


Interspecific geographic range size–body size relationship and the diversification dynamics of Neotropical furnariid birds

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Among the earliest macroecological patterns documented, is the range and body size relationship, characterized by a minimum geographic range size imposed by the species' body size. This boundary for the geographic range size increases linearly with body size and has been proposed to have implications in lineages evolution and conservation. Nevertheless, the macroevolutionary processes involved in the origin of this boundary and its consequences on lineage diversification have been poorly explored. We evaluate the macroevolutionary consequences of the difference (hereafter the distance) between the observed and the minimum range sizes required by the species' body size, to untangle its role on the diversification of a Neotropical species-rich bird clade using trait-dependent diversification models. We show that speciation rate is a positive hump-shaped function of the distance to the lower boundary. The species with highest and lowest distances to minimum range size had lower speciation rates, while species close to medium distances values had the highest speciation rates. Further, our results suggest that the distance to the minimum range size is a macroevolutionary constraint that affects the diversification process responsible for the origin of this macroecological pattern in a more complex way than previously envisioned.

KEY WORDS: Diversification models, macroevolutionary constraint, macroecological pattern, phylogenetic signal.

One of the earliest macroecological patterns documented is the relationship between geographic range size and body size (Brown 1981; Brown and Maurer 1987, 1989). Studies at wide taxonomic and geographic scales have shown that the relationship between these macroecological variables forms a roughly triangular-shaped envelope (Brown 1981; Brown and Maurer 1987, 1989; Taylor and Gotelli 1994; Gaston and Blackburn 1996a,b; Diniz-Filho and Tôrres 2002; Rosenfield 2002; Diniz-Filho et al. 2005; Agosta and Bernardo 2013; Hernández et al. 2013). This pattern means that small species can reach the full range of observed geographic range, while the species with increased body sizes are compelled to attain only larger ranges (Fig. 1).

Brown and Maurer (1987, 1989) described this relationship through a model defined by three boundaries, suggesting that these limits restrict the traits space to a triangular form through differential speciation and extinction rates: (i) an upper bound, set by the maximum range size that species can potentially occupy (geographic restriction); (ii) a left-hand bound, corresponding to physiological constraint imposed on the minimum body size that a species of a given taxon can reach (physiological restriction); and (iii) a lower bound, representing the minimum geographical range size (MGRS) for a species of a given body size (Gaston and Blackburn 1996a), which positively correlates with body size (Brown 1981). The most conspicuous and biologically attractive

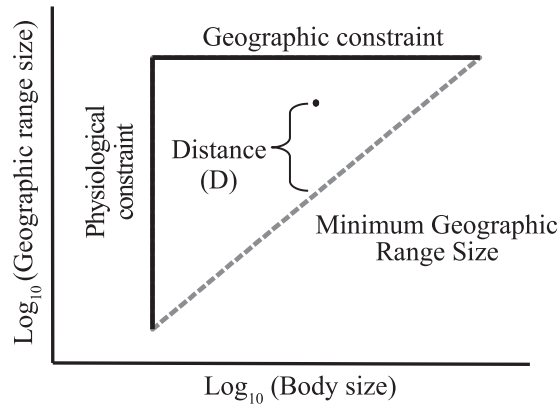


Figure 1. The theoretical model describing the geographic range size–body mass relationship proposed by Brown and Maurer (Brown and Maurer 1987, 1989). The gray dashed line indicates the probabilistic boundary defined by the minimum geographic range size (MGRS) needed for the survival of a species of given body mass, while the black solid lines indicate absolute boundaries. The Distance (D) indicates the distance to the lower polygon boundary.

aspect of this pattern is its lower boundary (i.e. MGRS) that could have great importance for conservation biology (Gaston and Blackburn 1996a).

Three main hypotheses have been proposed to explain the origin and maintenance of minimum range size and its correlation with body size: (i) the increase of the minimum range size with body size could be the result of the tendency of larger species to disperse more quickly and efficiently than smaller species. In this sense, larger species can use a bigger portion of their potential distributional range (Gaston 1994; Gaston and Blackburn 1996a). This could also be due to the fact that larger species are evolutionarily older than smaller species (Gaston 1994). Likewise, (ii) it can be a by-product of two interspecific patterns: the Rapoport's and Bergmann's rules (Pagel et al. 1991). These rules generalize an average decrease of range size (Stevens 1989) and body size toward the tropics (Bergmann 1847), respectively. If so, the product of both patterns would incidentally result in an increase of the minimum range size along with body size. And furthermore, (iii) the minimum viable population size proposed by Brown and Maurer (Brown and Maurer 1987, 1989) (hereafter B&M hypothesis)—i.e., the energetic constraint on minimum range size hypothesis (Agosta and Bernardo 2013)—suggests that given that larger species require larger home ranges to obtain resources for their survival (Mcnab 1963; Armstrong 1965; Schoener 1968; Lindstedt et al. 1986; Swihart et al. 1988), these species may also require larger geographical ranges to maintain viable population sizes. Thus, the various ecological restrictions imposed by the minimum range on the species and their populations cause large species to not survive in small geographical ranges. Therefore,

