

ARE RANGE-SIZE DISTRIBUTIONS CONSISTENT WITH SPECIES-LEVEL HERITABILITY?

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The concept of species-level heritability is widely contested. Because it is most likely to apply to emergent, species-level traits, one

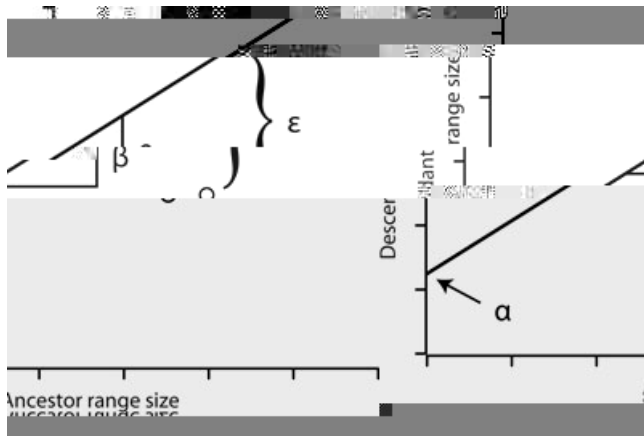


FIG. 1. A “Jablonski plot” displays the range size of the ancestor species on the *x*-axis and the descendant on the *y*-axis. The three parameters of the linear equation (intercept α , slope β , and the standard deviation of the error ϵ) are entered into the model as parameters.

ratio and intraspecific variability, Rabosky and McCune 2010); accordingly, most of the discussion of species-level heritability has concerned the potential for heritability of range sizes (Jablonski 1987; Webb and Gaston 2003; Hunt et al. 2005; Webb and Gaston 2005; Mouillot and Gaston 2007; Waldron 2007). Emergent traits contrast with “aggregate” species traits, such as body size, where the species-level trait is merely a statistical aggregate of the trait values of individuals. Although such traits may be highly heritable (Webb and Gaston 2005), they are not expected to be affected by higher level selection, because the potential for rapid individual-level selection overwhelms any species-level effects (Williams 1966).

Although range-size heritability is a theoretical possibility, the empirical evidence for it is controversial (Jablonski 1987; Webb and Gaston 2003; Hunt et al. 2005; Webb and Gaston 2005; Waldron 2007). The primary reason for the controversy is that empirical tests have been limited, because it is rarely possible to measure the range sizes of extinct ancestral species. One approach to solving this problem is to estimate range size by the geographical extent of the fossil record of well-preserved species. Jablonski (1987) did this for species of Cretaceous molluscs from the Gulf and Atlantic coastal plains of North America, and showed that the range sizes of species were correlated with those of their immediate ancestors. The relationship is demonstrated in a plot with the geographic range of a species on the *y*-axis and the geographic range of its immediate ancestor on the *x*-axis; each point in the plot represents a pair of species (ancestor-descendant). We call this type of plot a “Jablonski plot” (Fig. 1).

The statistical significance of the relationship described by Jablonski (1987) has been disputed (Webb and Gaston 2003; Hunt et al. 2005; Webb and Gaston 2005), and the analysis has not yet

been carried out for other taxa, primarily because of the lack of suitable fossil data. However, an alternative approach to measuring range-size heritability was suggested by Webb and Gaston (2003), who proposed that if range sizes were heritable, the range sizes of extant sister species should also be more similar than expected by chance. Thus, they proposed to estimate range-size heritability as the “asymmetry” of ranges of sister species, defined as the ratio of the smaller range size to the larger. Such an approach potentially offers important advantages, as it does not require fossil data and thus could be applied to the many datasets of extant species. For a clade of 103 sister species pairs of birds, Webb and Gaston (2003) showed that empirical range-size asymmetries were not different from those expected from a null model.

Webb and Gaston’s (2003) test of range-size asymmetry has been critiqued on two fronts. Waldron (2007) objected that the vicariant division of the ancestor range at speciation would tend to make range sizes of sister species asymmetrical rather than symmetrical, thus invalidating the null model of Webb and Gaston (2003). Hunt et al. (2005) also criticized the null model of Webb and Gaston (2003), because it assumes that the species range-size distribution (SRD) of the organisms is uniform. Using a null model based on the empirical SRD, Hunt et al.’s (2005) reanalysis supported the interpretation of range-size heritability.

