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**TITLE:** Niche evolution and diversification in a Neotropical radiation of birds (Aves: Furnariidae)

**RUNNING HEAD:** Furnariid Niche Evolution and Diversification

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## **ABSTRACT**

Rapid diversification may be caused by ecological adaptive radiation via niche divergence. In this model, speciation is coupled with niche divergence and lineage diversification is predicted to be correlated with rates of niche evolution. Studies of the role of niche evolution in diversification have generally focused on ecomorphological diversification but climatic-niche evolution may also be important. We tested these alternatives using a phylogeny of 298 species of ovenbirds (Aves:

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Furnariidae). We found that within Furnariidae, variation in species richness and diversification rates of subclades were best predicted by rate of climatic-niche evolution than ecomorphological evolution. Although both are clearly important, univariate regression and multivariate model averaging more consistently supported the climatic-niche as the best predictor of lineage diversification. Our study adds to the growing body of evidence suggesting that climatic-niche divergence may be an important driver of rapid diversification in addition to ecomorphological evolution. However, this pattern may depend on the phylogenetic scale at which rate heterogeneity is examined.

**KEYWORDS:** diversification, adaptive radiation, niche, morphology, climatic-niche, Furnariidae

**DATA ARCHIVAL:** Morphometric data were deposited as an associated document file in Microsoft Excel format in MorphoBank (<http://www.morphobank.org>) as part of the Ecomorphological Evolution of the Furnariidae project from a previous study (Derryberry et al. 2011). All locality data is accessible through the open access resources of ORNIS, Macaulay Library, Xeno-Canto, and eBird.

## INTRODUCTION

The ecological theory of adaptive radiation posits that rapid diversification is driven by ecological adaptive radiation in which speciation is coupled with niche divergence (Schluter 2001). In this model, diversification rates should be positively correlated with rates of niche evolution. Although theoretical and empirical studies aimed at identifying clades with elevated diversification rates are widespread (Magallón and Sanderson 2001; Alfaro et al. 2009; Rabosky et al. 2014a), the predicted association between increased diversification rate and rapid niche evolution is seldom tested.

Niche evolution can occur in two general, non-mutually exclusive ways. First, species may diverge in traits directly related to resource use such as micro-habitat preferences (MacArthur 1958; Pianka 1969; Roderick and Gillespie 1998) and foraging strategies (Wagner et al. 2009). Here, niche divergence can be measured by morphological differences related to resource acquisition (Lack 1971; Liem 1973; Losos et al. 1997). We use the term ecomorphology for these types of morphological traits (Losos 1990). Empirical evidence indicates that ecomorphological divergence can reduce competition among lineages (Losos et al. 1997), which is often invoked to explain cases of rapid diversification (Grant 1999; Schluter 2000; Gavrillets and Losos 2009).

Alternatively, species may diverge in macro-habitat preferences (Baldwin 1997; Ingram 2011) or in climatic tolerances (Rice et al. 2003; Graham et al. 2004; Martínez-Cabrera and Peres-Neto 2013). These traits can be represented by the climatic-niche, which is the range of climatic conditions that a species occupies (Peterson et al. 2011). Speciation rates can be accelerated by adaptation to local climates, habitats or both (Endler 1977; Doebeli and Dieckmann 2003). Climatic-niche evolution also allows colonization of new geographic regions with further opportunities for allopatric speciation (Hughes and Eastwood 2006).

If niche evolution is associated with speciation, rates of niche evolution should be positively correlated with metrics of lineage diversification. Empirical evidence of this association is growing. Rabosky et al. (2013) found a strong positive relationship between rates of morphological evolution and rates of speciation in the ray-finned fishes. Across 16 phylogenetically non-overlapping clades of salamanders, Adams et al. (2009) found no correlation with net diversification rates. However, across these same clades, Rabosky and Adams (2012) found that temporal variation in diversification rates obscured the positive relationship between rates of morphological evolution and species richness. The four prior studies of which we are aware that examined the role of climatic-niche divergence found a positive relationship with lineage diversification rates (Kozak and Wiens 2010; Martínez-Cabrera and Peres-Neto 2013) and species richness (Title and Burns 2015). However, no empirical study has

examined the relative importance of climatic-niche versus ecomorphological divergence on lineage diversification.

Here, we examine the role of niche evolution in diversification using the Neotropical bird radiation of ovenbirds, woodcreepers, leaftossers and miners (Passeriformes: Furnariidae) as a model system. Furnariidae constitutes one of the most species-rich bird families in the world (Remsen 2003). Furnariids are insectivorous yet utilize a large diversity of microhabitats and associated foraging substrates, some highly specialized (Remsen 2003). Most members of the family specialize on a single foraging substrate such as tree trunks, bromeliads, bamboo stems, bare ground, suspended dead leaves, a single species of palm tree, fallen logs and even the intertidal zone. This diversity of foraging substrates is reflected in the family's extensive interspecific variation in tail, foot, leg and bill dimensions (Figure 1). Indeed, the ecomorphological diversity of Furnariidae exceeds that of other closely-related families (Claramunt 2010). The ecomorphological diversity of Furnariidae is mirrored in the outstanding diversity of environments they occupy. Furnariid species occur in virtually every terrestrial ecosystem in South America, from the bases of Andean glaciers at 5000 m above sea level to the lowland Amazon rainforest (Stotz et al. 1996; Remsen 2003). While some clades have diversified primarily within a single habitat class or environment, others appear to have speciated across habitats and climatic gradients (Remsen 2003; Sabat et al. 2006; Irestedt et al. 2009).

