

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 of the central discussions has focused on the potential heritability of geographic range size. However, a central argument against range-size heritability has been that it is not compatible with the observed shape of present-day species range-size distributions (SRDs), a claim that has never been tested. To assess this claim, we used forward simulation of range-size evolution in clades with varying degrees of range-size heritability, and compared the output of three different models to the range-size distribution of the South American avifauna. Although there were differences among the models, a moderate-to-high degree of range-size heritability consistently leads to SRDs that were similar to empirical data. These results suggest that range-size heritability can generate realistic SRDs, and may play an important role in shaping observed patterns of range sizes.

KEY WORDS: range evolution, Range-size distribution, range-size heritability, simulation model, species-level selection.

Hierarchical models of natural selection (Rice 1995; Diniz-Filho 2004; Jablonski 2007; Simpson 2010) posit that selection processes are not restricted to individuals, but may also operate at higher levels of organization (e.g., on species). The prerequisite for selection to act on a given trait is that it is heritable (Lewontin 1970; Stanley 1975; Jablonski 1987), that is, that offspring inherit trait values from their parents. However, the existence of heritability of species-level traits, such as geographic range size, is widely disputed (Jablonski 1987; Freckleton et al. 2002; Webb and Gaston 2003; Hunt et al. 2005; Mouillot and Gaston 2007; Waldron 2007; Mouillot and Gaston 2009; Rabosky and McCune 2010).

Hierarchical selection models treat the processes of speciation and extinction as an analogy to the birth and death of individuals (Lewontin 1970). By extension of this analogy, species-level heritability refers to the similarity of the traits of species and their

immediate ancestor (Jablonski 1987; Webb and Gaston 2005). In traditional population genetics, population-level narrow sense heritability is often calculated from regressions of the traits of parents and offspring (Falconer and MacKay 1996). Similarly, species-level heritability may be inferred from a regression of the trait of a species and the trait of its immediate ancestor on the phylogenetic tree (Jablonski 1987). Importantly, such a positive correlation between the traits of ancestor and descendant species, along with differences in speciation or extinction probability among species of different traits, would be sufficient for a process of species-level selection to occur (Lewontin 1970).

Species-level selection should primarily affect “emergent” traits, which are traits that exist only at the species level (Vrba and Gould 1986; Grantham 1995). Probably the clearest example of such an emergent trait is a species’ geographic range size (Diniz-Filho 2004; Jablonski 2007; other examples include sex

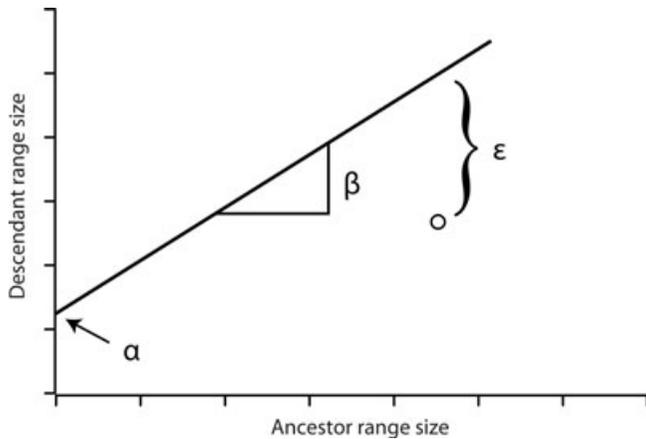


Figure 1. A “Jablonski plot” displays the range size of the ancestor species on the *x*-axis and the descendant on the *y*-axis. The three parameters of the linear equation (intercept α , slope β , and the standard deviation of the error ϵ) are entered into the model as parameters.

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 size distribution; for instance, What form would the species–range size distribution take if range sizes were heritable? or, equivalently, Is the form and phylogenetic structure of the species–range size distribution compatible with a scenario of range size heritability? The answer to this second question would generally appear to be no.”