the theoretical line that defines the minimum range acts as a probabilistic bound around which the probability of species arising or persisting could decrease linearly with respect to the range–body size combination in the traits space (Agosta and Bernardo 2013). Complementarily, Kelt and Van Vuren (2001) found an analog polygonal relationship for the home range–body size relationship, suggesting that the boundaries that define that polygon are the proximate manifestations of the mechanism envisioned in the B&M hypothesis (Diniz-Filho et al. 2005). This highlights the need for consideration of the minimum viable population size acting over evolutionary time (Diniz-Filho 2004; Diniz-Filho et al. 2005).

Given that the minimum viable population size would be acting across evolutionary timescales, and the range size–body size relationship emerges above the species level, macroevolutionary processes could explain the observed pattern. In this sense, macroevolutionary processes play an important role in understanding some macroecological patterns, such as those associated with body size (McShea 1994; Alroy 1998; Cumming and Havlicek 2002; Knouft and Page 2003; Avaria-Llautureo et al. 2012) and geographical range (Taylor and Gotelli 1994; Webb and Gaston 2000; Roy et al. 2001; Goldberg et al. 2011). Thus, the range size–body size relationship could be the result of the speciation and/or the extinction process associated with opportunities or constraints imposed by the presence/absence of the value of a given trait (Maddison et al. 2007; FitzJohn 2010) and/or by the geographical range inhabited by the species (Goldberg et al. 2011). From this standpoint, proximity to the minimum range size would be related to high extinction rates and/or low speciation rates due to macroevolutionary constraints imposed by geographic range close to the minimum range size required for population survival of a species with a given body size—a mechanism that may account for the low species number around this boundary at present (Gaston and Blackburn 1996b). Consequently, this boundary represents the minimum range for the evolutionary survival of the species, which positively correlates with body size. Conversely, greater distances to the minimum range would generate macroevolutionary opportunities, decreasing the extinction rates and/or increasing the speciation rates of the species.

While the effect of phylogenetic relationships on geographical range size–body size macroecological pattern has been suggested (Hernández et al. 2013), the macroevolutionary processes involved in the generation and maintenance of this pattern and how its boundaries can affect lineage diversification have been poorly explored. In this work, we evaluated the macroevolutionary consequences of the species' position on this bivariate trait space to untangle the role of minimum range size on the diversification dynamics of a Neotropical bird species-rich clade. Specifically, we evaluated if the distances to the minimum range are

differentially correlated to diversification rates. For this, we used as a study model the Neotropical passerine birds of the family Furnariidae, along with models of trait-dependent diversification, to test the hypothesis that the distance to minimum range boundary is a macroevolutionary constraint to lineage diversification.

Materials and Methods

MACROECOLOGICAL DATABASE AND PATTERN EVALUATION

We compiled a database of body mass (g) (as a measure of body size) and range size (km²) for 278 of ca. 300 species (93%) belonging to the family Furnariidae (Passeriformes: Tyranni) (Table S1). This is a clade of exclusively Neotropical birds, so we worked with a systematic and biogeographic defined biota, confining the analyses to organisms within phylogenetic lineages that are subject to similar evolutionary and geographical constraints, as suggested by Brown and Maurer (Brown and Maurer 1989). Both variables were log₁₀-transformed prior to analysis to correct for heteroscedasticity and nonlinearity in the models.

DATED PHYLOGENY OF FURNARIIDAE

We used the calibrated species-level molecular phylogeny of the Furnariidae published by Derryberry et al. (2011). This calibrated tree contains 284 of the ca. 300 recognized for this family (Clements et al. 2016). The phylogenetic tree is deposited in TreeBASE (study S11550). For further details on phylogenetic reconstruction and calibration, see Derryberry et al. (2011).

ESTIMATING THE MINIMUM GEOGRAPHIC RANGE SIZE (MGRS)

Quantile regression has been used to detect polygonal relationships between macroecological variables (e.g., Hernández et al. 2013). To evaluate the presence of minimum range size in the range size-body mass relationship, we searched for the lower boundary of this relationship, determining the linear regression of the lowest significant quantile by mean quantile regression. For this, we used the “rq” function implemented in package *quantreg* (Koenker 2016) in R (R Core Team 2016). To estimate standard errors and *P*-values for the coefficient model (i.e., body mass), we used a randomization process using “wild” bootstrap method (10,000 replicates) proposed by Feng et al. (2011). We then defined the distance from the minimum range size, for each species, as the difference between its range size and the range size predicted for that species by the regression line from the lowest significant quantile.