If niche divergence drives speciation then we predict that rates of niche evolution should be correlated with variation in metrics of lineage diversification. We used ecomorphological data and climatic data for the entire radiation of Furnariidae to examine correlations between rates of niche evolution and both species richness and diversification rate across phylogenetically non-overlapping clades. We also employed a Bayesian modeling framework (Rabosky 2014) to determine if the dynamics of lineage diversification are similar to the dynamic of niche evolution.

## MATERIALS AND METHODS

### *Phylogeny and taxon sampling*

Data collection and phylogenetic comparative analyses were based on a previously published analysis of 284 of the 301 recognized species in the family Furnariidae (Derryberry et al. 2011; Remsen et al. 2014; TreeBASE 11550), including all recognized genera. For our analyses, we used a random sample of 1000 time-calibrated trees from the posterior distribution of a Bayesian joint estimation of topology and divergence times (BEAST v1.5.2) based on three mitochondrial genes and two nuclear introns, as well the maximum clade credibility (MCC) tree (Derryberry et al. 2011). Seventeen species were not sampled in the phylogeny yet their sister species' (or in two cases, sister clades) were known based on established taxonomic affinities (Remsen et al. 2014). For the PGLS analysis, we manually inserted these unsampled species into the phylogeny by adding a terminal branch to the midpoint of their sister lineage's branch using the R package *addTaxa* (Mast et al. 2015).

### *Ecomorphology*

To describe ecomorphological variation, we made linear measurements of 11 variables from the four major functional units of avian external anatomy related to resource acquisition: the bill, wings, legs and tail. The measurements examined were bill length, bill depth, bill width, wing length, wing length to the 10<sup>th</sup> primary, wing length to the first secondary feather, tarsus length, hallux length, maximum and minimum tail length, and tail feather width. Details on these measurements can be found in Claramunt (2010). We measured an average of 4.2 specimens per species (range: 1–19). All measurements were taken with a Mitutoyo Digimatic Point Caliper by S. Claramunt and loaded directly into an electronic spreadsheet using an input interface. Morphometric data were deposited as an associated document file in MorphoBank (<http://www.morphobank.org>) as part of the

Ecomorphological Evolution of the Furnariidae project. Measurements of two species not included in the morphological analysis of Derryberry et al. (2011) were made by G. Seeholzer (*Asthenes heterura* and *Pseudoseisura cristata*) and included in the analysis.

We analyzed size and shape variation separately. We log-transformed all variables to analyze these log-normal measurements in an arithmetic scale for proportional measurements (Gingerich 2000) and computed the mean for each species. We calculated the size of each species as the mean of the 11 log-transformed ecomorphological variables, i.e. the logarithm of the geometric mean size (Mosimann 1970). We calculated a vector of shapes for each species by subtracting its size from each of its log-transformed ecomorphological variables (Mosimann 1970; Mosimann and James 1979). We partitioned these 11 shape variables into their respective functional units (bill, wings, legs and tail) and conducted a phylogenetic principal components analysis on each unit (PPCA, Revell 2009). We used the function ‘phyla.pca’ in the *phytools* library in R (Revell 2012) on the covariance matrix of the mean species values for each functional module’s shape variables; we used a Brownian motion correlation structure based on the MCC tree. Following the Kaiser criterion for PCAs on the covariance matrix, we retained the first principal component from each functional unit’s phylogenetic PCA. Hereafter we will refer to these principal components as bill shape, wing shape, leg shape and tail shape. Our biological interpretations of the PC axes are summarized in Table 1. Factor loadings, eigenvalues and percent variance are presented in Table S1.

### *Climatic-niche*

The realized climatic-niche is the range of climatic conditions that a species occupies (Soberón and Peterson 2005). We quantified the realized climatic-niche using bioclimatic data extracted from occurrence records for each species. We gathered 23,588 georeferenced locality records (mean = 79.4 records/species, range = 1:786) representing all furnariid species. We obtained

the locality records from three general sources: specimens, audio recordings and observational records. Specimen records were obtained from ORNIS ([www.ornisnet.org](http://www.ornisnet.org)). Audio records were obtained from Macaulay Library of Natural Sounds (Cornell Lab of Ornithology) and Xeno-Canto ([www.xeno-canto.org](http://www.xeno-canto.org)). The coordinates of all documented records (both specimens and audio recordings) included in this study were vetted for accuracy using gazetteers. The third group of records came from observational data gathered by the eBird citizen science initiative (May 2013 release, Sullivan et al. 2009), which are extensively vetted by expert review ([www.ebird.org](http://www.ebird.org)). To further ensure accuracy, we applied additional filters to the observational records. For each species, we then thinned all localities so that no two localities occurred within 1 km of each other, the resolution of the climatic data, except for species represented by ten or fewer localities.

For each locality record, we extracted elevation and 19 bioclimatic variables from the BioClim database of present-day climatic conditions (Hijmans et al. 2005) and obtained each variable's mean value for all species. As for the shape data, to reduce the dimensionality of the climatic data, we conducted a PPCA (Revell 2009) on the mean species values for the bioclimatic variables using the MCC tree. To increase the interpretability of the PCA axes, we removed redundant variables from the dataset prior to ordination. Our final bioclimatic variable set included elevation, four temperature variables and five precipitation variables (Table S2). Because the bioclimatic variables were in fundamentally different units for temperature (°C) and precipitation (mm) we used the correlation matrix as opposed to the covariance matrix in the phylogenetic PCA (Flury 1997). Following the Kaiser criterion for PCAs on the correlation matrix, we retained the first three eigenvectors, which had eigenvalues greater than one. These first three eigenvectors explained 75% of the climatic variation. Our biological interpretations of the climatic-niche axes are summarized in Table 1. Factor loadings, eigenvalues and percent variance are presented in Table S2.