Here, we address Webb and Gaston’s (2005) questions regarding the impact of range-size heritability on the form of SRDs. Although the phylogenetic structure of range sizes has been addressed by several authors (e.g., Freckleton et al. 2002; Jones et al. 2005), this study is the first to address the form of the SRD expected with a scenario of range-size heritability (but see Pigot et al. 2010 for a different approach).

To evaluate the effects of range-size heritability on the shape of SRDs, we constructed a relatively simple stochastic branching model of speciation and extinction, and incorporated varying degrees of range-size heritability. We calibrated the model with data on the SRD of the extant South American avifauna and used the model results to answer the question: Can a model of range-size heritability generate an SRD that resembles empirical data for extant assemblages? This approach presents a new angle on the

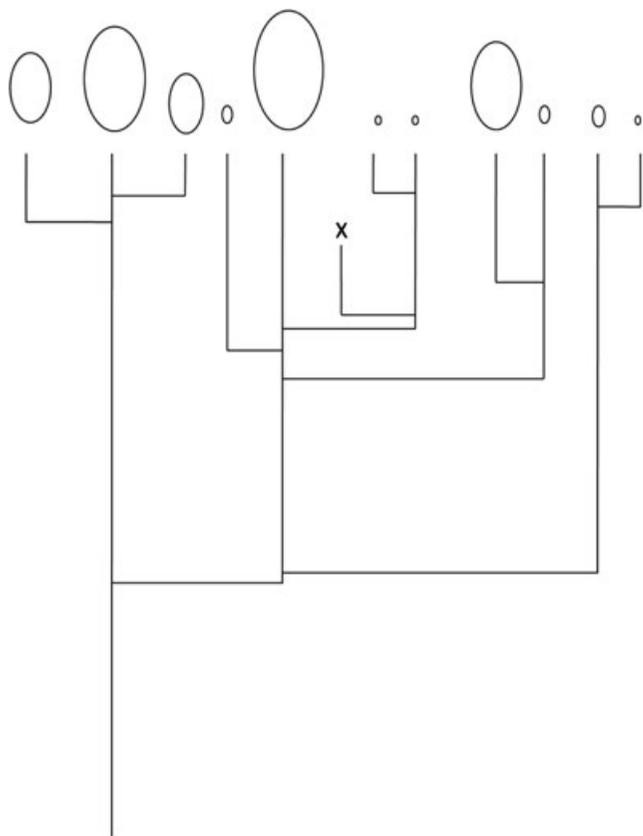


Figure 2. The range size of each species is determined by a branching process of speciation and extinction. Lineage termination (at point X) occurs with a probability that is inversely proportional to range size. The sizes of the ovals shown reflect the relative sizes of ranges, generated by the log-space 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 following a hump-shaped trajectory, e.g., Liow and Stenseth 2007), the model implements range sizes as a single value, representing the range size attained after an indeterminate period of post-speciation range expansion (Waldron 2007). Although this approach does not include all of the details of range-size dynamics, it does provide a parsimonious representation of the effect of range-size inheritance on the range-size frequency distribution.

The degree and type of range-size heritability from ancestors to descendants were varied systematically, and for each realization of the model, the range-size distribution at the final time step was

compared to the empirical species-range distribution of the South American bird assemblage. We then used the distribution of fit values to identify the set of parameters that systematically lead to the best fit with empirical patterns. To assess the sensitivity of the results to the exact assumptions of the model, we also carried out extensive sensitivity analyses, where we varied the implementation of all individual components of the model and quantified the effect on the conclusions.

An implication of the modeling approach is that range sizes evolve in a speciational fashion, that is, the range size characterizing each species is determined by applying the heritability model at the speciation event. However, models of trait evolution are often implemented based on Brownian motion, in which the differences between ancestor and descendant species are caused by the long-term buildup of gradual anagenetic changes. To facilitate comparison with these studies, we also investigated the results of letting range sizes evolve by Brownian motion.

