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LINEAGE DIVERSIFICATION AND MORPHOLOGICAL EVOLUTION IN A LARGE-SCALE CONTINENTAL RADIATION: THE NEOTROPICAL OVENBIRDS AND WOODCREEPERS (AVES: FURNARIIDAE)

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Patterns of diversification in species-rich clades provide insight into the processes that generate biological diversity. We tested different models of lineage and phenotypic diversification in an exceptional continental radiation, the ovenbird family Furnariidae, using the most complete species-level phylogenetic hypothesis produced to date for a major avian clade (97% of 293 species). We found that the Furnariidae exhibit nearly constant rates of lineage accumulation but show evidence of constrained morphological evolution. This pattern of sustained high rates of speciation despite limitations on phenotypic evolution contrasts with the results of most previous studies of evolutionary radiations, which have found a pattern of decelerating diversity-dependent lineage accumulation coupled with decelerating or constrained phenotypic evolution. Our results suggest that lineage accumulation in tropical continental radiations may not be as limited by ecological opportunities as in temperate or island radiations. More studies examining patterns of both lineage and phenotypic diversification are needed to understand the often complex tempo and mode of evolutionary radiations on continents.

KEY WORDS: **Morphological Evolution, Phylogenetics, Adaptive Radiation.**

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A central aim of evolutionary biology is to understand the historical processes driving species diversification. Both the fossil record and recent molecular phylogenetic studies that address the tempo of diversification typically yield a pattern of early, rapid cladogenesis followed by a decline in diversification rate (Stanley 1973; Harmon et al. 2003; Kadereit et al. 2004; Ruber and Zardoya 2005; Kozak et al. 2006; McKeena and Farrell 2006; McPeek 2008; Phillimore and Price 2008; Gavrilets and Losos 2009), although not every radiation shows density-dependent diversification (Alfaro et al. 2009a; Esselstyn et al. 2009; Slater et al. 2010). A common interpretation of a decline in diversification is that ecological opportunity facilitated an initial burst of speciation into new adaptive zones but then diversification rate declined as niches filled over time (Gavrilets and Vose 2005; Rabosky and Lovette 2008a). This inference of process from pattern is based on the ecological theory of adaptive radiations, which hypothesizes that ecological opportunity at first fuels but then limits radiations, predicting a pattern of diversity-dependent diversification and a slowdown over time in adaptive trait evolution (Simpson 1944; Schluter 2000). The process of increased competition for limited niches and phenotypic and genomic constraints on trait evolution could explain a pattern of slowdown in the rate of diversification (e.g., Simpson 1953; Foote 1997). On the other hand, a recent study suggests that simple geographic speciation, without the intervention of niche processes, can also generate a pattern of declining speciation through time (Pigot et al. 2010). Clearly, additional studies of both lineage accumulation and trait evolution across taxonomic groups are needed to understand the range of processes underlying evolutionary radiations.

Our understanding of the processes driving diversification is incomplete. Most studies to date have used incomplete phylogenies. Missing species can yield a false pattern of decline in diversification rate over time (Nee et al. 1994; Nee 2001), potentially leading to an over-association of radiations with diversity-dependent diversification (Cusimano and Renner 2010). In addition, the majority of studies have focused on radiations that are highly spatially limited (e.g., on islands or in lakes) (Baldwin and Sanderson 1998; Lovette et al. 2002; Gillespie 2004; Losos and Thorpe 2004; Seehausen 2006). With their relatively simple geography and small areal extent, island and lake radiations may experience similar histories of initial high niche availability and low competition, followed by a filling of niches over time. In contrast, the ecological histories of continental radiations are likely much more complex and varied and may yield a different tempo and mode of diversification (Irschick et al. 1997; Barraclough et al. 1999). Because most biodiversity resides on continents (May 1994), understanding the processes underlying diversification in ecologically and historically complex continental biotas is critical. Of the continental radiations examined in detail (e.g., McPeek and Brown 2000; Kozak et al. 2006; Rabosky and Lovette 2008a), many occupy only a small portion of the continent on which they occur, and few exhibit the high morphological diversity and species richness that characterize island and lake radiations. Testing evolutionary models of diversification in densely sampled, ecomorphologically diverse, species-rich continental radiations is essential to understand fully the historical processes that produce high species richness and phenotypic diversity.

We tested models of lineage accumulation and phenotypic evolution in one of the most well-recognized and largest (293+ species) of avian continental radiations (Fitzpatrick 1982; James 1982; Remsen 2003): the Neotropical ovenbirds and woodcreepers (Furnariidae, sensu Sibley and Monroe 1990; Remsen et al. 2011). When compared to the seven other families in the infraorder Furnariides (Moyle et al. 2009), the Furnariidae is characterized by a high rate of cladogenesis and a high diversity in morphological traits associated with feeding behavior and locomotion (Claramunt 2010a). The Furnariidae also represent a truly continental radiation: 97% of currently recognized species and 100% of genera occur within South America (Remsen 2003). In contrast to most Neotropical groups, furnariids are a predominant component of the avifauna in nearly all terrestrial habitats in South America (Ridgely and Tudor 1994; Marantz et al. 2003; Remsen 2003). Furnariids are found from the snow line at over 5000 m in the Andes down to the richest bird communities in the world in lowland Amazonia, and from perpetually wet cloud forests to nearly rainless deserts. The prevalence of furnariids throughout the Neotropical landscape as well as their exceptional diversity make them a particularly appropriate group for investigating diversification at a continental scale (Haffer 1969; Fjeldså et al. 2005).

Many geological and ecological processes could affect the pattern of lineage accumulation in a radiation that spans both an entire continent and a time period including major climatic shifts (e.g., to a more arid climate $\sim$ 15 Ma; Pleistocene climatic cycles) and geological events (e.g., the uplift of the Northern Andes between 2 and 5 Ma). Here, we employ likelihood methods for detecting temporal shifts in diversification rates to provide insight into the underlying causes of diversification in this family. We assess the consistency of the best-fitting model with scenarios of a slowdown in lineage accumulation through time due to ecological constraints (Gavrilets and Vose 2005) or to stable geographic range dynamics (diversity-dependent models) (Pigot et al. 2010), with hypotheses of shifts in diversification rate associated with major geological and climatic events or evolution of key traits (a discrete change in rates), and with a hypothesis of constant rate of diversification (pure-birth and birth–death models). We also test models that allow both speciation and extinction rates to vary, because moderate levels of extinction may obliterate the signal of early rapid diversification (Rabosky and Lovette 2008b). We next test competing hypotheses for the tempo of

phenotypic evolution in the Furnariidae, including a slowdown in the rate of phenotypic evolution, a constraint on trait evolution toward selective peaks (an Ornstein–Uhlenbeck [OU] process) and a Brownian motion (BM) process. To distinguish these hypotheses, we use three approaches, including likelihood models of continuous trait evolution (Pagel 1999), a node-height test (Freckleton and Harvey 2006), and disparity through time plots (Harmon et al. 2003).

