa outlined in the previous paragraph. These were marked as "author calibration" in our dataset (n=32). They were classified as "supporting" the island rule if they reported an evolution of body-size distribution that followed the island rule as defined above (see Fig. S1); "questioning" if their findings were not in line with the predictions, e.g. if larger species were even larger on islands or vice versa in small species or if there was no observable change in size between mainland and island populations; and "undecided" if the results were ambiguous.

Authorship network

A network of all authors of the articles in the dataset was created using the open-source software gephi (Bastian et al. 2009). The network was based on two types of relationship: (a) scientists that had co-authored a paper and (b) scientists that named other scientists in the Acknowledgements of a paper. Relationships of type (a) are inherently non-directional and the direction of type (b)-interactions was ignored for the construction of the network. Linkage between authors by acknowledgement was not included in the statistical analysis and only done for visual purposes. Every node of the network corresponds to one author that had written one or several articles included in the present study. We compared the level of support for the island rule between the most productive author groups that published a sufficient number of articles, and we investigated if these groups differed in their methodological approach, the observed changes in size they looked at and their taxonomic focus.

Addressing HARKing

Since there is no way to identify HARKing if the authors do not write that their results were only connected to the island rule post hoc, it is hard to correct for it. Indeed, we are not aware of a previous study that has tried to correct for HARKing. We propose an admittedly crude correction that we applied to our dataset: In comparison to the original results, we performed a second analysis where we excluded all studies published by authors that had not published another study on that subject. Emphasizing that having published on the island rule only once does not disqualify any of the given studies per se, we expected this group of publications to be most susceptible to HARKing. Thus, we first aggregated and weighted the results by author group, where the weight was the square root of the number of studies published by the respective author group (following Willer et al. 2010; Zaykin 2011; Heger and Jeschke 2014); the aggregation was then done as follows: for each author group, the median level of support for the island rule of the papers that this group had published (both original author interpretation and mode-based assessment) was identified. In a second step, we accounted for HARKing by excluding author groups with only one publication on the topic.

Statistical tests were carried out in R, version 3.3.2 (R Core Team 2013). Kruskal-Wallis tests and Mann-Whitney tests (in R termed Wilcoxon rank-sum test with unpaired data) were performed using the stats-package from R, version 3.3.2, and G-tests using the R-package deducer, version 0.7-9 (authors: Pete Hurd and Ian Fellows).

Results

Support for the island rule is lower for a consistent definition of this hypothesis

The original authors of the studies in our dataset reported higher levels of support for the island rule overall than the more consistent assessment of the island rule outlined here (combination of mode-based assessment and author-calibration studies) (Mann-Whitney test, V = 5470, $P < 0.05$). Following the authors' original interpretation of their results, 59.4% of all studies supported and 25% questioned the island rule, with 15.6% being undecided. In comparison, the present study found only 50.4% of articles being supportive and 43.6% questioning the island rule, the remaining 6.0% of the articles being undecided (Fig. 1). There was no significant difference in island rule support between studies that had explicitly addressed the island rule as a hypothesis and those that tested comparable phenomena but did not explicitly mention the island rule (Mann-Whitney test, V = 1749, $P = 0.64$).

Island dwarfs & giants

Of those articles that gave clear information about the type of size change predicted (n=129), most studies only focused on one direction (i.e. dwarfism or gigantism, n=90). Very few included a mixed type of body-size change (n=12), and 27 articles used methods to test the island rule from which the necessary information to estimate mode-based support could not be derived, e.g. analyses of patterns of body size distribution. Support for the island rule differed significantly between types of predicted body-size change, both for the original authors' interpretation (Kruskal-Wallis-test, $Chi^2 = 9.52$; df = 4; $P < 0.05$) and this study's assessment (Kruskal-Wallis-test, $Chi^2 = 11.57$; df = 4; $P < 0.05$) (Fig. 2). Dwarfism was predicted by the largest number of studies (n=59), and it was the only type of prediction that was supported by more than 50% of both the original authors and the present study's assessment. Support for the island rule following the assessment of the original authors mostly differs from our assessment when comparing studies that look at mixed directions in body-size change.