Our study quantifies the realized climatic-niche, which is the manifestation of intrinsic physiological tolerances as well as biotic interactions (competition, predation, disease, etc.), dispersal



capabilities, and history (Pearson and Dawson 2003). Although the underlying trait of interest is the fundamental niche (Peterson et al. 2011), we know of no practical method of disentangling the effects of these processes on the realized climatic-niche from presence information alone. Further, our aim is to compare relative levels of differentiation in the climatic-niche among furnariid species rather than to precisely delineate the climatic-niche of any one species. We therefore assume that the differences in the realized climatic-niche among species are proportional to the differences in their fundamental climatic-niche. We also note that the differences in the realized climatic-niche among furnariid species correspond to biologically meaningful differences in overall vegetation and macro-habitat preferences at the continental scale encompassed by this study. Although more complex modeling approaches are often used to quantify climatic niches (Phillips and Dudik 2008; Peterson et al. 2011), at phylogenetic and geographic scales similar to our study, such models have been found to give results equivalent to a phylogenetic PCA on mean species values (Title and Burns 2015).

#### *Rate correlations among clades*

We divided the furnariid tree into a set of non-overlapping clades by extracting the most inclusive clades from the tree whose crown ages were as old or younger than a predefined age threshold. Visually, this is akin to drawing a line down a phylogeny at a given age and extracting the clades that are as old or younger than the line (Fig. 1). We used the stem age of *Craniroleuca* as our threshold. Because topologies and branch lengths differ across the posterior distribution of trees, the stem age of *Craniroleuca* varied from tree to tree. The *Craniroleuca* clade was defined by the nodal location of the most strongly supported rate shift in the BAMM diversification analysis (see Results) and constituted a monophyletic group for all trees in the posterior distribution. We kept only clades with a minimum of five species and a maximum crown age not exceeding the stem age (given the tree) of the *Craniroleuca* clade. Due to variation in topology and branch lengths across the posterior, our approach resulted in varying numbers of clades for each tree ranging from 8 to 21, with a median

of 16 clades. Division of the MCC tree resulted in 16 clades. Information on clade membership and phylogenetic relationships for the MCC tree division can be found in Table 2, Table S3 and Fig. 1.

We analyzed the relationships between diversification rates and species richness with rates of trait evolution among clades using phylogenetic generalized least-squares regression (PGLS, Freckleton et al. 2002; Revell 2010). We estimate rates of lineage diversification using a birth-death model, *bd* function in the *laser* R package (Nee et al. 1994). We estimated the rate of niche evolution for each clade as the Brownian rate parameter ( $\sigma^2$ ) for each niche axis (size, bill shape, wing shape, leg shape, tail shape, ePC1-ePC3) for all clade divisions from the posterior distribution of trees. To obtain the correlation structure we used a tree with a single random representative of each clade. Predictor variables in our models were the three climatic-niche axes (ePC1-ePC3), the four shape axes, and body size. We also included crown age as a predictor. We compared models resulting from all possible combinations of these predictor variables ( $n = 511$ ) for the birth-death diversification rate and log species richness. We ran each model across the 1000 sets of parameter estimates for each of the 1000 trees sampled from the posterior distribution. For each tree in the posterior we compared models using  $AIC_c$  and computed  $AIC_c$  weights (Symonds and Moussalli 2011). We report all model parameters as the median value from across the posterior distribution. All PGLS analyses were conducted in the R v. 3.1.2 statistical computing environment (R Development Core Team 2011) using the ‘*pgls*’ function in the *caper* package (Orme et al. 2013).

### *BAMM Diversification Dynamics*

The analysis of rate correlations among clades allows for variation across clades but assumes that lineage diversification rates are uniform within clades. To test this assumption, we modeled the diversification dynamics of Furnariidae as a heterogeneous mixture of diversity-dependent and constant-rate diversification processes (i.e. rate regimes). We used the Bayesian modeling framework

BAMM (Rabosky 2014), which employs a transdimensional Markov Chain Monte Carlo process to estimate the posterior distribution of the likely locations of regime shifts. A given rate regime is characterized by its own dynamic rate that may vary through time. Shifts between regimes may occur anywhere on the phylogeny. BAMM models the number of total shifts across the tree under a compound Poisson process and makes no *a priori* assumptions about the locations of regime shifts. Each unique configuration of shift presences and absences on one or more branches in the phylogeny is referred to as a distinct shift configuration and the MCMC samples shift configurations in proportion to their posterior probability (for additional information see Rabosky 2014; Rabosky et al. 2014). BAMM estimates rates of both speciation and extinction, rather than a composite diversification rate. Because our question is focused on the effect of niche divergence on speciation (Rabosky et al. 2014a), we focus on estimated speciation rates.

We used BAMM 2.5 to run three separate analyses with different starting seeds for 50 million generations. We determined appropriate priors using `setBAMMpriors` function in the R package `BAMMtools` 2.0.2 (Rabosky et al. 2014b). We checked for convergence with log-likelihood plots and ensured effective sample size of the log-likelihood and the number of shift events were both above 200. We accounted for incomplete taxon sampling analytically by providing the proportion of species missing for furnariid clades (Table S5). We also examined whether the posterior distribution sampled by BAMM was sensitive to the prior distribution of the proposed number of rate shifts (Moore et al. 2016), as specified by the hyperprior parameter `expectedNumberOfShifts`. We ran BAMM using `expectedNumberOfShifts` equal to 1, 10, 50, 100, 250, and 500.