Methods and Materials

MOLECULAR DATA

We sampled 285 of the 293 recognized species (97%) and all 69 recognized genera in the Furnariidae (Table S1). For most species (89%), we sequenced two or more vouchered specimens to validate species identification or for calibration purposes, but we did not include the second individual in subsequent analyses. As outgroups, we included representatives of all closely related families in the infraorder Furnariides (Moyle et al. 2009): Formicariidae, Rhinocryptidae, Grallariidae, Conopophagidae, Melanopareiidae, and Thamnophilidae, as well as representatives of Tyrannidae and Tityridae.

We used standard methods to extract genomic DNA from pectoral muscle and to amplify and sequence six genes (see Material and Methods in Supporting information). For the majority of individuals, we amplified and sequenced three mitochondrial genes and one nuclear intron: *NADH dehydrogenase subunit 3* (ND3; 351 bp), *cytochrome oxidase subunit 2* (CO2; 684 bp), *NADH dehydrogenase subunit 2* (ND2; 1041 bp), and β-*fibrinogen intron 7* (Bf7; ∼840 bp). For at least one individual per genus, we also included a large portion of the single exons of the *recombination activating genes* RAG-1 (2904bp) and RAG-2 (1152bp). Most RAG sequences were obtained from Moyle et al. (2009). For three individuals for whom we were unable to amplify one of these genes (*Philydor pyrrhodes*, *Lochmias nematura*, and *Sittasomus griseicapillus*), we used a sequence obtained for another individual of the same species.

We edited sequences using Sequencher 4.6 (Gene Codes Corporation, Ann Arbor, MI) and aligned sequences manually using Mesquite version 2.6 (Maddison and Maddison 2009). The final alignment included 6954 base pairs and was deposited in TreeBASE (Study ID S11550). Protein-coding sequences were translated into amino acids to confirm the absence of stop codons and anomalous residues. Preliminary phylogenetic analysis suggested that Bf7 sequences for the tribe Synallaxini were probably not orthologous; therefore, we excluded these sequences from further analyses. These sequences may represent a pseudogene and were not deposited in GenBank. All remaining sequences were deposited in GenBank under accession numbers JF974355-JF975363.

PARTITIONS AND SUBSTITUTION MODELS

We estimated the optimal partitioning regime using the strategy described in Li et al. (2008) to designate partitions based on their similarity in evolutionary parameters (see Methods and Materials in Supporting information). We determined that a fully partitioned dataset (16 partitions) was the optimal partition strategy for the concatenated dataset (Table S2).

We used model selection techniques to determine the best substitution model for each partition under the optimal partition regime. With the tree obtained in the primary maximum-likelihood analysis, we used PAUP (Swofford 2003) to obtain likelihood values for all substitution models featured in Modeltest 3.7 (Posada and Crandall 1998) and calculated values of the Bayesian information criterion (BIC) (Posada and Crandall 1998; Sullivan and Joyce 2005). We identified the GTR + Γ + I model as the best model for the majority of the partitions, and the HKY + Γ + I model as the best model for the first and second codon positions of RAG 1 and all three codon positions of RAG 2.

PHYLOGENETIC INFERENCE

We conducted a joint estimation of topology and divergence times in a Bayesian framework in the program BEAST version 1.5.2 (Drummund and Rambaut 2007) under an uncorrelated lognormal model (UCLD) (Drummund et al. 2006). We unlinked substitution model, rate heterogeneity, and base frequencies across partitions. We used a Yule prior for tree shape and the default priors for the substitution model and relaxed clock parameters. A UPGMA tree was used as the starting tree. No restrictions were placed on the topology so that topological uncertainty was factored into the divergence date estimates. Because furnariid fossils are rare, relatively recent, and of uncertain relationships (Claramunt and Rinderknecht 2005), we used biogeographic events to place priors on the age of the root and on the divergence times of the most recent common ancestor (tMRCA) of 12 sets of taxa (see Methods and Materials in Supporting information).

To optimize the Markov chain Monte Carlo (MCMC) operators, we performed incrementally longer runs and adjusted the scale factors for the operators as suggested by the BEAST output. Once scale factors stabilized, we ran analyses for a total of 150 million generations across seven independent runs. Using Tracer 1.5 (Drummund and Rambaut 2007), we determined that replicate analyses converged, and all parameters met benchmark effective sample size values (>200). We identified and discarded the burn-in. Converged runs were combined in LogCombiner (Drummund and Rambaut 2007) and used to estimate the posterior distributions of topologies and divergence times as well as the maximum clade credibility (MCC) tree.

DIVERSIFICATION ANALYSES

We performed all analyses in R (R-Development-Core-Team 2008) using the Ape (Paradis et al. 2004), Geiger (Harmon et al. 2008), and Laser (Rabosky 2006) libraries. We used the MCC tree after excluding both the outgroup and ingroup samples used solely for calibration purposes (final included $n = 285$).

We used maximum-likelihood methods to compare models of lineage diversification and chose the best model using AIC. Using functions in the Laser library, we fit the following models of diversification: pure-birth (PB), birth–death (BD), Yule model with two rates (Y2R), linear (DDL) and exponential (DDX) diversity-dependent diversification, and three models that varied either speciation (SPVAR), extinction (EXVAR) or both (BOTHVAR) through time (Rabosky 2006; Rabosky and Lovette 2008b). We compared the fit of the best rate-variable model and best rate-constant model by computing the test statistic:

$$\Delta\text{AIC} = \text{AIC}_{\text{constant}} - \text{AIC}_{\text{Variable,}}$$

where $\text{AIC}_{\text{constant}}$ is the AIC score of the best rate-constant model and $\text{AIC}_{\text{variable}}$ is the AIC score of the best rate-variable model. A positive ΔAIC implies that the rate-variable model fits the data better than the rate-constant model. To avoid conditioning our results, we determined the distribution of ΔAIC over the posterior distribution of trees sampled using MCMC. To test for any over fitting of the data, we simulated 5000 phylogenies under a rate-constant model and compared the fit of the best rate-constant and rate-variable models to this null distribution. We simulated these phylogenies with 293 tips dropping eight of those tips to reflect sampling in the furnariid phylogeny (285 species with eight missing taxa).