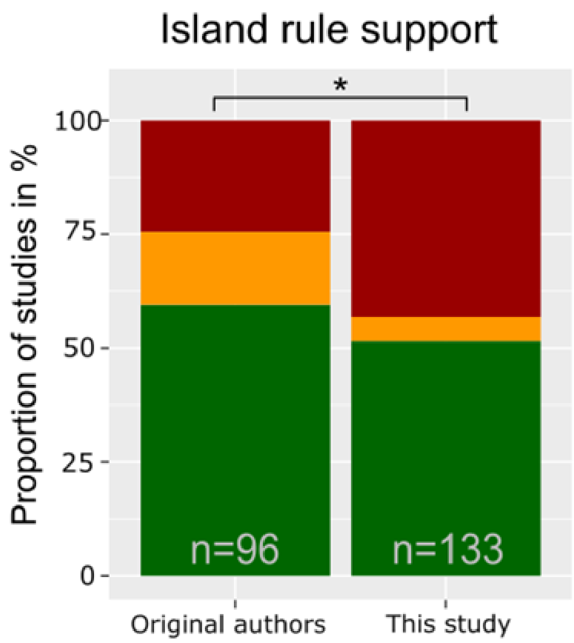

Figure 1 *Proportions of studies supporting (in green), questioning (in red) or being undecided about (in yellow) the island rule. Original authors: original author (OA) interpretations of the results of articles included in the present study. This study: re-evaluated results according to the criteria defined in the main body text (significantly different from OA support, p<0.05). Here, additional studies were considered where authors did not necessarily draw conclusions about the island rule themselves but that reported data to test the island rule; thus, the sample size is larger here.*

Taxonomic groups

Mammals, birds and squamate reptiles were the only taxa included in the comparison among taxonomic groups, as other groups had insufficient sample sizes. There were no significant differences in the level of support among taxonomic groups for the original authors' interpretation (Kruskal-Wallis-test, $Chi^2 = 4.89$; df = 2; n = 80; $P = 0.18$), nor for this study's assessment (Kruskal-Wallis-test, $Chi^2 = 2.69$; df = 2; n=114; $P = 0.44$). However, studies focusing on squamate reptiles tended to show a lower support than those on birds and mammals (Fig. 2).

Author groups disagree on island rule support

A network of authors was created that linked researchers if they had either co-authored a publication or acknowledged the other researcher in their publication. In this way, six fragmented networks connected by co-authorship were formed, each one comprising more than 10 authors (groups A-F in Fig. 3). These six groups were linked by acknowledgements between each other and additional interconnecting authors, leading to a larger network encompassing 169 out of 365 authors (Fig. 3). Those authors that are not linked to the core network by acknowledgements are arranged towards the periphery of the larger network in the centre of Fig. 3. In-depth analyses were restricted to the author groups A and B with a sufficient number of publications: group A (consisting of 24 authors) has published 15 articles in the dataset, and group B (consisting of 10 authors) has published 9 articles. The remaining four of the six groups have published between 4 to 6 papers each and were excluded from in-depth analyses.

These two author groups A and B significantly differed in how their publications supported the island rule; this was the case for the authors' original interpretation (G-test, G = 12.22, df = 2, $P < 0.01$) as well as this study's assessment (G-test, G = 10.24, $P < 0.01$). Note that Figure 3 shows the median value of island rule support for publications of every individual author, but the statistical analyses reported here are not based on these author-aggregated values but refer to the results of the individual publications of each author group. There were no significant differences between the studies performed by the two author groups regarding their approach (Table S1).