Range-Size Heritability

The simulation begins with a single ancestor species with a given range size r , that gives rise to all the extant species at the end of the simulation. At each time step, each species in the assemblage may go extinct with a probability E . Each surviving species may then speciate with a probability S , thereby adding a new species to the assemblage. Thus, multiple speciation and extinction events are possible within a single time step, although extinction always precedes speciation. This is a discrete-time version of Kendall's standard birth–death model (Kendall 1948).

The core of the simulation is the equation relating the range sizes of ancestor and descendant species. As the results are likely to depend on the exact implementation of range-size heritability, we employed three different models and compared the results.

In the most basic model, the range size of the descendant species is a linear function of the range size of the ancestor species (see Fig. 1):

$$D = \alpha \times \delta + \beta \times A + N(0, \epsilon \times \delta),$$

where δ is the domain size (1689; see below), D and A are the range sizes of the descendant and ancestor, N indicates a normal distribution, and the slope (β), intercept (α), and error term (ϵ) are model parameters. This linear model describes a situation where the range sizes of species are determined by the combined influence of the range size of the ancestor (indicating range-size heritability) and the global mean (indicating nonspecific constraints on range sizes). The relative influence of these two components is measured by β . α equals the global mean at $\beta = 0$, and will decline with increasing β when global mean range is kept constant. This model corresponds to the implicit assumptions of the empirical

Jablonski plot (Jablonski 1987), in which geographic ranges of ancestor and descendant species are plotted on the x and y axes and fit with a simple linear regression.

The second implementation assumes a linear relationship between ancestor and descendant range sizes when plotted on a log–log scale:

$$\log(D) = \alpha \times \log(\delta) + \beta \times \log(A) + N(0, \varepsilon \times \log(\delta)).$$

The logarithmic scale describes a situation where processes act multiplicatively, which may be more realistic for measures such as range size: it is likely to be easier for a large-ranging species to expand its range by, for example, 100 km², than for a small-ranging species (Borregaard and Rahbek 2006). Using log axes also has important implications for the error term. An error term that is constant in log space will increase with the predicted value when back-transformed into linear space. This will lead to variance heteroscedasticity, that is, the variability will be greater for large range sizes.

Finally, we implemented a model that is linear in logit space:

$$\text{logit}(D/\delta) = \alpha + \beta \times \text{logit}(A/\delta) + N(0, \varepsilon),$$

$$\text{logit}(p) = \log(p/(1-p)), 0 < p < 1.$$

A linear relationship in logit space corresponds to a logistic model, in which the potential for growth or retraction is highest at intermediate values, where both the number of occupied areas and the number of empty areas are high. As ranges approach the extremes (the size of the smallest measuring unit below or the size of the continent above), the potential for range-size change diminishes. This type of model explicitly incorporates the effect of a bounded domain on range dynamics, and has been suggested to be the most suitable for range sizes (Hanski and Gyllenberg 1997; Williamson and Gaston 1999).

For all three models, we also investigated the result of implementing a Brownian dynamic of range evolution, by varying the size of the process error ε (i.e., the linear model variance) to be proportional to the time since speciation of the ancestor. The results of these analyses are presented in the Supporting Information.

Model Design

We implemented the model to be as simple and tractable as possible. Where we had to incorporate explicit assumptions in the model design, we assessed the sensitivity of the results to several contrasting settings. Thus, we implemented different models for speciation probability, type of speciation, and the effect of boundaries.