We assessed the evidence for multiple shifts using Bayes factors with `BAMMtools`' function `computeBayesFactors`. We identified the most likely shift locations by analytically removing shift configurations with shifts that occurred at very low frequencies in the posterior following (Rabosky et al. 2014b). To do this we calculated the prior and posterior probability of models with one rate shift and models with no rate shifts for each branch, which we used to compute the marginal odds

(hereafter nodal marginal odds).

We also explored niche diversification dynamics using BAMM. However we found that the posterior distribution was sensitive to the prior for the number of rate shifts. This sensitivity was likely due to combination of rate heterogeneity and the inadequacy of underlying model of trait evolution, Brownian motion (see *Model Fitting and Model Adequacy*) for the traits examined. We present these results and discussion of BAMM's behavior with respect to our trait data (climatic-niche and morphology) in the Supporting Information.

### *Model Fitting and Model Adequacy*

We estimated the rate of trait evolution for PGLS from a Brownian motion (BM) model. Prior to drawing conclusions based on a BM model it is important to assess the adequacy of BM for modeling the evolution of both morphological traits and the climatic-niche (Boettiger et al. 2012; Boucher et al. 2014) and if not adequate, to determine in what ways the data deviates from a BM model. Tests of relative model fit (AIC rankings) do not give any information about how good, in absolute terms, a model describes the evolution of a trait.

We determined the absolute fit of BM to our data as well as alternative models of trait evolution that allowed for constraints (Ornstein-Uhlenbeck (OU)), rate variability through time (delta model), and punctuational evolution (kappa model). We compared summary statistics derived from the empirical maximum-likelihood parameter values of the model to a distribution of these same summary statistics derived from 1000 datasets simulated under the same model (Pennell et al. 2015). Six summary statistics are calculated for each dataset based on independent contrasts (Felsenstein 1985) which capture the common ways that continuous trait data may deviate from the expectations of BM. Because these summary statistics are used for testing deviations from BM, for the non-BM models we transformed the tree so that the branch lengths were, 1) proportional to the amount of

variance expected accrue along it based on the parameter values of the model, and 2) standardized so that the distribution of trait data on the tree was equal to that of a BM model with  $\sigma^2$  of 1 (Pennell et al. 2015). We fit models with the R package *geiger* (Harmon et al. 2007). We transformed trees, simulated data, and calculated summary statistics with the R package *arbutus* (Pennell et al. 2015).

We compared these four alternative models of trait evolution across the entire Furnariidae phylogeny and for the subclades in the PGLS analysis (both using the MCC tree). For each trait-by-model combination we simulated 1000 datasets and compared the distribution of the simulated summary statistics to the empirical ones. We report p-values that represent the two-tailed probability that the observed summary statistic falls within its simulated distribution. The lower the p-value the more likely that the model is inadequate (Pennell et al. 2015). We considered tests with p-values < 0.05 to be evidence of significant deviation from the proposed model. For comparison, we also determined the relative fit of the four models to our data using  $AIC_c$ .

## RESULTS

### *Model Fitting and Model Adequacy*

Model adequacy tests revealed widespread deviations from the expectations of the models of trait evolution when assumed over the entire Furnariidae radiation (Table 3). Of all niche axes, size, bill shape, and wing shape appeared to deviate the least from the expectations of kappa and Brownian models. For both models, the only major deviation came from the  $C_{VAR}$  statistic, which suggests rate heterogeneity (Pennell et al. 2015) but nonetheless supports a speciation model for these ecomorphological niche axes. This was not the case for leg shape, tail shape, and the three climatic-niche axes, all of which deviated considerably from the expectations of all models analyzed.

We recovered strikingly different results for the model adequacy tests of each subclades selected for the PGLS analysis. We found that BM was overwhelmingly supported as the best-fit model across clades and niche axes relative to the OU, delta, and kappa models (Table 4). In most cases, observed summary statistics fell within the distributions simulated under pure BM (Table 4), indicating that the niche axes did not deviate significantly from the expectations of BM motion at the subclade level.

Many of the subclades were small with less than ten tips (Table 2). For such clades, there will not be a strong signal of departures from a BM model, even if they are evolving under an alternative (but similar) model such as OU (but see Cooper et al. 2015 regarding a bias towards OU models for small clades). Regardless, our goal was not to determine the mode of trait evolution precisely but to estimate the rate of trait evolution. We found the BM model to be a good approximation for this purpose at this level of sample size. Trying to use more complex models of trait evolution just to estimate the rate of evolution may not be justified and may result in biased estimates (Cooper et al. 2015, Ho & Ané 2014).