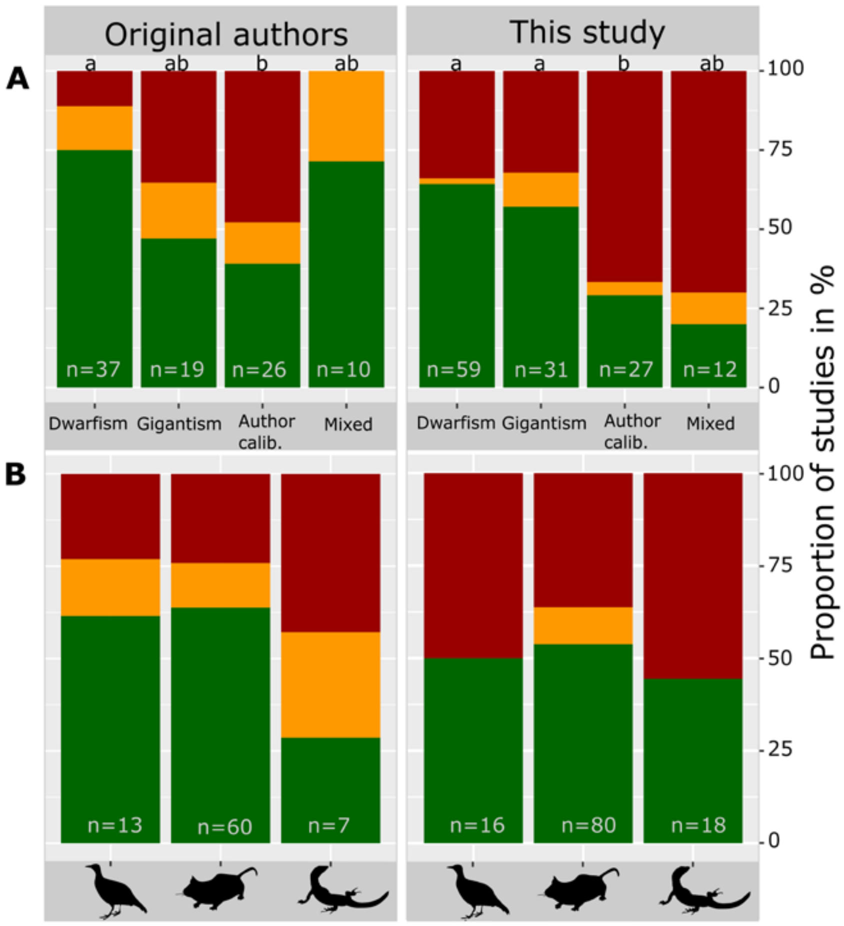

Figure 2 *Support for the island rule (original authors' interpretation and re-evaluated results according to the criteria defined here) for (**A**) different directions of predicted body-size change (dwarfism, gigantism, author calibration, mixed) and (B) taxonomic groups (mammals, birds and squamate reptiles). Supporting studies are in green, undecided studies in yellow and questioning studies in red. Letters indicate significant differences between bars (Mann-Whitney tests, p < 0.05).*

