

TECHNICAL NOTE

Minimal models provide maximally parsimonious explanations

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Abstract

We are delighted that Diniz-Filho et al. agree with the main premise of our paper, and we welcome their critique, as constructive debate will help foster a better understanding of size evolution on islands. Our perspective on each of their criticisms is discussed in greater detail below.

KEYWORDS

body size, dwarfism, evolutionary drift, gigantism, insular evolution, island rule, null models, parsimony

Diniz-Filho et al. take issue with several aspects of our study, the first of which concerns problems that arise when ratios are regressed against their denominator. We fully agree that there are problems with this approach. However, *'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'* (Biddick & Burns, 2021). We also did not rely solely on the analyses of ratios; we regressed island sizes against mainland sizes and assessed the corresponding regression coefficients while exploring the assumption of equivalent generation times. Continuing efforts to identify better statistical methods for testing the island rule are undoubtedly useful. However, they are tangential to the aims of our paper.

Next, they argue that our assumption of bounded trait domains is contradictory to the island rule phenomenon because *'the island rule is precisely about insular species evolving sizes outside the range of variation in the mainland'* (Diniz-Filho et al. 2012), and that *'phyletic size extremes are common in insular taxa'* (Meiri et al., 2011). However, the island rule does not focus on the evolution of size extremes *per se*. It actually describes the convergent evolution of intermediate body sizes on islands (Lomolino et al., 2012), which occurs when small species evolve to become larger, and large species evolve to become smaller. Furthermore, Meiri et al. (2011) conclude that it is a *'popular misconception*

that islands have more than their fair share of size extremes'. Size boundaries are an attribute of all life on earth, due to physiological limits to both small and large body size. Regardless of how trait boundaries are established, our simulations indicate that the island rule will always arise via drift, if given enough time.

Diniz-Filho et al. rightly argue that several factors associated with body size are relevant to the island rule. First, species-level variance in body size increases with body size itself. This may add to greater sampling error in the size of traits. However, all of our analyses were conducted on log-transformed axes, which should help equilibrate variance values. Second, the rates of evolution typically covary with body size, with larger animals evolving more slowly than smaller animals. We had yet to consider this factor, so we would like to thank Diniz-Filho et al. for pointing it out, and feel that it would be a worthwhile topic for future study in animals. However, it might not be as important in our particular application, as generation times are unlikely to vary with the size of plant organs (e.g. leaf area) as they do with the body size of mammals.

Lastly, Diniz-Filho et al. conduct four new analyses to investigate whether stochastic processes can generate the island rule. We applaud their efforts here and regret that we neglected to cite earlier efforts to model the island rule

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using neutral evolutionary processes (e.g. Diniz-Filho and Raia, 2017). However, it is important to note that they used a modified approach to our original model and applied it to an entirely different data set. Nevertheless, three out of four of their analyses predicted the island rule via stochastic drift.

Exploring the validity of assumptions is an important feature of our approach and we appreciate Diniz-Filho et al.'s efforts to do so further. When our simple null model fails to predict empirical patterns, it suggests that one (or more) of its simplifying assumptions has been violated (see Gotelli & Graves, 1996). An example that we highlight in our paper is that seed sizes evolve convergently to become larger on islands (i.e. gigantism), rather than obey the island rule, which we interpret as a violation of our simple null model's core assumption of no natural selection (Biddick & Burns, 2021). Continued exploration of our assumptions will hopefully lead to a better understanding of repeated patterns in the evolution of plants and animals on islands.

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