To test for lineage-specific shifts in diversification rates, we used the MEDUSA algorithm (Modeling Evolutionary Diversification Using Stepwise AIC), which fits a series of BD models with an increasing number of breakpoints (rate shifts), and estimated the maximum-likelihood values for each set of birth and death parameters (Alfaro et al. 2009b). The method then uses a forward selection and backward elimination procedure to determine the simplest model with the highest likelihood to describe the given set of branch lengths, age, and species richness data. The threshold for retaining additional rate shifts was an improvement in AIC score of 4 units or greater (Burnham and Anderson 2003).

Another way of investigating models of diversification is to analyze the relationship between clade age and clade size. Older clades have had more time to accumulate diversity than younger clades (Labandeira and Sepkoski 1993; McPeek and Brown 2007). However, this positive relationship between age and diversity may breakdown due to clade volatility (differential extinction of clades with high and low diversification rates) (Gilinsky 1994; Sepkoski 1998), among-lineage variance in diversification rates, or ecological constraints on clade growth (Ricklefs 2006). A strong correlation between clade age and clade size, on the other hand, suggests a constant model of diversification. To assess the relationship between clade age and size in furnariids, we compared the age and species richness of 63 monophyletic groups as determined by the MCC tree. These groups corresponded in most cases to currently recognized genera, except that we included six previously monotypic genera within other genera based on the results of our phylogenetic hypothesis. For the crown age of each clade, we used the mean estimated age from the posterior distribution of trees. For clade size, we counted the number of recognized species (including those not included in the molecular phylogeny, $n = 8$; Remsen et al. 2011). Using a generalized least squares model correcting for phylogeny (Freckleton et al. 2002), we tested the prediction that clade age and clade size are positively correlated. We ran this analysis both including and excluding monotypic genera.

Extinction can affect the pattern of lineage accumulation. Simulation studies suggest that extinction can remove the signature of an early-burst radiation (i.e., an initial high rate of diversification followed by a slowdown over time), particularly under scenarios of a decline in speciation rate with a background of high relative extinction (Rabosky and Lovette 2008b, 2009). We evaluated and compared maximum-likelihood estimates of relative extinction and 95% profile-likelihood confidence intervals from the BD, SPVAR, EXVAR, and BOTHVAR models and the MEDUSA analysis. Because estimating extinction from molecular phylogenies can be problematic, we also examined theoretical expectations for scenarios of declining net diversification with a background of high relative extinction. To examine this idea under realistic parameters, we generated expected LTT curves under three scenarios of declining diversification rate (20-fold, 10-fold, and fivefold decline) each with an identical high relative extinction rate ($\varepsilon = 0.82$ [i.e., the relative extinction rate of suboscines (Ricklefs et al. 2007)]). Curves are theoretical expectations from Nee et al. (1994). We found parameters that would result in (1) three different declines in net diversification rate under an identical ε and (2) a total of 285 surviving lineages after one time unit ($t = 1$). The net diversification rate was modeled as $r(t) = \lambda_0 e^{-zt}(1 - \varepsilon)$ following Rabosky and Lovette (2009). The code used to run this analysis in R can be found in Supporting information (ExtinctionLTT.R).

MORPHOLOGICAL EVOLUTION ANALYSES

To describe ecomorphological variation, we measured 11 variables that represent the size and shape of major functional modules of avian external anatomy: bill, wing, tail, and feet. We included measurements for all species in the phylogeny except *Asthenes luizae*. We measured an average of 4.2 specimens per species (range: 1–19). Only three species were represented by a single

specimen, and most were represented by more than three. Bill length was measured from the anterior border of the nostril to tip of the bill, and bill width and depth (vertically) at the level of the anterior border of the nostrils. We took three wing measurements, all from the carpal joint and without flattening the natural curvature of the closed wing: (1) wing length to the longest primary, as a general measure of wing extent; (2) wing length to the tenth primary, the most distal one in furnarioids, which is related to the shape of the wing tip; and (3) length to the first secondary feather, which represents the width of an open wing. Tail maximum and minimum length were taken from the base of the central rectrices to the longest and shortest rectrices, respectively. The third tail measurement, an index of tail width, was measured as the width of the central rectrix at its midlength. We measured tarsus length and hallux length (including the claw) as measures of leg length and foot size, respectively. All measurements were taken with a Mitutoyo Digimatic Point Caliper by the same person (S. Claramunt) and loaded directly into an electronic spreadsheet using an input interface. Morphometric data were deposited as an associated document file in Microsoft Excel format in MorphoBank (http://www.morphobank.org) as part of the Morphological Evolution of the Furnariidae project. All morphological variables were log-transformed so that the differences between observations in the logarithmic space are proportional to differences in the original space (Ricklefs and Travis 1980).

We used AICc to compare the fit of three models of continuous trait evolution (Pagel 1999): a random walk model (BM Model), a model of constrained trait evolution toward an optimum (OU Model), and a model of deceleration ($\delta < 1$) or acceleration ($\delta > 1$) of trait evolution through time (Delta Model). To account for intraspecific variation in trait values, we incorporated standard error when fitting each model.

We then ran a node height test, which tests for accelerations or decelerations in trait evolution, by comparing the independent contrasts (IC) for a trait with the respective node height (estimate of relative age) (Freckleton and Harvey 2006). For each trait, we calculated IC incorporating measurement error (Felsenstein 2008). We then summed IC values across traits for a composite IC. We obtained node heights from the MCC tree. Using a linear model, we tested the prediction from the ecological theory of adaptive radiations of a negative correlation between the absolute values of the independent contrasts and node height. A negative correlation would imply that species are dividing niche space more finely through time, consistent with a niche-filling model. To meet model assumptions, we used the Box–Cox method (R-Development-Core-Team 2008) to determine the most appropriate transformation of the IC values for a linear model. The best transformation was a power transformation, with values raised to the power of 0.2.