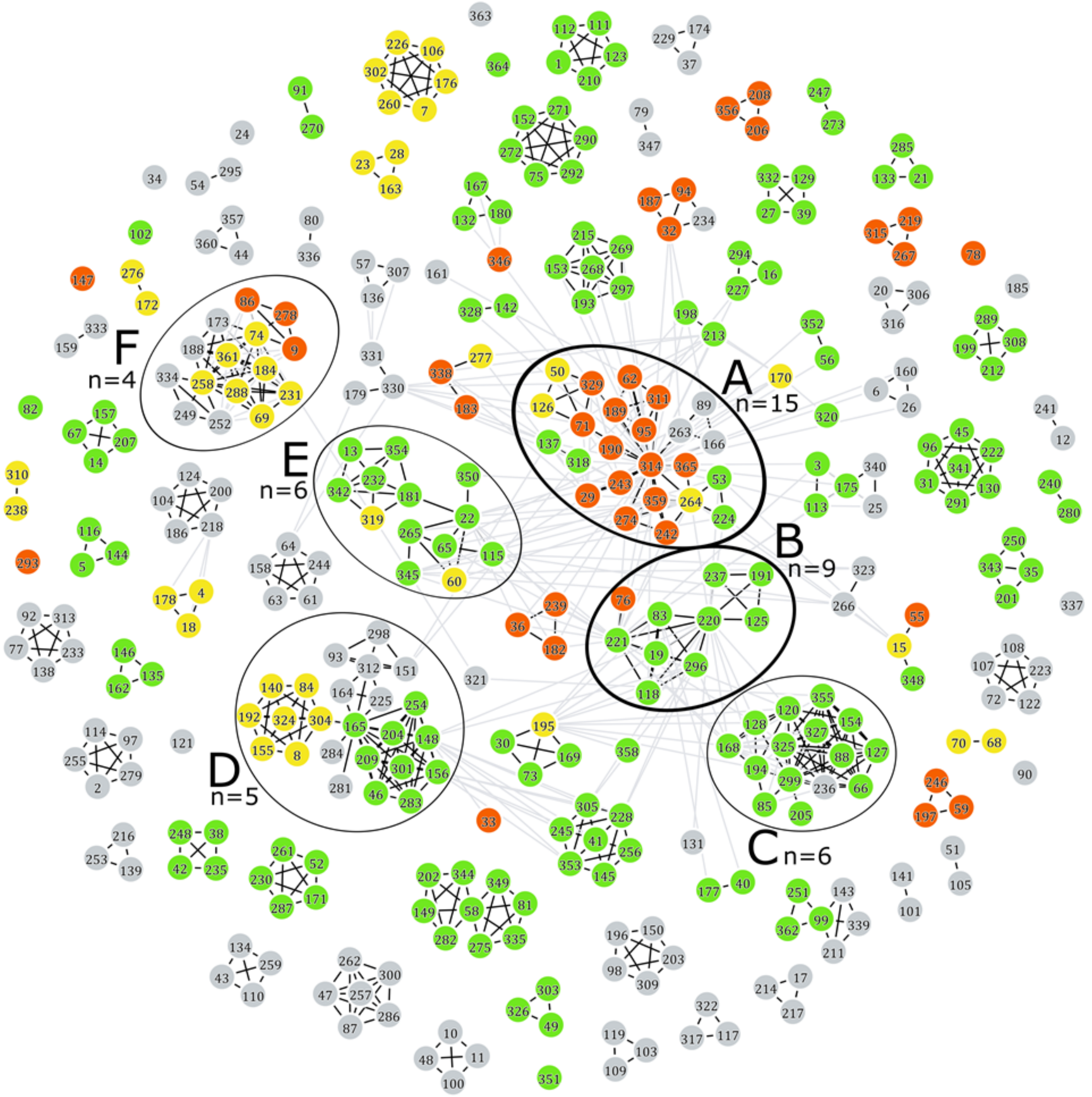

Figure 3 *Authorship network of researchers that have published articles on the island rule. Colours indicate that an author's studies are, according to the original author interpretation, largely supporting (in green), questioning (in red), or undecided (in yellow) about the island rule, taking the median across studies; grey (not assignable) was mainly due to authors not interpreting their results in light of the island rule. Each author was assigned to an anonymous ID number shown in the figure. Black lines connect authors that have co-authored a scientific publication. Grey lines indicate that one or both connected researchers have mentioned the other in the acknowledgement section of one of their articles. Black circles indicate the author groups that encompass at least 4 articles; n is the exact number of publications by each author group. Group A and B were selected for in-depth analysis (group A: 24 authors, 15 articles; group B: 10 authors, 9 articles).*

Author group-based weighting & HARKing

Given that the results of a study are not necessarily independent of the researchers conducting it, the sample size should be the number of author groups rather than the number of studies (see also Discussion). We thus re-analysed the data, this time aggregating the results of studies per author group and weighting each group by the square root of the number of studies it published (see Methods). This led to a slightly higher level of support for the island rule as compared to the unweighted results (Table 1). When addressing HARKing by excluding author groups that had only published a single study, support for the island rule dropped to 50% (original authors' interpretation) and 42% (this study) (Table 1). Groups that had only published a single study reported very high levels of support (74%, original authors' interpretation; 58%, this study's assessment).