We applied a nonphylogenetic model because there is no quantile regression (to our knowledge) that incorporates information about the phylogenetic relatedness between species. However, when using a phylogenetic linear regression, we found low phylogenetic signal in the error term (Table S2) (see Revell 2010

for the importance of estimating phylogenetic signal on the error term). Moreover, nonphylogenetic methods provide unbiased estimates of regression lines (Rolf 2006), and our primary purpose in this step is to estimate the line corresponding to the minimum range size. For each species, this line is used to derive the distance from that species’ range size to the minimum range size predicted by the line. Later, phylogenetic correlation between species is accounted for by QuaSSE, to correlate the distance to the minimum range size (obtained in this first step here) with diversification rates (see section Diversification Analyses).

PHYLOGENETIC SIGNAL

The patterns of similarity among species in macroecological variables (e.g., body mass and range size) have been shown to be closely related to lineages’ evolutionary histories (i.e., phylogenetic signal). Therefore, we evaluated the effect of phylogenetic relationships on similarity trait patterns, evaluating the phylogenetic signal of body mass, range size, and the distance from the minimum range size. For this, we used the lambda (λ) parameter defined by Pagel (Pagel 1999), where $\lambda = 1$ indicates that phylogenetic relationships effectively predict the species traits’ similarity pattern under a Brownian evolution model; $\lambda = 0$ indicates complete independence between phylogeny and species traits (under Brownian evolution model). Intermediate λ values indicate different phylogenetic signal levels. To evaluate and compare these scenarios of the phylogenetic signal, we used the software BAYESTRAITS v3.0 (<http://www.evolution.rdg.ac.uk/BayesTraits.html>), using a Bayesian approach, comparing the fit of the Pagel’s lambda models via Akaike Information Criterion for Bayesian samples (AICM; Baele et al. 2012), as implemented in the software TRACER v1.6 (Rambaut et al. 2014). Briefly, the AICM is an ordinary AIC (Akaike Information Criterion) but using the estimation of the marginal likelihood (and not the maximum likelihood score from a ML analysis) of any given model from a Bayesian analysis. Then, applies the same formulation that an ordinary $AIC = 2Lh + 2n$, where *Lh* is the marginal likelihood of the Bayesian model, and *n*, the parameter number in the model.

DIVERSIFICATION ANALYSES

To assess if the distance to the minimum range acts as a macroevolutionary constraint (or opportunity) on lineage diversification, we tested if the distances to this boundary have differential effects on the diversification rates of furnariids. Based on the previously defined boundary, we used the residuals obtained from the linear regression of the lowest significant quantile as a distance measure to the lower boundary (Fig. 1).

We used the Quantitative-State Speciation and Extinction model (QuaSSE) implemented in the *diversitree* R software (FitzJohn 2012). This method allows fitting several models where

speciation (λ_{sp}) and extinction rates (μ) are constant, linear, sigmoid, or hump-shaped functions of a quantitative trait. Moreover, it allows the incorporation of a diffusion term, ϕ , which captures the directional component in the trait's evolution (FitzJohn 2010). Extrapolating to a macroevolutionary level, under the B&M hypothesis, the diversification rate (speciation minus extinction) of lineages is expected to be a positive linear function of the distance. However, positive diversification-distance measure relationships can be the result of a different interplay between extinction and speciation rates. Thus, to differentiate between those processes, we fit two sets of QuaSSE models: (i) one set where the extinction rate was constant while speciation rates varied as functions of the distance (variable speciation models), (ii) and another where the speciation rate was fixed while extinction rates varied as functions of the distance (variable extinction models). We used the Akaike information criterion (AIC) to select the best-fit model between variable speciation and extinction models.

Considering that trait-dependent diversification models have recently been criticized for tending to exhibit a high Type I error rate (Davis et al. 2013; Rabosky and Goldberg 2015), we evaluated whether our results were the product of a statistical artifact by using a parametric bootstrap approach. In this approach, we simulated 200 random traits (i.e., distance values) on the dated phylogeny under a Brownian model, using the “fastBM” function in the *phytools* R package (Revell 2012). This procedure ensured that the simulated traits did not affect the diversification process. For these simulations, we used the diffusion parameters estimated by the constant QuaSSE models (in which both speciation and extinction rates are constant across traits values) and ancestral root values estimated from Maximum-Likelihood ancestral estimation, using the “fastAnc” function implemented in the *phytools* R package (Revell 2012). Then, for each simulated set we fit constant QuaSSE models and the best-fit model for the observed data and compared them to obtain the log-likelihood difference ($\Delta\text{Log-Lik}$) values across simulated traits. We used the distribution of simulated $\Delta\text{Log-Lik}$ values to estimate a *P*-value as the proportion of simulated values that are as extreme as the $\Delta\text{Log-Lik}$ obtained in the observed data. A *P*-value less than 0.05 supports the effect of the distances to the minimum range size on the diversification of furnariid birds (Rabosky and Goldberg 2015).