### *PGLS Regressions*

We examined correlations between species richness and rates of diversification with rates of niche evolution (Table 2) using PGLS regression across the posterior distribution of furnariid trees. We found that the rates of evolution of the primary and tertiary climatic-niche axis (ePC1, ePC3), bill shape, leg shape, and size were all significant univariate predictors of diversification rate and species richness (Fig. 2). The best univariate predictors of diversification rate were bill shape (median adj.  $R^2 = 0.565$ ) and ePC1 (median adj.  $R^2 = 0.538$ ). In contrast, ePC1 was the best predictor of species richness (median adj.  $R^2 = 0.552$ ) followed less closely by bill shape (median  $R^2 = 0.464$ ). To determine the relative effect of each predictor while controlling for the influence of all other

predictors we used AIC model averaging (Burnham and Anderson 2002). We found considerable model uncertainty when we compared all possible univariate and multivariate models, indicated by universally small AIC<sub>c</sub> weights (wtAIC<sub>c</sub> < 0.05), further justifying a model-averaging approach. The summed AIC<sub>c</sub> weight (wtAIC<sub>c</sub><sup>\*</sup>) is a cumulative estimate of the importance of a predictor controlling for all other predictor variables. We found that the primary climatic-niche axis (ePC1) was the best predictor of both diversification rate and species richness based on its high summed wtAIC<sub>c</sub> (Table 5a). The next best predictor was leg shape, but it did not approach the importance of ePC1. Finally, we found ePC1 to be a stronger predictor of species richness than diversification rate relative to the other predictors (Table 5).

The *Cranioleuca* clade had the highest diversification rate as well as some of the highest rates of climatic-niche and ecomorphological evolution, potentially driving the significant positive associations but our results were robust to the exclusion of the *Cranioleuca* clade (Fig. S1, Table S6).

#### *Bayesian Analysis of Lineage Diversification*

We found strong evidence for heterogeneity in speciation rates across Furnariidae. Bayes factor model support for one vs. two and two vs. zero shifts were essentially equal (Bayes factor = 24.6 and 24.8, respectively). The most strongly supported rate shift occurred at the base of the genus *Cranioleuca* (Fig. 3a), whereas the location of the second shift was undetermined. After filtering non-core shift locations with low marginal odds, we identified 25 distinct shift configurations that were sampled more than expected based on the prior alone. These configurations cumulatively accounted for 95% of the posterior probability (Fig. 3b). Of the core shifts in these configurations five included a rate shift at the base of or within the *Cranioleuca* clade and occurred in 76% of the posterior distribution. This clade contains all members of the arboreal spinetails, *Cranioleuca*, among which are embedded the monotypic genera *Limnocyttus* and *Roraimia*, as well as the six species of the

paraphyletic genus *Thripophaga*, the softtails. These results were consistent across all three independent BAMM runs and were robust to changes in the prior expectations for the number of rate shifts (Fig. S3).

The rate shift at the base of the *Cranioleuca* clade had a substantial effect on the rate of speciation. The mean time-averaged speciation rate across the posterior distribution of shift configurations for *Cranioleuca* was 0.45 species per myr (90% HPD 0.19 – 0.65), over three times greater than the mean, 0.16 species per myr (90% HPD 0.14 – 0.17), for the rest of Furnariidae.

## DISCUSSION

We examined patterns of variation in rates of niche evolution and their relative power to explain variation in rates of lineage diversification. As predicted by several evolutionary theories including the ecological theory of adaptive radiation (Schluter 2000) and punctuated equilibrium (Gould and Eldridge 1977, Ricklefs 2004), we found that rates of bill shape evolution and, to a lesser degree, size and leg shape evolution, were associated with variation in diversification rates and species richness among furnariid clades (Fig. 2). However, we also found that the rate of climatic-niche evolution was a strong predictor of diversification rates and species richness. When these alternative models were compared using an information-theoretic approach, we found that the rate of climatic-niche (ePC1) evolution was the best predictor of diversification rates and species richness among furnariid clades after controlling for all other predictors (Table 5).

Our results provide further support to the growing body of evidence that variation in rates of climatic niche evolution are associated with variation in lineage diversification (Kozak and Wiens 2010; Martínez-Cabrera and Peres-Neto 2013; Title and Burns 2015). Although more studies are needed to determine the generality of this relationship, these results suggest that, at least at relatively shallow phylogenetic time scales, variation in rates of climatic-niche evolution may be at least as



important to generating variation in net diversification rates and species richness among clades as morphological evolution (although see Kozak et al. 2006). Indeed, both have clearly played a role in the diversification of Furnariidae. To the best of our knowledge, our study is the first to directly compare the relative importance of variation in rates of ecomorphological versus climatic-niche evolution on lineage diversification.

### *Lineage Diversification*

Diversification analyses of Furnariidae using stepwise model-selection methods (MEDUSA, Alfaro et al. 2009) found evidence for increased diversification rates near the base of the sub-family Furnariinae as well as near the base of *Cranioleuca* (Derryberry et al. 2011; Claramunt et al. 2012). While our results also confirm a rate shift occurred at the base of *Cranioleuca*, we found limited support for rate shifts elsewhere in the tree (Fig. 3). Furthermore, of the rates shifts that were sampled by BAMM apart from those subtending *Cranioleuca*, none corresponded in even approximate location to the rate shift at the base of Furnariinae inferred in previous analyses (Derryberry et al. 2011; Claramunt et al. 2012). The solitary rate shift at the base of *Cranioleuca* is not particularly surprising given that this genus has almost double the species richness of any other similarly aged clade.

Although we accounted for missing biological species analytically, it is possible that the species richness of Furnariidae may be underestimated by the taxonomy used in our phylogeny due to a preponderance of distinct evolutionary lineages within any given biological species in the Neotropics (Tobias et al. 2008; Sanín et al. 2009; D'Horta et al. 2013; Sousa-Neves et al. 2013). We conducted a preliminary investigation of the impact of missing tips by repeating the BAMM diversification analysis on a tree including an additional 66 distinct evolutionary lineages, i.e. subspecies (Tobias et al. 2013). Our results were robust to the addition of evolutionary units below the

species level to the tree; we again found that the only significant speciation rate shift present in the tree occurred at the base of *Cranioleuca* (Fig. S2).