For mammals only, the island rule was highly supported by the original authors when correcting for author groups (70%, Table 1). This correction is important here, as 6 of 14 studies in our analysis that question the rule for mammals are linked to author group A. The level of empirical support dropped to 57% even for mammals when taking this study's assessment, but it was still higher than for all taxa combined.

Table 1 *Island rule support for differently weighted data and consideration of author groups.*

a Unweighted data (cf. Fig. 1)

	Authors (n=96)	This study (n=133)
Questioned	25.0%	43.6%
Undecided	15.6%	6.0%
Supported	59.4%	50.4%

b Author groups, weighted by √n

	Authors (n=58)	This study (n=81)
Questioned	21.1%	42.0%
Undecided	13.9%	4.7%
Supported	65.0%	53.3%

c Author groups, weighted by √n & without single-studies groups

	Authors (n=18)	This study (n=18)
Questioned	28.8%	49.2%
Undecided	21.5%	8.6%
Supported	49.7%	42.2%

d Author groups, weighted by √n, mammals only

	Authors (n=34)	This study (n=48)
Questioned	20.5%	34.4%
Undecided	9.9%	8.2%
Supported	69.6%	57.3%

Discussion

Based on a systematic literature search, we identified 143 articles with relevant empirical data to address the island rule. We found that a consistent approach for assessing the level of support for the island rule yielded a significantly lower level of support than simply combining the original interpretations of authors. This evaluation of study results was done with a mode-based approach as outlined above. We have chosen this approach because it allows to include most available studies in the analysis. When picking a particular approach for an overall analysis, one needs to be careful not to introduce a bias caused by the approach. This does not seem to be the case here, as the level of support for the island rule was not lower for studies using a mode/threshold-based approach (gigantism, dwarfism, mixed) than for other studies (author calibration) (Fig. 2A).

Meiri et al. (2011) suggested that the *"[...] perceived pattern [i.e. extrema in body sizes on islands] may simply reflect an ascertainment bias, i.e. we may be more likely to notice animals of extreme body size when they happen to live on islands"* (p. 2). Similarly, Gould (1997) suspected Cope's rule of a general trend in body-size evolution towards organisms to be based on *"our tendency to focus on extremes that intrigue us, rather than full ranges of variation"* (p. 1). Our results indicate that part of the research literature on the island rule might indeed be prone to this sort of ascertainment bias and that the general application of the island rule to a wide range of taxonomic groups is problematic.

The island rule for different taxa: birds keep up with mammals

While the island rule was historically restricted to mammals, many studies are now available for other taxonomic groups, particularly reptiles and birds. The level of support for the island rule was very similar between birds and mammals, but a large fraction of studies questioning the rule in mammals stems from one author group. In an early study, Grant (1965) stated that in contrast to small mammals which are larger on islands, in birds only bill size and tarsus length tend to increase and that there is no decrease, respectively, as predicted by the island rule. Clegg and Owens (2002) extended Grant's dataset and found significant support for the island rule over a large number of avian taxa. The discrepancy can be explained by the taxonomic focus of the studies or the unfavourable use of wing size as a proxy for body size in Grant (1965) (Lomolino 2005). This is an important point, as the comparison between and within mammals, birds and reptiles (not to mention fishes, molluscs and insects) is complicated by the use of different proxies for body size.