We measured the time course of morphological diversification using disparity-through-time (DTT) plots (Harmon et al. 2003). Disparity is the dispersion of points in multivariate space and is usually measured as the mean squared Euclidean distance among species. However, we used the total variance instead (Van Valen 1974). The total variance is closely related to the mean squared Euclidean distance (Pie and Weitz 2005) but allowed us to take measurement error into account. We partitioned the total variance into two components, intraspecific and interspecific, using a random effect one way ANOVA, and used only the interspecific variance for the analysis. We also calculated the expected total variance under a BM model of trait evolution at each time point based on 10,000 phylogenetic simulations. We estimated the Brownian rate for the simulations using function fitContinuous incorporating measurement error. We plotted the mean subclade disparity for the observed and simulated data against node age. We also calculated the morphological disparity index (MDI), which is the area between observed and simulated clade disparity curves in standardized axes (Harmon et al. 2003). To determine the probability of obtaining a negative MDI value when the true model is BM, we computed the MDI value between our data and each of 10,000 simulated datasets. Negative values of MDI indicate that disparity through time is less than predicted under BM and that most variation is partitioned as among basal clades. Such a pattern indicates that clades tend to occupy different regions of morphological space, which is a common feature of adaptively radiating lineages (Harmon et al. 2003). The code used to run this analysis in R can be found in Supporting information (Variance Through Time functions.R).

Results

PHYLOGENETIC INFERENCE

A joint estimation of topology and divergence times in a Bayesian framework in the program BEAST version 1.5.2 (Drummund and Rambaut 2007) yielded a phylogenetic estimate for the Furnariidae with good resolution and high nodal support (>80% of nodes with posterior probability >0.95; Figs. 1 and S1).

LINEAGE DIVERSIFICATION

Lineage accumulation in the Furnariidae occurred at a constant rate during most of the 30 million year history of the radiation with a shift to a lower rate 1.7 million years ago (Fig. 2). A Yule model with two rates (Y2R) provided the best fit (rate 1 = 0.16 lineages/Ma, rate 2 = 0.05, shift point = 1.17 Ma) based on model selection using AIC. The best-fit rate-constant model was a PB model. When we compared the fit of these models (ΔAIC) to the posterior distribution of furnariid phylogenies sampled using MCMC, we found a positive distribution, implying that the Y2R

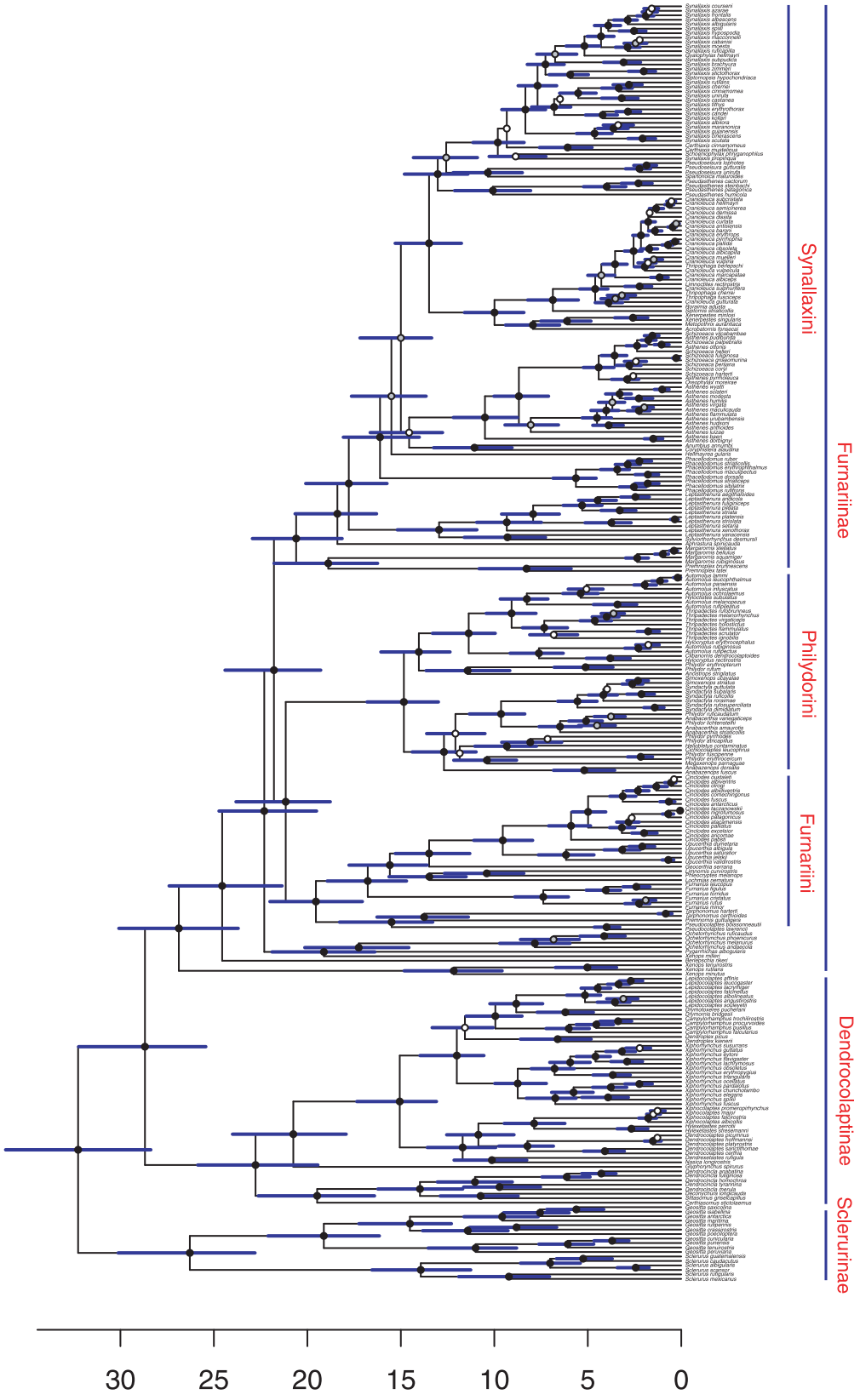

Figure 1. Bayesian estimate of phylogenetic relationships and divergence times among species of ovenbirds and woodcreepers (family Furnariidae) as inferred from a partitioned analysis of three mitochondrial and three nuclear genes. Bars at nodes indicate the 95% highest posterior density for the inferred divergence time estimates. The color of the circles at nodes indicates posterior probability support, > 95% (black), 95–75% (gray), <75% (white).