Webb and Gaston (2005) countered that Hunt et al.’s (2005) use of the empirical SRD was potentially circular: if range sizes were heritable, this itself would affect the SRD of assemblages. They write:

“Results [of modelling range size heritability] can also be applied to more general questions regarding the species–range

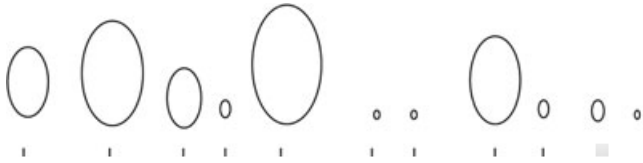


FIG. 2. The range size of each species is determined by a branching process of speciation and extinction. Lineage termination (at point X) occurs with a probability that is inversely proportional to range size. The sizes of the ovals shown reflect the relative sizes of ranges, generated by the log-space model for range inheritance.

study of range-size heritability, and demonstrates that it may play an important role in generating present-day patterns.

Materials and Methods

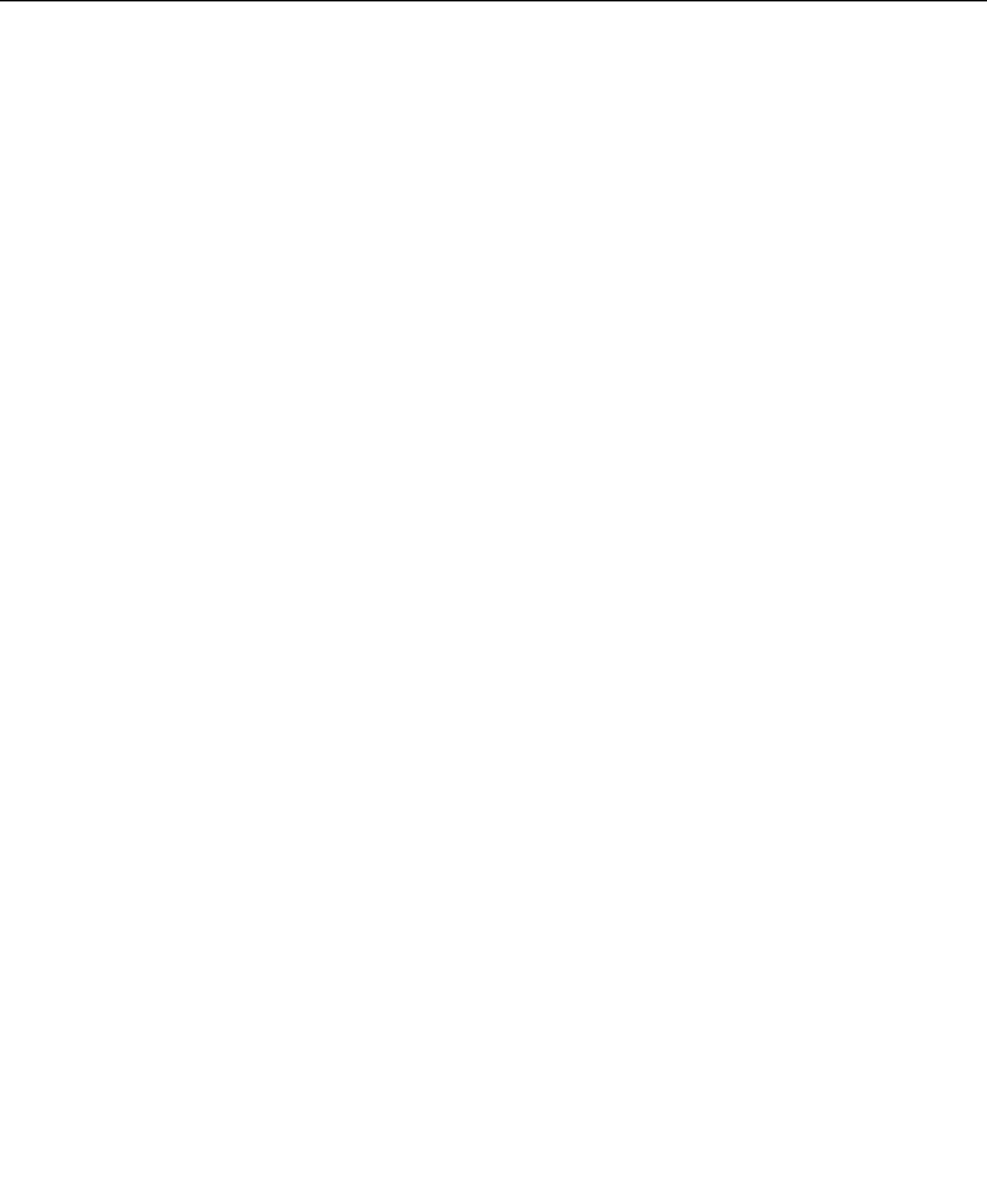
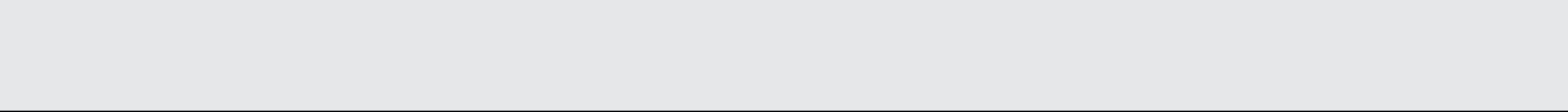
The simulation models a simple branching process of speciation, in which the range size of each new species is determined by that of its immediate ancestor (Figs. 1 and 2). Although the range sizes of species are not constant over their lifetimes (often fol-