The probability of a given species undergoing speciation in a time step may be constant, or it may depend on the range size of the species. The latter assumption is supported by some

empirical studies, which have demonstrated a negative correlation between range size and speciation probability (Jablonski and Roy 2003). It has also been suggested that the relationship between range size and speciation rate should be positive (Moullot and Gaston 2007), or even hump-shaped (Rosenzweig 1995; Gaston and Chown 1999) although hump-shaped relationships may be empirically indistinguishable from negative relationships because the increasing part of the curve (i.e., small range sizes) is absent from the fossil record (Jablonski and Roy 2003). To reflect the uncertainty in the relationship between range size and speciation probability, we thus evaluated scenarios of positive, negative, and no relationship. To model negative correlations, we set the probability of speciation in one time step for each species as $S = 1 - \text{range size}/\text{mean range} \times 0.01$. The constant 0.01 is an arbitrary value, which is set low to minimize the number of species undergoing speciation in the same time step. Because the simulation output is the distribution of all species, changing this value, for example to scale with realistic species existence times, would not affect the results. To model positive correlations, speciation probability was $S = (\text{range size}/\text{mean range}) \times 0.01$. Under a model of no relationship, we set the probability of speciation as 0.01 for all species in each time step, regardless of their range sizes.

Extinction probability, on the other hand, is regarded as unambiguously related to range size: small-ranging species are more likely to go extinct than widespread species (Jablonski 2008; Purvis 2008; although a recent meta-analysis failed to demonstrate this, Lorenzen et al. 2011). The extinction probability in each time step was calculated as $E = (1 - \text{range size}/\text{mean range}) \times 0.005$, where the constant 0.005 was chosen to ensure that speciation events outnumbered extinction events. Hence, species numbers grew throughout the simulation, from one ancestral species at the start of the simulation to the preestablished bound of 2869 extant descendant species at the end. To ensure that most simulations did not end with extinction of the entire assemblage, each simulation was preceded by a short burn-in period so that no extinctions were allowed until the assemblage contained at least 20 species.

Another key assumption of the model is the predominant type of speciation. The simulation implemented two speciation mechanisms: “range splitting” and “founder event” speciation (Waldron 2007). Range-splitting speciation models a vicariance event that splits a species into two isolated populations (Mayr 1963). This was implemented by removing the ancestor species and adding two descendants with range sizes generated from the Jablonski model (Fig. 1). Founder event speciation models a new species as a population that buds off the range of an existing species, for example, as in an island–mainland scenario. In founder-event speciation, the ancestral species was kept, and one descendant was created with a range size generated from the Jablonski model. We also implemented a “mixed” scenario, where 50% of speciation events were of each type (results not shown).

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 procedure was replicated five times.

Model Evaluation

To evaluate the model, we compared its predictions to the range sizes of South American birds. The correspondence of the simulated SRD to the empirical data was quantified using the Kolmogorov–Smirnov two-sample D^* statistic (Sokal and Rohlf 1995). To assess the validity of regression analyses of range-size heritability, we also performed a linear regression analysis of range sizes of ancestor and descendant species remaining at the end of the simulation. The model parameters (slope and intercept) were then compared with the parameters used to create the model.

To compare the strength of heritability to the phylogenetic signal of range size over the entire phylogeny, we calculated Pagel's (1999) λ for a small subset of the final phylogenies. As calculating λ from phylogenies with ~ 3000 tips is very computationally intensive, this was only done for 1000 randomly selected simulation runs from each of the three heritability models. λ values were calculated for the phylogeny of all species extant at the end of the simulation, using the R package "motmot" (Thomas and Freckleton 2012).

Simulation output was analyzed and visualized in R (R Development Core Team 2011). All simulations were implemented in C++, compiling with MinGW gcc within the Code::Blocks open source IDE.

Results

Speciation probability, speciation mechanism and the choice of boundary assumption all affected the shape of the SRD to some degree. However, the results did not vary qualitatively between different combinations of these assumptions. The main exception was for speciation probability, in that assuming a positive relationship between speciation probability and range size consistently resulted in a poorer fit to empirical patterns (see Supporting Information). Hence, we describe below the results for one parameter combination, using constant speciation probability, allopatric speciation, and absorbing boundaries. The results of other model combinations are presented in Appendix S1. The fit of the modeled SRD was not sensitive to the initial range size, and we present results from using a starting range of 838 grid cells (half the domain size).