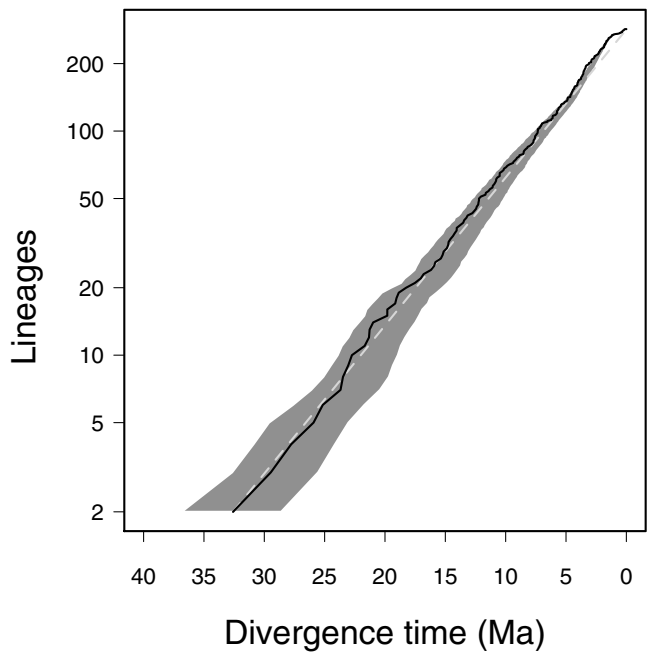

Figure 2. Near-constant lineage accumulation over time in the Furnariidae radiation. The black line represents the number of lineages through time for the maximum clade credibility tree, and the gray shaded area is the 95% quantile on the number of lineages at any given time drawn from the posterior distribution of phylogenetic trees. The dashed line indicates the expected number of lineages under a constant-rate model of diversification with no extinction.

Table 1. Summary of diversification models fitted to the branching times derived from the Furnariidae phylogeny before (above the line) and after (below the line) truncating the tree at 1.17 Ma.

Model	Log likelihood	ΔAIC[1]
Yule-2-rate	505.01	0
Diversity-dependent, linear	494.49	19.86
Diversity-dependent, exponential	492.58	22.86
Pure-birth	491.14	23.75
Speciation decline	492.37	25.28
Birth-death	491.14	25.74
Both variable	492.41	27.21
Extinction-increase	491.06	27.91
Pure-birth	476.47	0
Birth-death	476.59	1.76
Yule-2-rate	477.54	1.85
Diversity-dependent, linear	476.49	1.97
Diversity-dependent, exponential	476.47	2
Speciation exponential decline	476.61	3.73
Extinction exponential increase	476.58	3.77
Variable speciation and extinction	476.61	5.73

[1]Difference in AIC scores between each model and the overall best-fit model.

model fits the data better than a PB model. We then compared the fit of the Y2R and PB models to the null distribution from phylogenies simulated under a PB model. We found a distribution centered on zero with a long positive tail but with minimal overlap of the ΔAIC distribution tabulated from the posterior (Fig. S2). This result suggests that the Y2R model often provided a better fit than a PB model to simulated PB phylogenies. Despite this tendency to overfit the data, the Y2R model fits the observed data better than a PB model. After truncating the tree at the time of the rate shift, a rate-constant model received the strongest support (lower AIC indicates better model fit: PB AIC = –951; Y2R AIC = –949). All other models tested, including diversity-dependent diversification, received lower support (Table 1).

When we allowed rates of speciation and extinction to vary among lineages using the MEDUSA algorithm, we found strong support for two rate shifts from the background diversification rate ($r = \lambda - \mu = 0.1$; $\varepsilon = \mu/\lambda = 2.2 \times 10^{-05}$): one shift near the base of the Furnariinae approximately 23 Ma ($r = 0.16$; $\varepsilon = 2.5 \times 10^{-08}$), and a second shift near the base of the genus *Cranioleuca* approximately 3.5 Ma ($r = 0.58$; $\varepsilon = 2.5 \times 10^{-08}$).

We found a significant and positive relationship between genus age and species richness in the Furnariidae (phylogenetic GLS (Freckleton et al. 2002): including monotypic genera—$n = 63$, $R^2 = 0.57$, $F = 80.5$, $P < 9.5 \times 10^{-13}$; excluding monotypic genera—$n = 36$, $R^2 = 0.15$, $F = 5.8$, $P < 0.02$; Fig. S3). This correlation indicates that factors such as niche saturation or limits to clade size have not erased the signal of increased diversity over time (Rabosky 2009).

Maximum-likelihood estimates of extinction under a BD model indicate that extinction rates were orders of magnitude lower than speciation rates (relative extinction $\varepsilon = \mu/\lambda = 0$ [95% CI: 0, 0.105]). All other likelihood models that accounted for varying speciation and extinction rates (SPVAR, EXVAR, BOTHVAR) and for nonuniform processes (MEDUSA) provided estimates of extinction rates within this confidence interval. Low levels of extinction are unlikely to mask the signature of early burst radiations. Due to the difficulty of estimating extinction from molecular phylogenies, we also examined theoretical expectations for LTT curves in the context of declining rates of diversification and high relative extinction. When the decline in diversification is high (20- or 10-fold), the signal of early, rapid diversification is still apparent, even under high relative extinction (Fig. S4). When the decline in diversification is low (fivefold) under high relative extinction, then the result is a curve very similar to that seen under constant speciation with increasing extinction (i.e., an upturn in the number of lineages toward the present [Rabosky and Lovette 2008b]). None of these theoretical curves resemble the furnariid LTT curve, making it unlikely that the true pattern of diversification is one of declining speciation under high relative extinction.

Table 2. Summary of ΔAIC (difference between each model and the overall best-fit model) for three models of trait evolution for each morphological trait.

Morphological character	BMM[1]	DM[2]	OUM[3]
Wing length to the longest primary	**0**	1.9	1.9
Wing length to the tenth primary (wing tip shape)	**0**	1.6	1.4
Wing width	**0**	1.0	0.6
Tail maximum length	**0**	1.8	1.6
Tail minimum length	0.4	0	**0**
Tail width	1.4	0.4	**0**
Bill length	**0**	0.7	2.0
Bill width	**0**	1.2	2.0
Bill depth	**0**	2.0	2.0
Tarsus length	**0**	0.4	0.5
Hallux length	0.8	**0**	0.8

[1]Brownian Motion Model.
[2]Delta Model.
[3]Ornstein–Uhlenbeck Model.