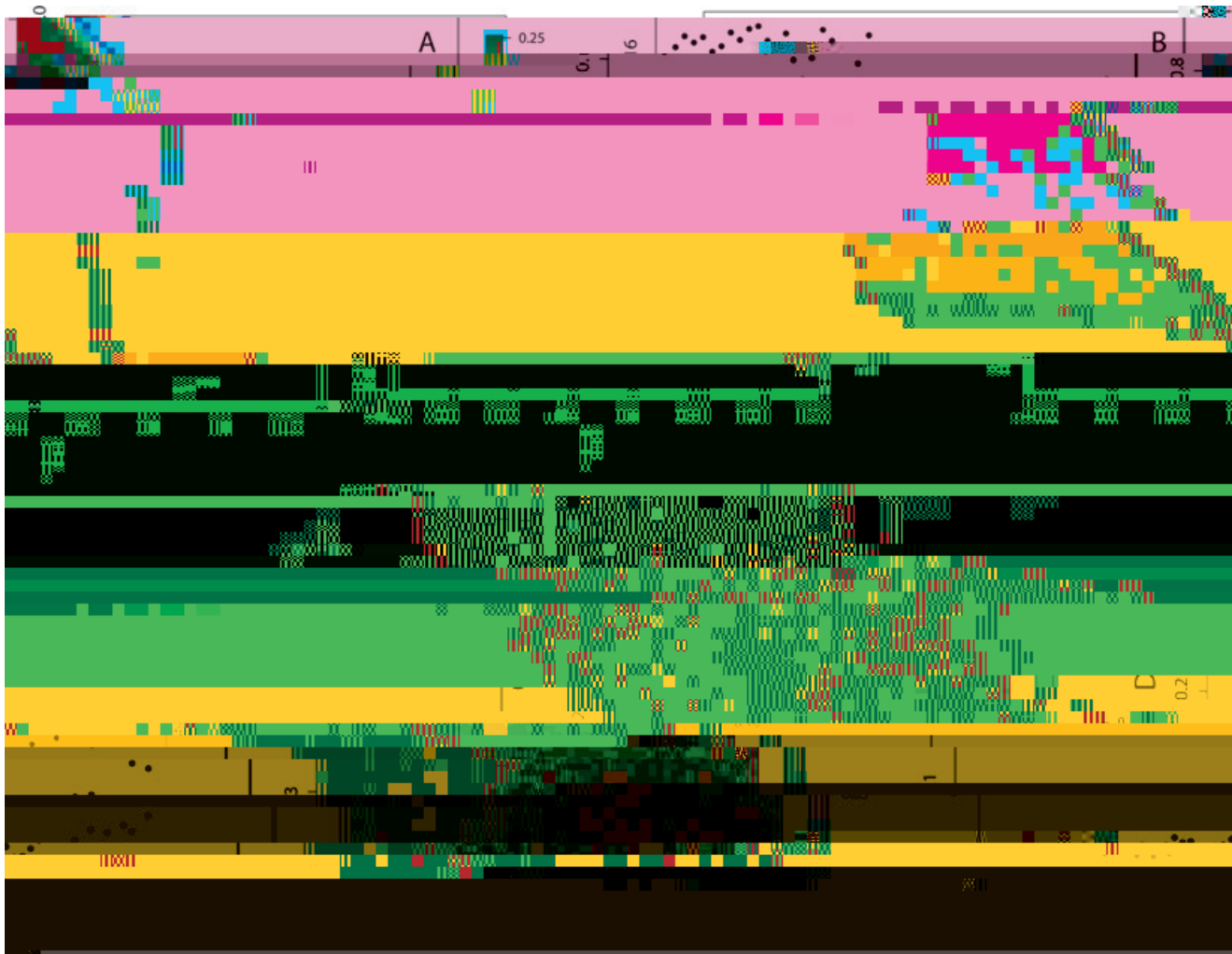
Jablonski plot (Jablonski 1987), in which geographic ranges of