Nonetheless, the use of the best-fit model between a set of candidate models (relative fit) does not ensure that it has an adequate model in absolute terms, that is that the selected model can actually predict our empirical dataset (i.e., absolute fit or model adequacy). Thus, to evaluate the model adequacy of the selected model, we implemented a posterior parametric predictive simulation procedure that evaluates to what extent it is a suitable model for describing the processes (i.e., trait dependent-speciation and extinction rates) that gave rise to our distance measure. For

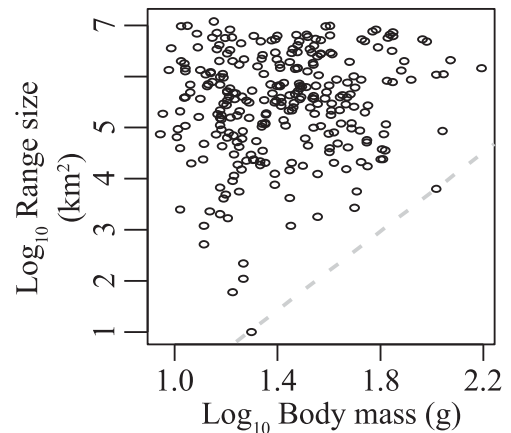


Figure 2. Empirical geographic range size–body mass relationship for furnariid birds. The gray dashed lines indicate the minimum geographic range size, measured as the lowest significant quantile in quantile regression. The Distance (D) indicates the difference between the observed and the minimum range sizes required by the species' body size.

this, we simulated 1000 datasets (i.e., trees and traits) under the best-fitting QuaSSE models for the distances and calculated four general descriptive statistics of these datasets: (a) mean, (b) variance, (c) kurtosis, and (d) skewness. The simulated trees in the above procedure were obtained fixing the maximum taxa number to 278, to obtain similar trees to the empirical one. Then, these descriptive statistics were calculated for our empirical dataset and compared with the frequency distribution of the statistics from the simulated datasets. For each simulated descriptive statistic, we calculated the 95% confidence limits of its density function. If the calculated descriptive statistics for the empirical dataset laid in the 95% interval density, the selected QuaSSE model was considered an adequate model.

Results

MACROECOLOGICAL PATTERN

Our results show the widely documented triangular relationship between range size and body size (Fig. 2). In addition, this pattern sustains the presence of a significant lower bound on the geographic range at the quantile = 0.001 ($t = 3.89$, $P = <0.005$; Fig. 2). This significant lower bound corresponds to the minimum range size for furnariids.

PHYLOGENETIC SIGNAL

There is a significant phylogenetic signal in all variables considered (Table 1). Body mass shows the stronger phylogenetic signal (0.921; 95% HPD: 0.8734–0.9663), whereas geographic range size shows a low phylogenetic signal (0.297; 95% HPD: 0.1393–0.4703). The distance to the lower limit shows

Table 1. Comparison of the phylogenetic signal models of body mass, geographic range size, and distance from minimum geographic range.

| | AICM ^a | S.E. | Parameter estimation |
|---------------------------------------|-------------------|-------------------------------|-----------------------|
| (A) Body mass | | | |
| $\lambda = 0$ | 23.5 | ± 0.005 | |
| $\lambda = 1$ | -251.3 | ± 0.012 | |
| λ estimated | -284.4 | ± 0.035 | 0.921 (0.8734–0.9663) |
| (B) Geographic range | | | |
| $\lambda = 0$ | 803.3 | ± 0.008 | |
| $\lambda = 1$ | 956.9 | ± 0.021 | |
| λ estimated | 769.4 | ± 0.018 | 0.297 (0.1393–0.4703) |
| (C) Distance (D) | | | |
| $\lambda = 0$ | 946.7 | ± 0.009 | |
| $\lambda = 1$ | 1040.3 | ± 0.014 | |
| λ estimated | 905.6 | ± 0.033 | 0.553 (0.3663–0.7287) |

^afrom 1000 bootstrap replicates.

Models in bold indicate the lambda model with better fit.

Lambda models were run for 2,000,000 iterations, sampling each 100th and burning the first 20,000 iterations.

Lower Akaike Information Criterion for Bayesian MCMC sample (AICM) values indicate better model fit. In parameter estimation, the λ estimations are reported along their HPD (High Posterior Density interval for the λ estimations).

intermediate levels of phylogenetic signal (0.553; 95% HPD: 0.363–0.7287).