There were very marked differences between the three models of range-size heritability (Fig. 3). For all three models, the simple branching process resulted in a broad variety of SRDs at different parameter values, but different parameter combinations led to the best fit to the empirical distribution. Whereas the linear heritability model did not generate SRDs that were similar to the empirical pattern for any combination of regression parameters, both the log-space and logit models produced results that were highly similar to the observed at certain parameter values. The ability to generate a variety of different outcomes is a desirable property in a model used for inverse estimation of parameters, as it increases the power of the model to discern between various parameter values.

For both the log-space and logit models, values of the slope parameter β yielded a good fit to the empirical distribution only when combined with a certain value of α (the intercept). This is because the combination of these two parameters determines the mean range size, and thus the location of the final SRD, and this effect overwhelms the individual effects of each parameter. When controlling for this interaction by varying α to the best-fitting level, the model fit is strongly dependent on β (Fig. 4B and D).

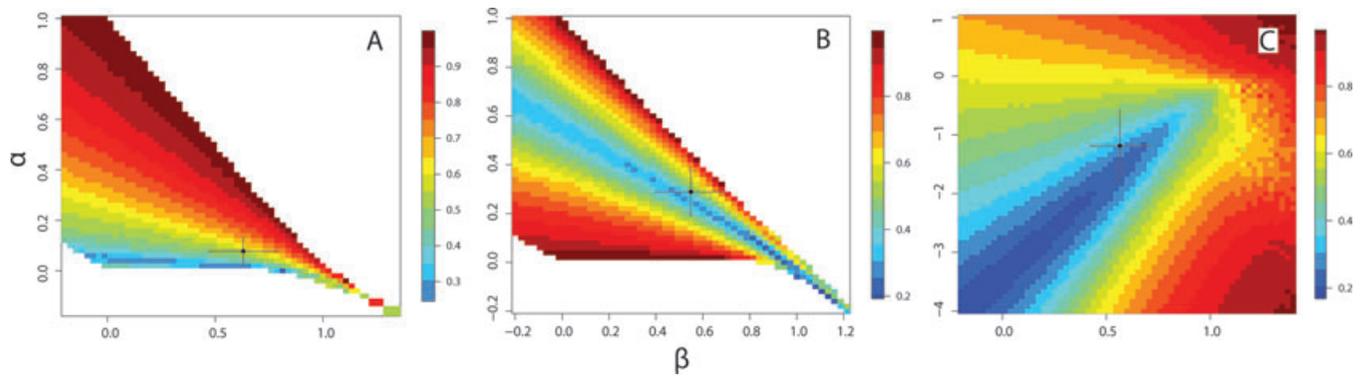


Figure 3. The fit of the model SRD as a function of input slope and intercept values. The color indicates the value of the D^* statistic. Dark blue indicates the best fit to the empirical distribution, dark red indicates the poorest fit, with green and yellow indicating an intermediate fit. The color scale is identical for all three graphs. The black dot with cross hairs indicates the mean and 95% confidence intervals of the slope and intercept estimates from the gastropod data of Jablonski (1987; reanalysis of the dataset published by Hunt et al. 2005). (A) Result using the linear-space model of range size heritability. (B) Results of the log-space model. (C) Results of the logit-space model.

The log-space and logit models lead to contrasting results: the log-space model lead to a good fit to the empirical SRD for high slope values (~ 0.8 – 1.0), whereas the logit model leads to a good fit for most slope values, except for the highest. Only very specific combinations of parameters resulted in SRDs with a D^* statistic lower (i.e., better) than 0.036, which is the D^* value corresponding to a significant difference at the 0.05 level.

A scenario of no heritability is equivalent to a slope value $\beta = 0$. The SRD generated using a slope of 0 using the log model is identical to a log-normal distribution, which is well known to reasonably approximate empirical SRDs; the best log-normal distribution had a D^* statistic ~ 0.16 . However, the empirical SRD is more strongly right-skewed than a log-normal distribution, and models with higher values of β produce more realistic SRDs. The logit model, on the other hand, demonstrated a good fit at $\beta = 0$, consistent with the observation that the empirical SRD is very close to logit-normal.