A final assumption is how the simulation deals with out-of-bounds ranges. Range dynamics occur in a bounded domain, in that ranges may not be smaller than the smallest unit of measurement, or larger than the size of the domain. This is explicitly accounted for within the logit-space model for heritability, but the models incorporating linear and log-transformed values sometimes generate values that fall outside the bounds of the geographic domain. We implemented two different approaches to deal with these ranges: (1) the range is discarded, and a new value generated, until a permissible range size is attained (repelling boundaries); (2) the new range size is set to one grid cell if it is too small or is set to the domain size if it is too large (absorbing boundaries). Because both procedures violate the assumption of linearity for the input heritability model, we only saved simulations where at least half the speciation events were unaffected by the boundary condition. The model was parameterized to be comparable to a high-quality empirical dataset of distributions for the South American avifauna (Graves and Rahbek 2005). The phylogenetic structure of this avifauna is reasonably comparable to the simulated data, because most species have been produced by speciation within South America. However, in contrast to the simulated clade, the avifauna is not completely monophyletic.

The domain size was set at 1689, which is the number of $1^\circ \times 1^\circ$ grid cells encompassing the continent of South America. The number of extant species generated by each simulation was set at 2869, which is the number of breeding species in South America (Rahbek et al. 2007). Preliminary analyses indicated that simulating additional species did not change the shape of the SRD: post-hoc inspection showed that most simulations had reached a stable average range size by the end of the simulation.

All parameter combinations were evaluated using a full factorial lattice design (Rangel et al. 2007). The range of values for each of the parameters of the heritability model (β , α , and ϵ) was divided into 60 levels, and simulations were run for each heritability model with all possible combinations of speciation probability, speciation mechanism, and boundary effects. We also evaluated the effect of changing the range of the initial species. The whole





F 4. The parameter combinations resulting in the best fit to empirical patterns. A and B display the results from the log-space model, C and D for the logit-space model. The linear model did not give a good fit to the empirical SRD. (A and C) The value of the process error ϵ that result in the best fit for all combinations of α and β . (B and D) The slope β that gives the best fit to the empirical SRD, when controlling for the effect of α . β

distribution that fit the empirical data more poorly. In the logit-space model, a good fit was generated even without range-size heritability, although incorporating a moderate degree of heritability did not detract from the fit. Although these results do not conclusively demonstrate that range-size heritability occurs in nature, they do counter Webb and Gaston's (2005) claim that observed SRDs are incompatible with the hierarchical branching processes of an evolving clade.

The idea of species-level heritability, which builds on quantitative genetics, is similar to "phylogenetic signal," a concept that has attracted considerable attention in later years (Harvey and Pagel 1991; Freckleton et al. 2002). The phylogenetic signal of a phylogeny has been extensively used to estimate the evolvability of traits, especially in the context of the evolution of environmental niches (Wiens and Graham 2005; Losos 2008). Although the theories of quantitative genetics and phylogenetic signal have developed in relative isolation, recent work demonstrates that a quantitative genetics framework can be fruitfully applied to hypothesis testing in comparative studies (Hadfield and Nakagawa 2010). Indeed, the phylogenetic signal estimator λ is mathematically equivalent to the overall heritability over a phylogeny, as defined in quantitative genetics (Housworth et al. 2004).

Importantly, although, measures of phylogenetic signal are based on the distribution of traits among extant species. Thus, using phylogenetic signal to measure species-level heritability assumes that the relationship between the traits of ancestors and descendants can be inferred from the distribution of traits among descendants. However, this may be a problematic assumption in the context of geographic range-size heritability.