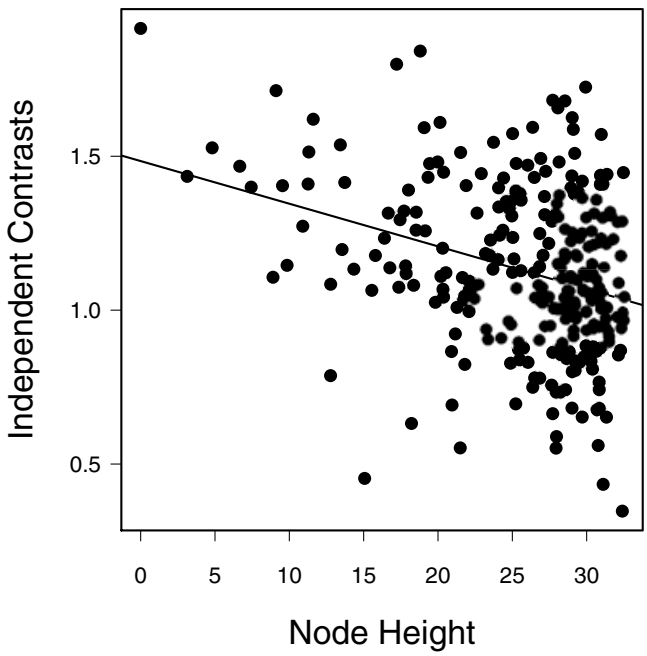

Figure 3. A negative relationship between node height and independent contrasts for morphological traits. Absolute value of the composite independent contrasts describing morphological space compared to the height (relative age) of the corresponding node. The negative relationship between node height and independent contrasts is significant ($n = 280$, $t = -5.44$, $P < 1 \times 10^{-7}$). The solid line is the best-fit line. Independent contrasts were power-transformed to stabilize variance. Lower contrast values indicate that paired comparisons are relatively similar in morphology. Node height is the distance from the root to a given node, such that the height of the root is zero.

MORPHOLOGICAL EVOLUTION

We found that a BM model provided the best fit for eight of the 11 traits. A model with a constraint on trait evolution toward an optimum (OU) described trait evolution best for two traits (tail minimum length and tail width), and the Delta model provided the best fit for one trait (hallux length). The difference in AICc values between these alternative models and the BM model were very low (ΔAICc < 2 units), suggesting that the OU and Delta models do not provide a substantially better fit than a BM model (Table 2).

We next used the node height test to detect accelerations or decelerations in trait evolution over time. Using this test, we found a significant negative relationship between the composite index of independent contrast scores and node height ($t = -5.44$, $P < 1\times 10^{-07}$; Fig. 3). This negative relationship held across individual traits. These results suggest that furnariids are dividing morphological space more finely through time, consistent with a niche-filling model.

The time course of morphological diversification indicated that relative disparity through time for morphological traits was less than that predicted under a BM model (Fig. 4). Supporting this qualitative assessment, our analysis yielded a negative MDI value (MDI = –0.156). There were no MDI values greater than zero, indicating that a BM process cannot explain morphological evolution in the furnariids. Values of disparity less than predicted under BM suggest that most variation is partitioned as among basal clade differences, indicating that basal clades tend to occupy different regions of morphological space.

Discussion

LINEAGE DIVERSIFICATION

The tempo of lineage accumulation in the Furnariidae was nearly constant through time (Fig. 2) apart from a few rate shifts near the base and near the tips of the furnariid phylogeny. Model selection and the MEDUSA analysis identified three discrete rate shifts. One of these shifts was a rate decrease that occurred recently (∼1 Ma) relative to the age of the radiation (∼33 Ma) and could be detected across the entire phylogeny. We determined that this rate shift is not a spurious result of the Yule two-rate model overfitting the data. Therefore, this shift may represent an artifact of missing phylotaxa or a real decrease in net diversification due to a geological or climatic event. In this family, many biological species comprise more than one divergent evolutionary lineage (cf. Tobias et al. 2008; e.g., Sanín et al. 2009). Many missing young lineages could yield a false signature of a recent shift to a lower rate of diversification. If true, then including these cryptic lineages may erase the recent rate shift. Another explanation for this pattern is that a real decrease in net diversification rate

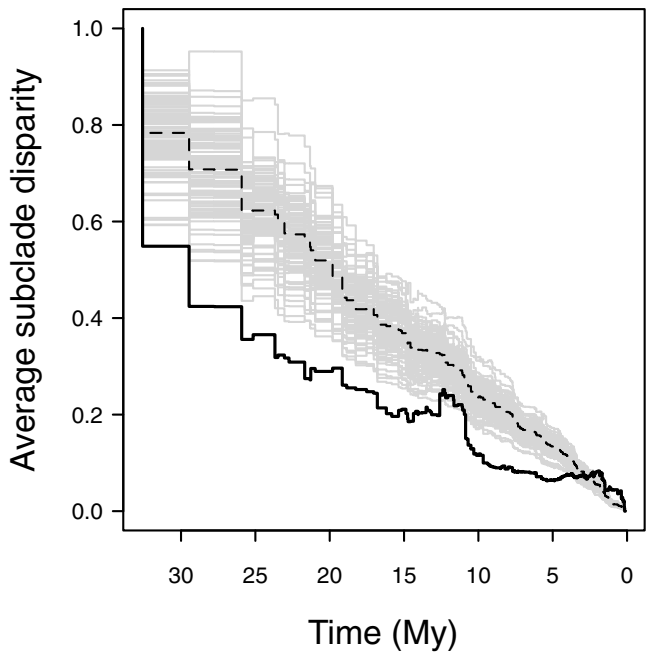

Figure 4. Relative disparity through time (DTT) for morphological traits was less than that predicted under a Brownian motion model. Disparity values closer to 1 indicate that most variation is found within subclades and values closer to 0 indicate that variation is partitioned among subclades relative to the entire clade. Solid line indicates actual disparity; dashed line indicates median expected disparity and gray lines indicate expected disparity for a sample of 100 simulations based on a Brownian motion model.

occurred approximately 1 Ma due to dramatic fluctuations in climate during the Pleistocene. At this time, distinguishing these two scenarios is not possible. However, it is important to note that neither diversity-dependent diversification nor an exponential increase in extinction can explain this recent decrease in the rate of diversification, because both models received low support (Table 1). Together, our results suggest that lineage accumulation occurred at a constant rate for most of the history of the Furnariidae.