The process error value ϵ that lead to the best fit depended on the combination of α and β , although for most parameter combinations, a relatively large process error was needed to produce a good fit (Fig. 4A and C). This indicates that the process error of the Jablonski model played an important role in generating realistic range-size distributions, and that a strictly deterministic model of range-size heritability is not consistent with empirical patterns.

To compare the model results, we reanalyzed the original gastropod data from Jablonski's (1987) paper in linear, log, and logit space (using the largest total range +1 as an estimate of the domain size). The estimated parameters for the slope and intercept are shown in Figure 3. For both the log and logit models, the 95% confidence intervals for these parameters include values that yield a relatively good fit to the empirical distribution, although they do not correspond with the areas that give the closest fit.

Post-hoc regressions of simulated descendant and ancestor range sizes performed reasonably well at estimating the true slope and intercept (Supporting Information Appendix 3). This result suggests that simple Jablonski plots are a reasonable method for estimating range-size heritability. However, the intercept was estimated with very large uncertainty in the log-space model.

The λ values of the phylogenies resulting from the simulation ranged from 0 to 1, and were fairly efficient at estimating the level of heritability incorporated in the model (expressed as the slope parameter β ; Fig. 5). Significant phylogenetic signal was only detected at relatively high β values, whereas the process error obscured most signal of heritability for β values lower than 0.5.

The models based on Brownian motion yielded similar results to those for the speciation model (Supporting Information Appendix 2), and led to a similar degree of fit between the simulated and the empirical data. However, the phylogenetic signal estimator λ was less efficient at identifying the degree of range-size heritability in the Brownian models, especially for the logarithmic heritability model (Supporting Information Figs. S2-3B).

Discussion

The main result of the analysis is that a simple evolutionary model can generate a realistic SRD, with characteristic right-hand skew and a predominance of small-ranged species. Contrary to Webb and Gaston's (2005) assertion, incorporating range-size heritability in the model lead to a better fit with the SRD of the South American avifauna, although this depended on the exact mechanics of range-size heritability. For the log-space model, the best fit was found when the slope of the heritability relationship was steep, whereas a model with no heritability resulted in a log-normal