Reptiles are in this respect relatively straightforward to include in a synthesis study, as their size is usually recorded as snout-vent length; this was the case for 14 of the 16 studies focused on squamate reptiles (excl. snakes) in our dataset. Many of these studies reported differences in body size of their focal taxon between mainland and island but did not test or explicitly refer to the island rule (7 out of 21). This might be an explanation for the altogether low support of the island rule in reptiles, as

HARKing was supposedly lower among these studies. However, further studies in various taxonomic groups are needed in the future to allow a real cross-taxonomic assessment of the island rule's validity.

Dwarfs & giants

Most of the articles in our dataset did not address the island rule in its broad sense but rather looked at either dwarfism or gigantism. In other words, they addressed sub-hypotheses (sensu Jeschke et al. 2012, Heger and Jeschke 2014) of the overarching island rule. Dwarfism has been studied more frequently than gigantism (Roth 1990; Losos and Ricklefs 2009; present study). In fact, and as mentioned above, the "rule of dwarfed island forms" (Kleinheit der Inselformen) pre-dates the island rule by far (Rensch 1924, who refers to F. Frech's formulation of 1908). Shai Meiri and colleagues even suspect that empirical support for the island rule has been inflated due to the focus on dwarfism in large mammals (Meiri et al. 2011). Indeed, comparing differences between studies focusing on dwarfism, gigantism and mixed decrease/increase, dwarfism was supported, whereas the latter showed lower levels of support.

During our analysis, we encountered another difficulty when trying to identify the direction of size change. This can be illustrated by the following example: The giant monitor lizards of Komodo are the largest lizards alive. Like many of their comparably large relatives, they cannot be found on the mainland. They are certainly larger than lizards "usually" are and as such do not follow the island rule which predicts that large-bodied taxa become smaller on islands (e.g. Meiri 2007). However, the inclusion of the fossil record, as did Hocknull et al. (2009), reveals that *Varanus komodoensis* might in fact be the small-bodied descendant of an even larger, mainland-based group (†*V. prisca* reached a length of up to 6m). In this light, the decrease in size from an even larger ancestral mainland population to the extant island-dwelling varanids follows the prediction of the island rule. This example shows that a thorough knowledge of phylogenetic relationships between the studied species is needed when investigating the island rule (see also Gould and MacFadden 2004).

Authorship networks

Over the past 50 years, teams of authors have gained predominance over individual authors in number and impact of publications in the natural sciences (Wuchty et al. 2007). The causes of this development are numerous (summarized in Katz and Martin 1997). To quantify patterns of collaboration in science, co-authorship has been used as a main indicator (e.g. Melin and Persson 1996; Newman 2004), and a network of scientific collaborations in a specific field of research can be illustrated by additionally including researchers mentioned in the Acknowledgements of publications (Cronin et al. 2003). This type of collaboration is also termed sub-authorship.

To identify core groups of scientific collaboration, we relied primarily on co-authorship, while sub-authorship connections were used for visual illustration. Co-authorship helped to identify several groups of authors but only two of them were large enough and had published a substantial number of articles relevant to the present study to be further analysed.

How well the island rule is supported depended strongly on the group of co-authors that performed a given study. This was shown for a comparison of the two most productive author groups. None of the studies performed by either of the two groups was affected by our mode-based reassessment, so the difference in support is only between the author groups themselves. Methodological aspects of their studies (taxonomic level, taxonomic focus, direction of body-size change, field vs museum vs literature studies, restrictions to mammalian datasets, corrections in statistical analyses, a focus on inter- vs. intraspecific change in body size) were similar and did not significantly differ between these groups. Of course, this does not mean that there are no methodological differences, however they are not as clear and apparent as the difference in level of empirical support reported by the two author groups.