DISTANCE MEASURE AND DIVERSIFICATION RATES

The AIC comparison between variable speciation and extinction models for distance to the minimum range size, shows that the best-fit model was a variable speciation model, where the speciation rates vary as a positive hump-shaped function of the distance (log-likelihood = -1262.6; Fig. 3; Table 2). In this model, species with the highest and lowest distance values had lower speciation rates ($\lambda_{\text{sp.min}} = 0.010$; Fig. 3), while species close to medium values (distances around 3.89) had the highest speciation rates ($\lambda_{\text{sp.max}} = 0.255$; Fig. 3). This model is characterized by a significant, although small, positive directional trend ($\varphi = 0.061$) and a low extinction rate ($\mu = 2.5 \times 10^{-6}$). The diversification rates (speciation minus extinction) follow the same pattern as the speciation rate, given the small extinction rate detected (Fig. 3). The simulation procedure shows that this model is statistically significant (Fig. 3) and an adequate model given that it can predict basic aspects of the statistical distribution of our empirical dataset (Fig. 4).

Discussion

The diversification dynamics of furnariid birds depends on the species range-body size combination, which defines its position

within the triangular-shaped envelope conformed by the range-body size relationship. However, contrary to the expectations of the B&M hypothesis, the diversification rate associated with the distance from the lower boundary of this pattern is not linear, showing instead that speciation rate is a positive hump-shaped function of this boundary. This finding suggests that this boundary acts as a macroevolutionary constraint, affecting the diversification dynamics that give rise to the origin and maintenance of this macroecological pattern in a more complex way than had been previously envisioned.

Our results support that the speciation rate is a positive hump-shaped function of the distance from the minimum geographic range, while the estimated extinction rate is constant, acting as background extinction rate across distance values (Table 2; Fig. 3). Therefore, the several ecological constraints imposed by the minimum geographic range do not generate a decrease in diversification rates around this boundary by increasing extinction rates, but rather, by decreasing speciation rates of ancestral furnariid species. Thus, our finding does not support the argument of the hypothesis that states that the distance to the minimum geographic range boundary is necessarily an evolutionary constraint on lineage diversification by selective extinction of species closer to the minimum geographic range (Brown and Maurer 1987, 1989; Gaston and Blackburn 1996b; Diniz-Filho 2004; Diniz-Filho et al. 2005). Instead, the minimum geographic range boundary acts as an evolutionary constraint just for the speciation process at both extremes of distance values. Accordingly, the explanation for this pattern is complex (as is the nature of the geographic range-body size pattern) and could involve different processes associated at each end of the distance range distribution frequency (Fig. 3).

The low speciation rates associated with species close to their minimum geographic range (i.e., small distance values) could be mainly explained alluding to the likelihood of vicariant process as a function of range size. The most common speciation model, mainly in birds, is allopatric speciation (Rosenzweig 1995; Phillimore et al. 2008; Price 2010; Fjeldsa et al. 2011), a process that is mainly caused by vicariant events (Rosenzweig 1995), which are more likely to occur in intermediate to large range sizes (Rosenzweig 1995; Price 2010; Pigot et al. 2010). Then, because species at low distances to minimum range represent species with relative small range sizes, the chance of incidence of geographic barriers is low. Thus, for these species there is a low probability of occurrence for speciation events, which is reflected in the low speciation rates found in this work. Also, our results suggest an evolutionary scenario for those species that currently are positioned at the boundary formed by the minimum geographical range. Our results show two species on this boundary (Fig. 2): *Cinclodes palliatus* and *Thriphopaga cherriei*, both classified ecologically by the International Union for the Conservation of