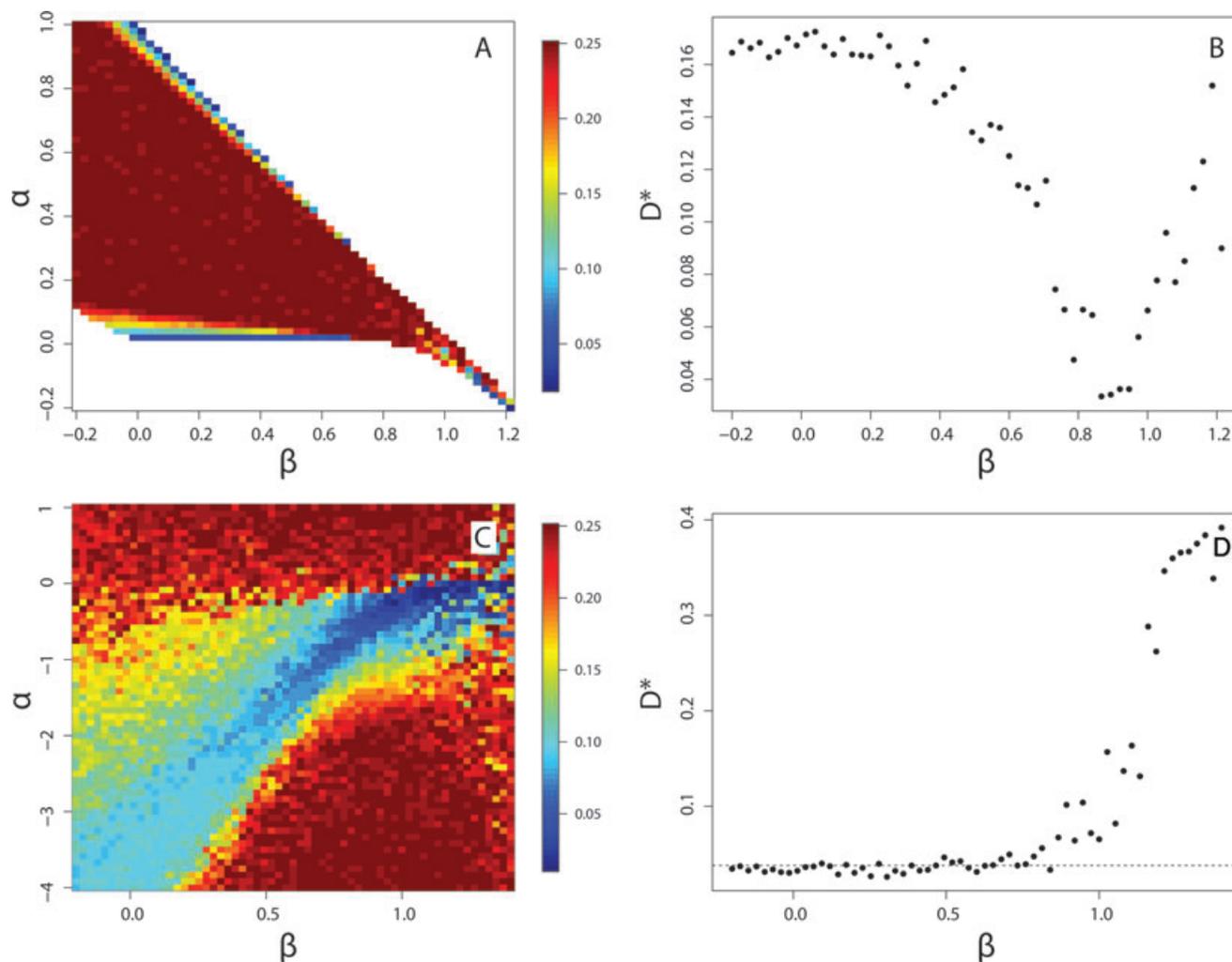


Figure 4. The parameter combinations resulting in the best fit to empirical patterns. A and B display the results from the log-space model, C and D for the logit-space model. The linear model did not give a good fit to the empirical SRD. (A and C) The value of the process error ε that result in the best 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 measures the strength of range-size heritability.