Species-level heritability of range sizes may happen through two clearly distinct mechanisms. First, it may be created because of phylogenetic conservatism of ecological traits. If ancestor and descendant species share traits that predispose them to attain a certain range size, their range sizes are predicted to be more similar. This could be high dispersal ability, which has been proposed to allow species to attain large ranges (Bohning-Gaese et al. 2006; van Bocxlaer et al. 2010). Similarly, ancestors and descendants are likely to occupy similar environmental niches (Peterson et al. 1999), inhabit the same habitats (Mouillot and Gaston 2009), and share the same geographic domain (Pigot et al. 2010), which again are strong determinants of range size. Second, range-size heritability may be caused by direct inheritance of ranges (Waldron 2007). At vicariance events, which may be the most common type of speciation (Wiens 2004), the original species is split into two distinct populations, which then evolve into two new species (Mayr 1963). These two species divide the range that was occupied by the ancestor: in effect, the physical range is inherited by the daughter species.

This dual causality limits the utility of phylogenetic signal as a measure of range-size heritability. The two types of inheritance

make contrasting predictions about the ranges of sister species: shared ecological traits will tend to make the ranges of sister species more similar, whereas asymmetric division of ranges at speciation events will tend to make the range sizes of sister species more dissimilar. As we do not know the relative strengths of these two types of heritability, the method of sister species comparisons (e.g., Webb and Gaston 2003; Webb and Gaston 2005) is not reliable. Although challenging, the problem of multiple mechanisms of heritability is not unique to species-level heritability. Indeed, traditional heritability also results from mixed causality—including numerous forms of maternal and environmental effects, epistasis, and complex interactions between genes, environment, and phenotype (Futuyma 1998).

In our model, a phylogenetic signal was generally only discernible under a regime of very strong heritability (Fig. 5). In empirical studies, the phylogenetic signal of range size has generally been moderate, with λ ranging from 0 to 0.66 in a recent review by Waldron (2007). This has typically been interpreted as an indication that geographic range size is not highly heritable. However, in the present study, λ values near 0.6 were consistent with large values of β (indicating strong heritability) that also lead to a good fit to empirical SRDs.

An innovative solution to the problems with sister-species comparisons was suggested by Waldron (2007), who used an explicit model of range division to generate an expected distribution of the symmetry of sister species' range sizes, and compared this to the empirically observed pattern. The analysis showed that sister species were actually more symmetrical than expected from direct range inheritance, thus to some degree supporting the assumption of range-size heritability. However, this kind of null model only considers direct range inheritance. In addition, it models only the terminal branching event, and thus does not emulate the patterns generated in a stochastic branching model of speciation and extinction. Many of these issues were addressed by Pigot et al. (2010), who followed up on the work by Waldron (2007) by incorporating random range splitting in a model of range evolution through time.

The observation

descendant with a small range. Because of this, with the passage of evolutionary time, many species with small ranges are generated, but relatively few species with large ranges are generated (see also Anderson 1985).

A good fit was also created by the logit model, which also introduces heteroscedasticity, with the variance being largest at range sizes equal to half the domain. The logit model explicitly emulates the limiting effect of evolution in a bounded domain, and the effect of this is sufficient to create realistic species-range distributions even in the absence of range-size heritability. Thus, stochastic speciation and extinction in an evolving lineage on a bounded domain is a simple mechanistic process that could account for the predominance of relatively small-ranged species in most empirical assemblages (as also argued by Anderson 1985; McGill et al. 2007).

When Jablonski's estimated heritability values for gastropods were plotted on the simulation parameter space they fall within the favorable zone of parameter values, although not in the region where the fit is best. We would not expect the fit to be perfect: the continental range sizes of extant birds are likely to be controlled by different processes than gastropod ranges inferred from fossil data. In addition, Jablonski's (1987) analysis may un-

Housworth, E. A., E. P. Martins, and M. Lynch. 2004. The phylogenetic mixed model. *Am. Nat.* 163:84–96.

Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on “on the heritability of geographic range sizes”. *Am. Nat.* 166:129–135.

Supporting Information

1. Results from all parameter combinations.
 2. Brownian motion models.
 3. Recovery of fit.
- g** 1. The fit of the model SRD as a function of input slope and intercept values.
- g** 2. A version of Figure 3 in the main text, based on the Brownian motion model.