When we allowed clades to vary in speciation and extinction rates using MEDUSA, we found evidence for at least two lineage-specific rate shifts. Both shifts were significant increases in diversification rate. The first occurred approximately 23 Ma (range: 17 – 27 Ma) near the base of the radiation containing most of the subfamily Furnariinae. Fjeldså et al. (2005) suggested that changes in cranial kinesis at the base of the Furnariinae may be in part responsible for high rates of diversification in this group. Ancestral character reconstructions or trait-dependent diversification analyses (Maddison et al. 2007) are needed to test this hypothesis. Of the three subfamilies, Furnariinae has the highest species richness, and at least one hypothesis (Irestedt et al. 2009) suggests that the radiation of this lineage was propelled by a major climatic shift to a more arid climate in South America beginning approximately 15 Ma (Zachos et al. 2001). Species in this subfamily tend to occupy more open environments and aridification creates more open environments, thus potentially facilitating speciation in this group. Our results do not support this hypothesis, because the shift in diversification rate appears to have occurred prior to the shift in climate. However, ruling out an association between diversification and climate shifts is difficult, because estimates of the timing of both often have large confidence intervals.

A second increase in diversification occurred approximately 3.5 Ma along the stem of a clade containing most, but not all, of the species in the genus *Cranioleuca.* Previous work has noted extremely low levels of interspecific genetic divergence in this species-rich group, suggesting rapid and recent diversification (García-Moreno et al. 1999), but the driving force behind this is not immediately apparent. Rapid diversification in this group does not appear to be the result of a key morphological or behavioral innovation (Claramunt 2010b). Species in this genus are typical furnariines that do not differ significantly in foraging behavior, nesting behavior, or morphology. However, plumage evolution can occur rapidly in this genus (Remsen 1984) and different traits seem to change independently from each other (Maijer and Fjeldsa 1997; Claramunt 2002). These two factors can produce multiple combinations of plumage characters in short evolutionary time. If some of these plumage traits confer reproductive isolation, then this could explain rapid speciation in this clade.

CLADE AGE VERSUS CLADE SIZE

For lineages diversifying at a nearly constant rate, older clades are expected to have had more time to accumulate diversity than younger clades (Labandeira and Sepkoski 1993; McPeek and Brown 2007). This process should generate a positive relationship between clade age and size. If species diversity were limiting diversification in the furnariids, then we would expect clade size to achieve a state of equilibrium, weakening the relationship between clade age and size. Instead, we found a significant, positive relationship between clade age and species richness, consistent with our finding of a nearly constant rate of lineage accumulation in the furnariids.

Several empirical studies on higher taxa have found a negative or no relationship between clade age and clade diversity (Magallon and Sanderson 2001 [Angiosperm clades]; Ricklefs 2006 [Avian tribes]; McPeek and Brown 2007 [Mammalian orders and Teleost fish orders]; Rabosky 2010b [Ant genera]). The correlation between age and diversity may breakdown due to clade volatility (Gilinsky 1994; Sepkoski 1998), among-lineage rate variation, or ecological constraints. Rabosky (2009, 2010b) tested whether these factors could explain the breakdown in the relationship between clade age and size in higher taxa. His results suggested that only ecological constraints, rather than clade

volatility or variance in clade diversification rates, are a strong enough effect to disrupt the expected positive relationship between clade age and diversity. If ecological constraints are the primary factor reducing the correlation between clade age and size, then furnariids appear to be less constrained by ecological factors than other higher taxa examined to date.

ROLE OF EXTINCTION

Extinction is of concern when evaluating lineage diversification because high levels of extinction can erase the signature of rapid initial lineage diversification (Rabosky and Lovette 2008b). We estimated a low level of relative extinction for furnariids ($\varepsilon = 0.10$), but estimates of extinction rates from molecular phylogenies can be incorrect (Rabosky 2010a). Estimating extinction from molecular phylogenies is problematic because BD models assume complete, resolved phylogenies and no constraints on clade growth. Simulation studies suggest that for phylogenetic trees with complete taxonomic sampling (in the case of the furnariids, 97% of species sampled), estimates of relative extinction are unbiased in the absence of among-lineage rate variation (Rabosky 2010a). As among-lineage rate variation increases in simulations, estimates of relative extinction become upwardly biased (Rabosky 2010a). Thus, our estimate of low relative extinction for the furnariids is more likely to be upwardly biased than too low an estimate. However, confidence intervals in these simulation studies are high, and it is possible that relative extinction in the furnariids is higher than we estimated.

Simulation studies suggest that moderate-to-high levels of extinction can remove the evidence of rapid early diversification followed by a slowdown (Rabosky and Lovette 2008b, 2009). A slowdown in diversification can occur via several different scenarios, including a decline in speciation, an increase in extinction, or both. In simulations of declining speciation with no extinction, lineage accumulation curves show the expected slowdown in diversification (Rabosky and Lovette 2008b). In simulations of increasing extinction under constant speciation, the number of lineages increases toward the present. This "pull of the present" can create an apparent excess of recent lineages. Thus, a slowdown in diversification due to increasing extinction through time yields a pattern of increasing diversification toward the present rather than a pattern of constant diversification. We do not find an upturn in the number of lineages in the furnariid LTT plot; instead, we find an LTT curve nearly indistinguishable from that expected under constant diversification (Fig. 2). This suggests that neither declining speciation under zero extinction nor increasing extinction under constant speciation can explain the pattern of furnariid diversification. This result is supported by model fitting in that neither the SPVAR nor the EXVAR (variable speciation or extinction through time) models received strong support. However, a more complex model of varying and nonuniform speciation and extinction rates could potentially generate a pattern nearly indistinguishable from a constant rate model.

There may be certain scenarios in which a decline in speciation coupled with a high level of relative extinction could yield a pattern of lineage accumulation difficult to differentiate from constant diversification. In simulations of a decline in speciation, the signature of the decline is reduced as the relative level of constant extinction is increased (Rabosky and Lovette 2009). Under relative extinction levels of 0 to 0.75, the signature of a decline in diversification is still apparent but less pronounced. And under extremely high relative extinction (0.99), there is an upturn in the number of lineages toward the present. However, relative extinction levels between 0.75 and 0.99 might result in a pattern similar to constant diversification. If furnariids have a high level of relative extinction, then it is possible that the true scenario of furnariid diversification is one of declining speciation with a high level of background extinction. However, none of the theoretical LTT curves generated under scenarios of declining diversification and high relative extinction rate ($\varepsilon = 0.82$ [e.g., estimated relative extinction rate in the suboscines (Ricklefs et al. 2007)]) resembled the furnariid LTT curve, making it unlikely that the true pattern of diversification is one of declining speciation under high relative extinction.