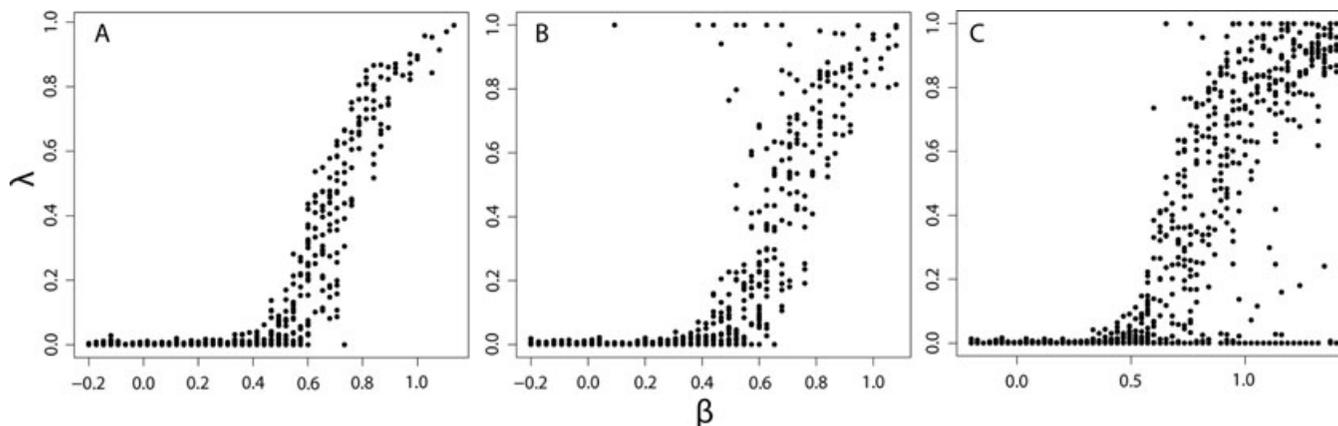


Figure 5. Phylogenetic signal λ as a function of the slope parameter β , which controls the strength of heritability in the simulation model. A significant phylogenetic signal is only detected at high heritability. A, B and C show the results from the linear, log-space and logit-space model, respectively.

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 that a simple function of range-size heritability can generate a realistic SRD is in itself an important result, because the causes of the strong right skew of empirical range distributions are not very well understood (Gaston 1996). In the log-space model, the right skew of the SRD appears to result from variance heteroscedasticity in the descendant range size: the descendant of a wide-ranging species might inherit either a large or a small geographic range, whereas the descendant of a small-ranging species is usually constrained to inherit a small geographic range. As a consequence, phylogenetic lineages in the model that start out with small range sizes tend to pass that trait on to their descendants. Large-ranged species would tend to produce large-ranged descendants, but would also sometimes produce a

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 underestimate the degree of heritability, due to uncertainties in the phylogenetic relationship of species and incomplete sampling of the fossil strata.

A potentially debatable assumption of our model is that species ranges are modeled as a single value for each species, which only changes at speciation events. Thus, the figure can be conceived as the range size attained after an indeterminate period of range expansion. This type of model differs from traditional models of trait evolution, which often employ a gradual anagenetic trait change following a Brownian process (Felsenstein 1985). However, because ranges are implicated in speciation events (i.e., vicariance speciation is preceded by the splitting of the ancestral range), ranges are affected by both anagenetic and cladogenetic processes in contrasting ways. Nevertheless, incorporating Brownian dynamics did not change the simulation results markedly.

In a recent article, Pigot et al. (2010) combined an approximately Brownian dynamic with discontinuous range dynamics at speciation events, and found that the results were compatible with empirically observed rates of speciation and extinction, and generated a realistic level of phylogenetic signal and skewness in the distribution of range sizes. Still, whereas this type of approach incorporates long-term range dynamics that will give rise to range-size heritability via direct inheritance of ancestral ranges, it does not account for trait-driven range-size heritability. Models that combine range-size heritability with the effects of vicariant speciation are clearly a fruitful area for future research. One especially promising approach may be process-based models that

directly incorporate the reciprocal effects of geographical range and speciation rates (Goldberg et al. 2011).

In conclusion, the large temporal scale involved in species-level processes means that we cannot study processes such as range-size heritability directly. In addition, phylogenetic comparative approaches have conceptual difficulties when applied to range sizes that may be impossible to ameliorate completely. Thus, simulation-based approaches like the one used here and by Waldron (2007), Pigot et al. (2010), and Goldberg et al. (2011) are likely to continue to play a major role in this field.

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Supporting Information

Appendix S1. Results from all parameter combinations.

Appendix S2. Brownian motion models.

Appendix S3. Recovery of fit.

Figure S1. The fit of the model SRD as a function of input slope and intercept values.

Figure S2. A version of Figure 3 in the main text, based on the Brownian motion model.

Figure S3. A version of figure 4 in the main text, based on the Brownian motion model.

Figure S4. A version of figure 5 in the main text, based on the Brownian motion model.

Figure S5. The estimated slopes and intercepts of “Jablonski plots” fitted to simulated ancestor-descendant relationships, plotted against the true slope and intercept values in the model.

Figure S6. The relationships in the log-space model.

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

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