Accounting for author biases and HARKing

Our findings suggest that the results of a study are not necessarily independent of the authors who performed the study. This result is ground-shaking for ecologists and other natural scientists who typically assume that there is no relationship between who performs a study and what they find. On the other hand, disciplines such as psychology or medicine have seen a frustratingly low level of study repeatability (e.g. Ioannidis 2005; Open Science Collaboration 2015). And we all know that some researchers tend to be in favour of certain important hypotheses in their field, particularly if they proposed a hypothesis themselves, whereas other researchers tend to disbelieve these hypotheses. Researchers are no robots and it seems naïve to assume that their identity does not influence the results of their studies.

If the outcome of studies depends on who performed them, the sample size in a synthesis of these studies should not be the number of studies but the number of author groups. Actually, however, we are not aware of a meta-analysis or other synthesis study that has done so. When doing so, it makes sense to assign higher weights for author groups with more publications. We did so here by using the square root of the number of publications. Rather than seeing this as the ultimate solution, however, we call for alternative suggestions how to deal with author-related biases. We hope this study motivates other synthesis studies on the island rule or other hypotheses in ecology and beyond that propose new approaches to account for such potential biases.

Another problem that is hard to address is HARKing (hypothesizing after the results are known). We propose the following mechanism leading to an unintentional bias due to HARKing: There are numerous ecological and evolutionary questions that biologists address on islands. If these biologists notice an unusual body size of their focal species on an island, there is a good chance that they will write a paper about that and publish their finding as support of the island rule now that they have found this result even if it was not their original intention to address the island rule. On the other hand, if they do not coincidentally notice an unusual body size, they will probably not write a paper questioning the island rule, since this hypothesis was never in their mind. This mechanism leads to a higher percentage of studies supporting than questioning the island rule, and it relates to researchers who not normally address this hypothesis. There are also researchers who have a strong interest in the island rule and regularly work on it. These researchers are predicted to publish a finding on the island rule independently of whether it is supporting or questioning it, as it is truly relevant to their work.

Based on this argument, we suggested as a first possibility to correct for HARKing to exclude studies done by authors who published only once on the island rule. We suspect these articles to be more susceptible to HARKing than articles of authors who had published several times on the topic. Of course, the big disadvantage of this approach is to exclude many studies with valuable results and to further reduce the sample size available for synthesis. It is a crude approach to control for HARKing and probably not the ultimate way to deal with this problem. We are thus calling for alternative approaches to control for HARKing. In any case, our results did show a higher support of the island rule by authors who only published once on it, thus supporting the above argument. Consequently, empirical support for the island rule dropped when correcting for HARKing according to the approach proposed here.

Conclusions & Outlook

Although we found differences in the level of empirical support for the island rule, it seems safe to conclude that only about half of the available empirical evidence is supportive, whereas the other half is questioning this important hypothesis of the field. This is basically what one can expect if the pattern is purely random, thus the island rule as currently used does not seem to be very useful. Its original definition by Lomolino (1985), however, that restricts it to mammals, is better supported.

Low values of empirical support have also been reported for other major ecological hypotheses, e.g. by Jeschke et al. (2012) for hypotheses about biological invasions. Also, Fox (2011) called for the identification of zombie ideas in order to move ecology forward. Hypotheses that are not empirically supported need to be revised or even abandoned. The island rule could be restricted to mammals, as it was originally formulated, or even to dwarfism, and there are other explanations for body-size changes on islands and mainlands. In fact, predator release, competitor release and resource limitation are ecological explanations for body-size changes that seem to be relatively well supported empirically (Supplementary Fig. S2 which was compiled with the studies in our dataset).

Finally, it is important to consider potential biases related to authors conducting studies and the effects of HARKing when synthesizing research. We have made relatively simple suggestions how they can be considered, but a broader discussion and alternative approaches are needed to cope with these and related challenges.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary Table S1 and Figures S1, S2

Appendix S2 Dataset collected for this study

Biosketches

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Author contributions: S.L. and J.M.J. conceived the ideas; S.L. collected and analysed the data; S.L. and J.M.J. wrote the manuscript.

Appendix 1 – Literature included in the analysis

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