MORPHOLOGICAL EVOLUTION

Theory suggests that as organisms diversify into new adaptive zones, morphological evolution should be rapid at first and then slow as ecological opportunities become limited (Simpson 1944). If morphological evolution in furnariids is a function of ecological opportunity, then we predicted that we would find support for (1) furnariids diversifying into new adaptive zones, (2) early and rapid morphological evolution followed by a significant slowdown, and (3) niche saturation. Consistent with the first prediction, the disparity through time plot indicated that furnariids partitioned morphological disparity among rather than within clades. This finding suggests that furnariid lineages evolved along distinct morphological trajectories through time, probably exploring different adaptive zones. Providing support for the third prediction, we found evidence that furnariids have divided morphological space more finely through time, as the absolute contrast in morphological trait values decreased from the root to the tips in the node height test. This pattern is usually indicative of niche saturation. However, model selection did not provide support for the second prediction of decelerating trait evolution (Delta < 1). Instead, evolution of most of the traits examined appears consistent with a BM process. Altogether, our results suggest that furnariids diversified early along different morphological trajectories and the difference among these trajectories (or adaptive zones) has become smaller over time, but morphological evolution has not slowed. Instead, traits appear to be evolving according to a random walk process.

The pattern of morphological evolution in furnariids is more consistent with an early burst of diversification, as found in *Dendroica* warblers (Rabosky and Lovette 2008a), than with a lineage experiencing nearly constant diversification through time. Partitioning of disparity among rather than within clades is more often associated with lineages undergoing early, rapid cladogenesis, whereas equal partitioning of disparity within and among clades is more often associated with lineages exhibiting constant diversification (Harmon et al. 2003). This pattern of association between disparity and diversity is often considered evidence that lineages exploring new adaptive zones undergo bursts of lineage diversification (Burbrink and Pyron 2010). We find evidence of furnariids exploring new adaptive zones, but not of an excess of early speciation events. Niche saturation is also more consistent with a radiation undergoing diversity-dependent diversification. For example, as the diversity of competing lineages present on an island increases, *Anolis* lizards divide morphological space more finely (Mahler et al. 2010). A study of the evolution of feeding adaptations in Old World leaf warblers (*Phylloscopus* spp.) also found evidence of niche saturation limiting phenotypic evolution (Freckleton and Harvey 2006). If speciation is linked to ecological opportunities, then niche saturation should be associated with a decline in speciation rate. However, in the furnariids, we find evidence of niche saturation but not of a decline in diversification. Only the likelihood models provided evidence of uniform morphological evolution with no evidence of limits on clade growth, consistent with a radiation undergoing constant lineage accumulation.

Inconsistency between disparity and diversity analyses could indicate either that morphological analyses are picking up a signature of early, rapid lineage accumulation that was not detected by the diversification analyses or that the pattern of disparity and diversity are not tightly linked in the furnariid radiation. As mentioned earlier, there are factors, such as moderate-to-high levels of extinction, that can erase the signature of early, rapid diversification (Rabosky and Lovette 2009). This signature might have disappeared from the phylogeny but remains apparent in the morphological data. A recent analysis of disparity and diversity in modern whales (Neoceti) also could not distinguish lineage diversification from a Yule model but found evidence of niche saturation and a negative MDI (Slater et al. 2010). This study concluded that the signature of an adaptive radiation might be retained in morphological traits even after it has been erased from the structure of a phylogeny. However, if this was the case in the Furnariidae, then we would have expected limitations on clade growth leading to a low correlation between clade age and size; instead, we found a significant correlation between clade age and size. This result does not provide evidence against ecological limits on lineage accumulation but does suggest that it is a less likely interpretation of the data. The furnariid radiation might instead exhibit real differences in patterns of disparity and diversity, indicating either that the furnariid radiation is on a trajectory to slow down but has not done so yet or that speciation is not linked tightly to ecological opportunities in this group.

Because the Furnariidae are an exceptional radiation, characterized by both a high rate of cladogenesis and high diversity in morphological traits (Claramunt 2010a), we predicted that this group would show signatures of an adaptive radiation (Gavrilets and Losos 2009), including a slowdown in lineage accumulation and in phenotypic evolution over time. Although we find some evidence of the latter, we did not find evidence of the former, which leads us to consider how the spatial and temporal distribution of ecological opportunities across radiations may affect patterns of lineage accumulation. Most island and lake radiations probably experienced one period of open niches that facilitated rapid speciation (Seehausen 2006; Gavrilets and Losos 2009). If these radiations were able to continue to colonize new areas, such as nearby islands, then a constant rate of diversification could be maintained via a series of new ecological opportunities. For example, the Southeast Asian shrew (*Crocidura*) radiation on the Southeast Asian archipelagos has a near-constant rate of lineage diversification that may be associated with its continued colonization of new islands (Esselstyn et al. 2009). However, in most island or lake radiations, once niches filled, diversification rate could only decline. For example, successive radiations of cichlids show early bursts and then declines in diversification (Seehausen 2006) as successive radiations of *Anolis* lizards show declines in phenotypic diversification (Mahler et al. 2010). In contrast, the Furnariidae span an entire continent and a time period including major climatic shifts and geological events; thus, they have experienced a series of ecological opportunities over time due to dynamic habitat and range changes.

Concurrent with the furnariid radiation in South America, dramatic geoclimatic changes, from the uplift of the Andes to the development of the Amazon riverine system, created abundant opportunities for both geographic and ecological speciation. Geological studies suggest that the central and northern Andes rose in a series of pulses over the past 25 million years (Gregory-Wodzicki 2000), creating new vegetation zones and changing the organization of the Amazon and Paraná river basins several times (Hoorn et al. 1995; Figueiredo et al. 2009). These biogeographic events created multiple barriers to dispersal as well as a series of new habitats into which furnariids could radiate. This continuous creation of new barriers and niches may have facilitated near-constant diversification in the furnariid radiation in spite of constraints on phenotypic evolution. As diversification patterns and ecological histories of continental radiations are examined with the attention given to island radiations, continental radiations will likely prove to be complex and varied in their tempo and mode of lineage and phenotypic diversification.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Maximum clade credibility (MCC) tree of the Furnariidae. MCC tree inferred using BEAST version 1.5.2.

Figure S2. Distribution of ΔAIC test statistic calculated from the posterior distribution of furnariid phylogenies sampled using MCMC (black) and from a null distribution of phylogenies simulated under a constant-rate model (gray).

Figure S3. Species richness increases with clade age.

Figure S4. Expected LTT curves under an identical high relative extinction rate ($\varepsilon = 0.82$) and different net diversification rates (20fold, 10fold and fivefold decline from left to right) with 285 surviving lineages.

Table S1. Accession numbers and locality information for samples included in the Furnariidae phylogeny.

Table S2. Statistics for selection of the best partitioning strategy.Supporting Information may be found in the online version of this article.

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