### *Brownian Motion and Niche Evolution*

We found that while the trait data deviated considerably from the expectations of BM at the scale of the entire Furnariidae tree, the subclade analysis failed to identify major deviations from BM (Table 3). We suspect that rate heterogeneity among clades is the most likely explanation for this discrepancy between the family-level and the subclade evaluations. First, rate heterogeneity is entirely expected for a family with such a large diversity of ecologies and morphological variation. Second, our results from the BAMM trait analyses found widespread rate heterogeneity in both the climatic-niche and ecomorphology, despite sensitivity to the prior (see Supplemental Material). Finally, we found that the  $C_{VAR}$  statistic from the model adequacy simulations consistently suggested rate heterogeneity in our dataset. It is possible that all the subclades evolved under BM (our model adequacy tests support this), but they are evolving at different rates (as seen in the PGLS and BAMM analyses), thus resulting in a poor fit of a single-rate BM in the entire tree.

### *Cranioleuca Speciation*

South American bird diversification has been attributed mostly to the allopatric divergence of populations separated by geographic barriers such as rivers and mountains (Mayr 1942; Ribas et al. 2012), however, this framework may not fully explain patterns of divergence within *Cranioleuca*. While some speciation events within *Cranioleuca* can be attributed to geographic isolation without climatic-niche divergence (*C. albiceps* – *C. marcapatae*), *Cranioleuca*'s elevated rate of

diversification is likely due to the additional species richness generated by rapid speciation across climatic gradients (Hendry et al. 2007).

The genus *Cranioleuca* has one of the widest elevational distributions of any Neotropical bird genus (0 – 4800 m). At the extremes, seven species occur in various habitats within the Amazon basin and yet others occupy high-elevation *Polylepis* woodland of the Andes up to 4800 m, the highest forested landscape in the world. Additionally, *Cranioleuca* has also diversified across both the wettest and driest regions of the Neotropics. These varied environments may have exposed members of *Cranioleuca* to strong selection for physiological adaptations to high elevation (McCracken et al. 2009; Cheviron and Brumfield 2011; Bulgarella et al. 2012; Dubay and Witt 2014) and for water conservation (Lillywhite and Navas 2004). Under such selective pressures, local adaptation will result in maladaptive migrants reducing gene flow across environmental gradients. In addition, local adaptation may also drive divergence in phenotypic characters associated with reproductive isolation (Schluter 2009). For instance, plumage evolution in *Cranioleuca* appears to occur rapidly (Remsen 1984) and there is evidence for color matching to habitat (Maijer and Fjeldsâ 1997; Claramunt 2002), which may result in modification of color patches used for reproductive displays. Additionally, divergence in vocalizations, the principal premating reproductive isolating mechanism in birds (Price 2007), may be influenced by morphological divergence in characters such as body size or bill morphology due to local adaptation (Derryberry et al. 2012), although *Cranioleuca* species are relatively uniform vocally (Maijer and Fjeldsâ 1997).

Perhaps the strongest evidence from within the genus for the role of climatic niche divergence in driving speciation comes from the *Cranioleuca antisiensis* species complex. A sedentary, arboreal insectivore, *C. antisiensis* occupies a compact, linear distribution in the Andes of Peru along an elevational gradient (950 - 4800 m) that spans dramatically different climatic-niches. Phenotypic variation in plumage, morphology and song are tightly correlated with the environmental gradient across which the species is distributed (G. Seeholzer *in prep*). Vocal variation is likely due to natural

selection for body size as per Bergmann's Rule (James 1970), which increases clinally more than twofold, 12.5 – 30.0 g. Divergence between the clinal extremes in these characters is so profound that these populations are often considered separate species.

### *Conclusions*

Given the tremendous ecomorphological variation of Furnariidae (Remsen 2003; Claramunt 2010) and the popularity of adaptive radiation models, it may not be surprising that variation in lineage diversification is significantly predicted by ecomorphological traits such as size, bill shape and leg shape. However, we found that variation in rates of climatic-niche evolution may be more important in generating variation in rates of lineage diversification and species richness within Furnariidae. Divergence in the climatic-niche is generally associated with allopatric distributions, the dominant mode of speciation in birds (Price 2007), and may influence diversification more directly. While ecomorphology is likely to diverge as a result of climatic-niche divergence this is not necessarily what restricts gene flow between populations. Still, ecomorphological divergence may still be important in the diversification of Furnariidae by providing a means of second sympatry, by reducing competition, that allows for the accumulation of regional species richness and further diversification within clades (Pigot and Tobias 2012). Examination of either ecomorphology or the climatic-niche separately, as has been done in all previous studies ( but see Adams et al. 2009; Kozak and Wiens 2010; Rabosky and Adams 2012), does not fully capture the different spatial scales at which the niche can interact with diversification. By quantifying both ecomorphology and the climatic-niche within a single phylogenetic framework, a more nuanced view of the influence of these important traits on diversification can be obtained.

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Figure 1. Phenotypic diversity of Furnariidae and clade selection for PGLS analyses. Depicted is the maximum clade credibility tree of Furnariidae with the 16 clades selected by the PGLS clade selection

algorithm highlighted in black for the MCC tree. The vertical dashed line represents the maximum age threshold (the stem-age of *Craniolueca*). Illustrations from the Handbook of the Birds of the World (Remsen 2003).