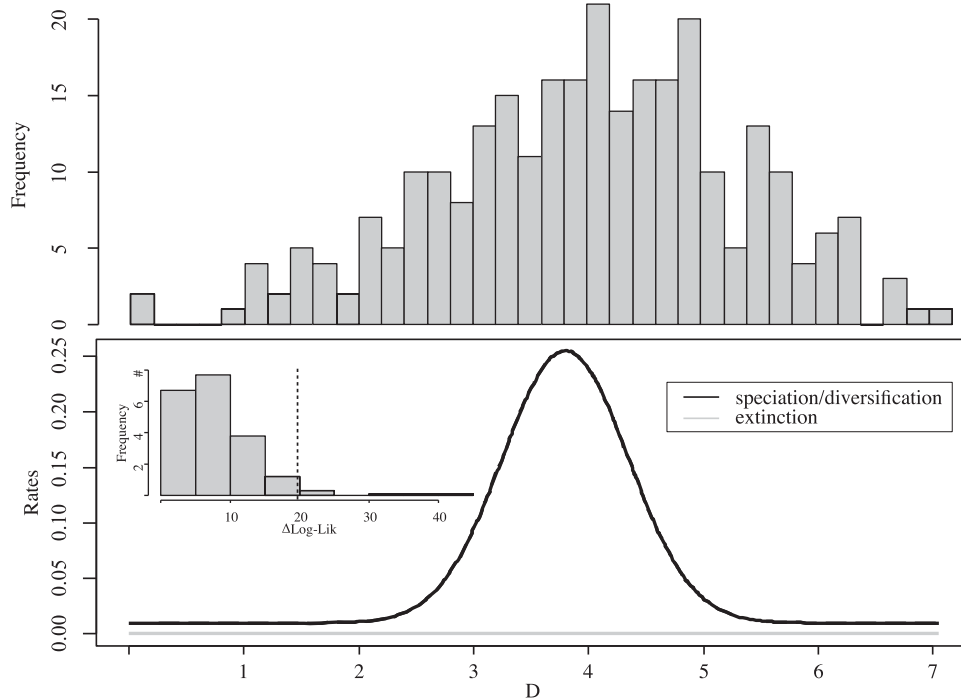


Figure 3. Top: histogram showing the frequency distribution of the distance from the minimum geographic range. Bottom: representation of best-fit model estimated with QuaSSE showing the speciation, extinction, and diversification rates as a function of the distance to the lower boundary (D) from body geographic range–body mass relationship. The histogram inside the plot shows the simulation results. The Log-Likelihood difference ($\Delta\text{Log-Lik}$) corresponds to the differences between the QuaSSE best-fit model and the constant QuaSSE model across 200 simulations. The gray dashed line shows the observed Log-Likelihood differences, which is significant for this model ($P\text{-value} = 0.02$). Note that as the extinction rate is very small compared to speciation rate ($\mu = 2.5 \times 10^{-6}$), the net diversification rate is indistinguishable from the speciation rate.

Table 2. Trait-dependent diversification model fits for distance to minimum geographic range size (D). Drift models are QuaSSE models in which drift parameter (directionality in trait evolution) is incorporated.

| | <i>k</i> | lnLik | AIC | ΔAIC | AIC _w |
|-----------------------------------|----------|---------|------|--------------------|------------------|
| Variable speciation models | | | | | |
| Null model | 3 | −1282.4 | 2571 | 31.6 | 0 |
| Linear | 4 | −1276.7 | 2561 | 22.2 | 0 |
| Sigmoidal | 6 | −1270 | 2552 | 12.9 | 0 |
| Hump | 6 | −1271.9 | 2556 | 16.6 | 0 |
| Drift linear | 5 | −1269 | 2548 | 8.84 | 0.01 |
| Drift sigmoidal | 7 | −1266.7 | 2547 | 8.2 | 0.02 |
| *Drift hump | 7 | −1262.6 | 2539 | 0 | 0.97 |
| Variable extinction models | | | | | |
| Linear | 4 | −1282.4 | 2573 | 33.5 | 0 |
| Sigmoidal | 6 | −1282.4 | 2577 | 37.5 | 0 |
| Hump | 6 | −1282.4 | 2577 | 37.5 | 0 |
| Drift linear | 5 | −1282.3 | 2575 | 35.3 | 0 |
| Drift sigmoidal | 7 | −1282.3 | 2579 | 39.3 | 0 |
| Drift hump | 7 | −1282.3 | 2579 | 39.3 | 0 |

*Indicates the best-supported QuaSSE model for D.

The parameters of the selected model are: $\lambda_{\text{sp.min}} = 0.010$, $\lambda_{\text{sp.max}} = 0.255$, x_{mid} (inflection point) = 3.89, $\mu = 2.5 \times 10^{-6}$, $\phi = 0.061$, diffusion = 0.019, $I.s2$ (variance of the normal distribution) = 0.0195.

k, number of free parameters (model parameter estimated); lnLik, logarithm of likelihood; AIC, Akaike information criterion; ΔAIC , delta Akaike information criterion; and AIC_w, Akaike information criterion weight.