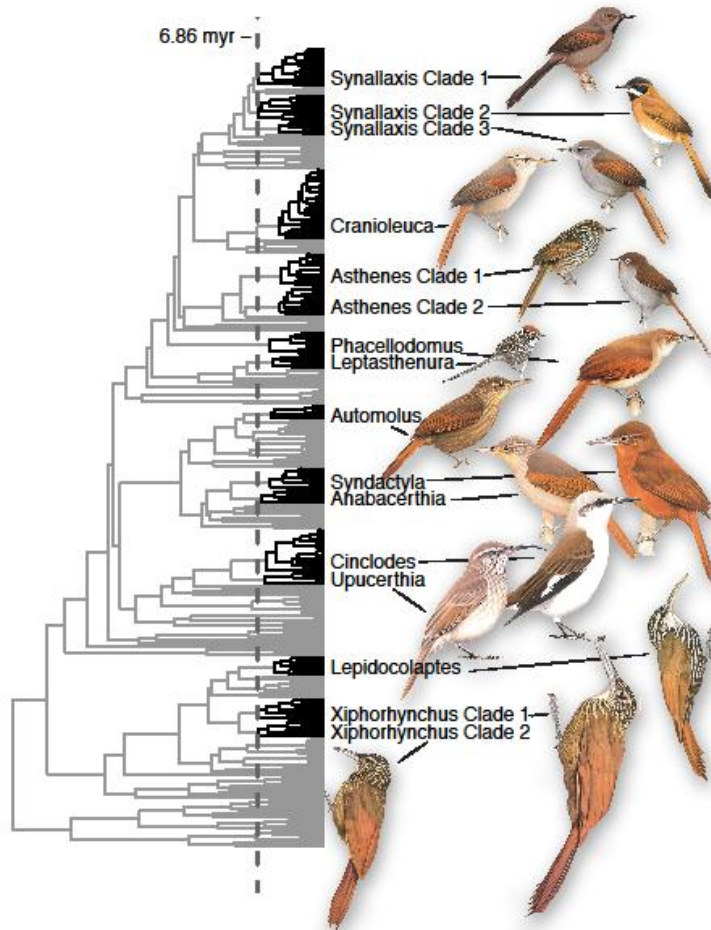


Figure 2. Diversification rates and species richness are positively correlated with rates of climatic-niche (ePC1, ePC3) and bill shape evolution, and, to a lesser degree, rates of size, and leg shape evolution. Plots depict relationships between the Brownian motion rate parameter for eight niche axes and (a) birth-death (bd) diversification rate or (b) species richness across 16 phylogenetically non-overlapping clades within Furnariidae. Data and regression parameters are median values from posterior distribution of trees, see Table 5 for model-averaged results from posterior. Regression lines plotted for P-values < 0.05. The *Craniolueca* clade is represented by a diamond.