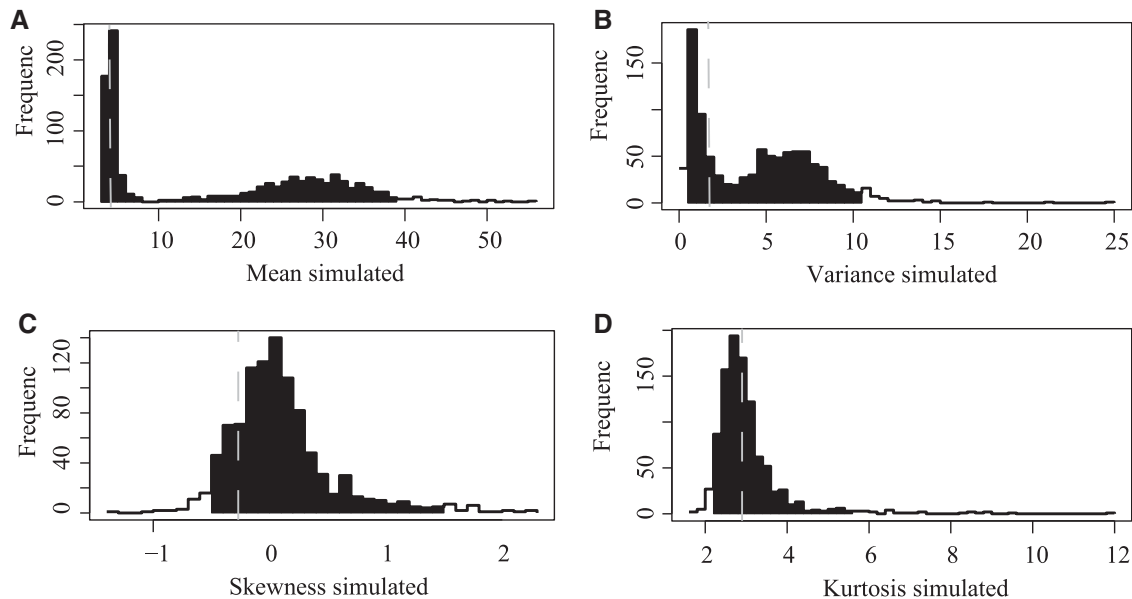


Figure 4. Results of the predictive simulation procedure designed to evaluate the model adequacy of the best-supported QuaSSE model for the distance (D) to the minimum range size. The statistic descriptors used in this simulation procedure were the mean (A), variance (B), skewness (C), and kurtosis (D). The black shaded area represents 95% of the density of the simulated statistical descriptors. The gray dashed vertical lines are the empirical values of each statistics descriptor.

Nature (IUCN) as Critically Endangered and Vulnerable, respectively, due to a combination of low population abundance and small range sizes (50–249 mature individual in 6300 km²; 250–999 mature individuals in 10 km², respectively; <http://datazone.birdlife.org/species>). However, the drift parameter (φ ; directionality in trait evolution estimated along the best-fit QuaSSE model indicates that the distance to this boundary has increased throughout evolutionary history ($\varphi = 0.06$), so if the evolutionary change toward larger relative range sizes is faster than the effects of the constraints imposed by minimum range, these species could cope with the potential conservation problems.

On the other hand, our finding of a low speciation rate associated with species far from the minimum geographic range (i.e., high distance values), does not support the general statement that emerges from the B&M hypothesis, since a linear increase in the diversification rate is expected as the range size–body size combination shifts away from the minimum range. Under the B&M hypothesis, it is expected that species whose relatives ranges are large have more opportunities for allopatric speciation provided by the greater likelihood of area fragmentation (Rosenzweig 1995; Owens et al. 1999). However, this scenario is not supported by our results, instead supporting the alternative scenario proposed by Gaston (1998), which states that the basic element for the speciation probability is the frequency distribution of geographic barriers size: “If most barriers are small-to-intermediate in size, relative to the range sizes of widespread species, then intermediate-sized ranges may indeed have a higher probability of speciation” (Gaston 1998). Also, it has been proposed that for species inhab-

iting larger range sizes, it is possible that there is a homogenizing effect of gene flow, lowering the speciation probability and diversification rates. For example, Claramunt et al. (2012) found an overall negative relationship between dispersal ability and the speciation rate for furnariids. They argued that this could be the result of a negative relationship between gene flow and genetic differentiation found in bird species at the population level (e.g., Belliure et al. 2000; Burney and Brumfield 2009), which would inhibit the speciation process (Claramunt et al. 2012). Consequently, lineages with high dispersal ability distributed over wide areas experience reduced speciation rates due to genetic homogenization via gene flow (Claramunt et al. 2012). Thus, the low speciation rates estimated in our model for species more distant from minimum range size would be supporting this last hypothesis.

Our overall results suggest that species are affected by minimum geographic range size, by means of its effects on the distance between the observed range size to this limit, restricting the speciation rate in the extreme values of the distance. This implies that the extant species position on this trait’s space was defined by the interplay of differential speciation rates imposed by this boundary, generating an area of higher speciation rate centered on medium distance values. We suggest that species on medium distance values experienced a “optimal blend” between range expansion and geographical subdivision, consistent with the “intermediate dispersion” model proposed in Claramunt et al. (2012). In this model is combined the mixed effect of the dispersal, barriers, and gene flow on the species diversification. Species with low dispersal ability are geographically restricted and thus have

few opportunities for allopatric speciation (Claramunt et al. 2012). On the other hand, species with high dispersal ability can potentially inhabit wider areas, experiencing reduced speciation rates because of genetic homogenization by gene flow (Claramunt et al. 2012).

Furthermore, it has recently been shown that the speciation rate of this clade is positively related to the habitat type, particularly to open habitats (Ledzma et al. 2017). These findings could be potentially related to our results. So if species are at medium distances from the minimum range and are also distributed in open environments, then the speciation rate could be enhanced. However, this and other hypothetical scenarios must be evaluated in future works.

In conclusion, our results support that the origin and maintenance of range size–body size pattern occur at macroevolutionary scale. We claim this because (i) range size, body mass, and the distance measure have a significant phylogenetic signal; and (ii) there is differential speciation related to the minimum range bound. Therefore, our study supports the long-standing idea proposed by paleontologists since the 1970s and 1980s (with relatively recent impact on macroecology; see Hernández et al. 2013) that suggests the existence of dynamic selective processes analogous to the action of natural selection on organisms within populations, but at species-level within a certain biota (Eldredge and Gould 1972; Stanley 1975; Gould and Eldredge 1977; Vrba and Eldredge 1984; Arnold and Fristrup 1986). Trait combinations that characterize the species are, to some degree, determined by how species interact with their environment and result in selective speciation, extinction, and/or colonization processes (Brown and Maurer 1987). In this sense, the minimum range size, which is the most conspicuous and biologically attractive aspect of range size–body mass relationship, has a direct effect on speciation rates leading to the species sorting process (the differential speciation/extinction among species of given biota [Vrba and Gould 1986]).

In this work, we addressed crucial caveats previously identified for state-dependent diversification models (e.g., Type I error rate and model adequacy; Rabosky and Goldeberg 2015), and our results are robustly facing these caveats. Still, there might be other potential biases. First, extinction rates are known for being difficult to estimate using methods based solely on extant species (see Stadler 2013). For example, at present, we do not observe large species with small ranges because they are unlikely to originate (low speciation rate) or because the extinction rate for these species are very high? In this sense, our results suggest that these species are not currently seen because their probability of origin is low. Thus, new methods that allow estimating more accurate extinction rates, using fossil data, if these are available, could help answer this question. A second potential bias is that the QuaSSE model assumes that a quantitative trait is continuous at speciation

events (FitzJohn 2010). Here, the distance to the lower boundary of this pattern (as a measure of range size) might violate this assumption: a new species is likely to start with a small geographic range and hence a drop of the distance right after speciation event (Rosenzweig 1995). If it takes some time before another speciation event can occur, then this sudden drop in measure could explain low speciation at low distance values. In other words: species closer to the lower boundary could have an overrepresentation of young species. Since QuaSSE cannot model a drop in the distance after speciation, the method might compensate by estimating a low speciation rate at low distance values. We recognize that this is a hard issue to be addressed because it would require the development a more flexible trait-diversification model. Finally, a bias may emerge by not accounting for the potential relationship between the diversification rates and a cofactor related to our studied variable. This would imply that the results obtained would represent only a byproduct of a relationship between a cofactor (*hidden* trait) and diversification rates, as has been recently discussed by Beaulieu and O'Meara (2016). For example, in Figure 2 only small-bodied species can reach the maximum distance values, which can produce a negative correlation between body size and the distance. If the body size influences the diversification rates, then the analysis would be confounded by using the distance as the only predictor used in the QuaSSE models. This model weakness does not allow comparing directly the contribution of multiple variables on the diversification rate (a realistic scenario). In this sense, although there is no direct extension of the QuaSSE model to multiple traits, TRC (Tip-Rate Correlation) methods represent a promising approach that can complement the trait-dependent diversification analyses (Harvey and Rabosky 2017). This class of methods assesses the correlation between traits (or several) of interest across the tips of a phylogeny and tip-specific estimates of speciation rates, overcoming the need for a fully parameterized model of diversification. Furthermore, these methods have the potential to incorporate of several traits in the analysis as well as many functional relationships between speciation rate and phenotypes (Harvey and Rabosky 2017). However, its current implementation allows for a single trait and linear relationships between diversification rate and this traits.

Finally, our study shows that a simple model based on the relationship between biologically relevant species traits (such as developed by Brown and Maurer [Brown and Maurer 1987, 1989]) coupled with a macroevolutionary approach based on birth-death dynamics, improves the understanding of how the trait–diversification relationship is related to the origin and maintenance of broad macroecological patterns.

AUTHOR CONTRIBUTIONS

C.E.H. and O.I.M. conceptualized the project. O.I.M. collected the dataset, conducted all statistical analyses and wrote the first draft of

the manuscript. C.E.H., E.R.S., J.A.L., and M.M.R. edit and revise the manuscript.

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DATA ARCHIVING

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Body mass and geographic range size for furnariid species in the phylogeny used in this work.

Table S2. Phylogenetic regression analysis between geographic range size and body size.