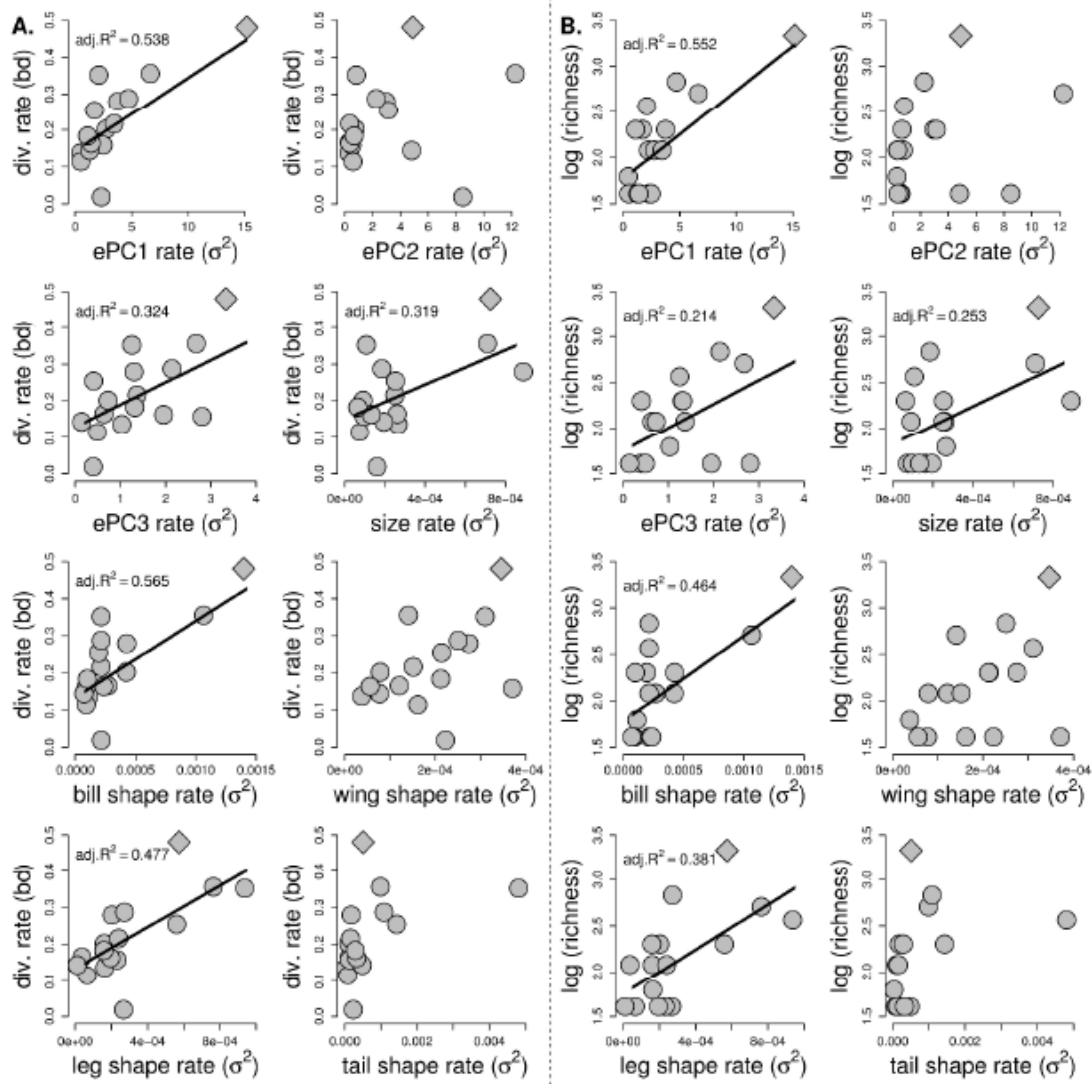


Figure 3. Evolutionary dynamics of speciation in Furnariidae inferred from BAMM. Depicted are the a) mean branch specific evolutionary rates inferred from BAMM. The grey circles are placed at nodes on the trees representing the core shift configuration with the highest posterior probability. b) The 95% credible set of shift configurations. These nine distinct shift configurations account for 96% of the posterior distribution. Grey circles represent rate shifts. Each branch is color-coded based on the mean of the marginal posterior density of the evolutionary rate for their respective BAMM analyses. Blues indicate slower evolutionary rates. Reds indicate faster evolutionary rates. Figures derived from analyses with hyperprior expectedNumberOfShifts = 1.

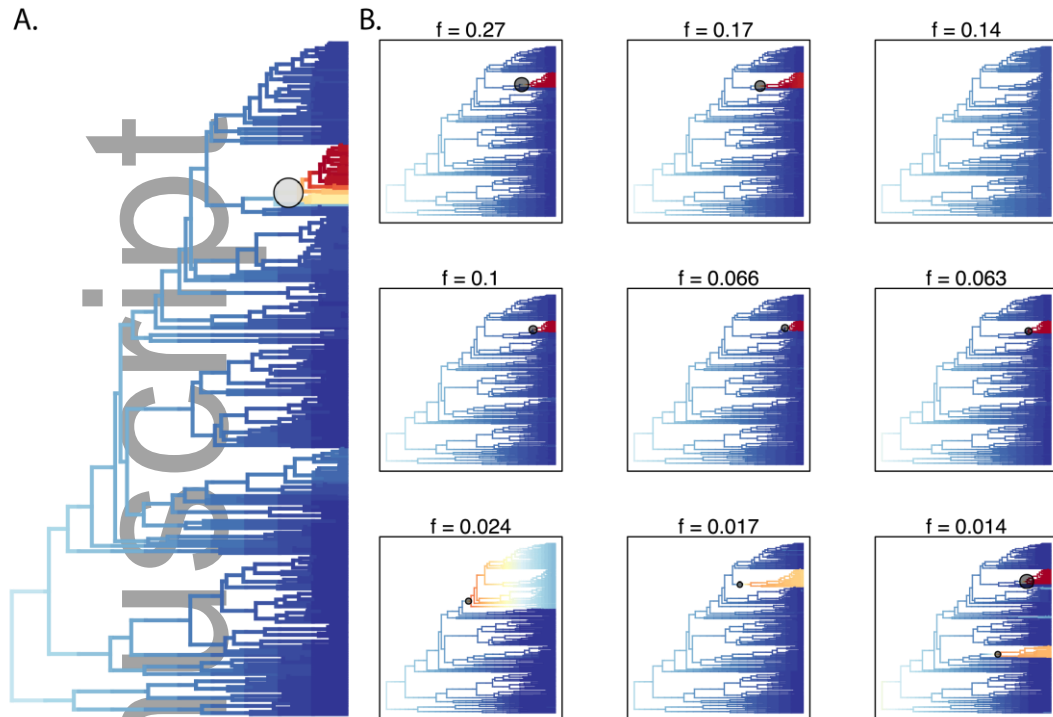


Table 1. The niche axes analyzed in this study, the top loading variables for each principal component axis (except size), and each axis' biological interpretation.

Niche Axis	Top Loading Variable(s)	Biological Interpretation
<u>Climatic-niche</u>		
ePC1	Mean Annual Precipitation	Precipitation
	Mean Diurnal Range	
ePC2	Elevation	Elevation & Temperature Evenness
	Isothermality	
	Temperature Seasonality	
ePC3	Precipitation of Warmest Quarter	Precipitation Seasonality & Temperature Evenness
	Temperature Annual Range	
	Isothermality	



Precipitation Seasonality		
<u>Ecomorphology</u>		
Size		overall body size
Bill Shape	bill length shape	relative bill length
Wing Shape	tenth primary shape	wing attenuation
Leg Shape	hallux shape	relative leg length
Tail Shape	even loadings across all tail shape variables	tail shape

Table 2. Species richness, crown age, birth-death rate and Brownian motion rate of niche evolution for 16 phylogenetically non-overlapping clades of furnariids. Clade division and parameter estimates from MCC tree.

Clade	Species Richness	Age (myr)	Birth-Death Rate	$\sigma^2$ Rate of Niche Evolution							
				ePC 1	ePC 2	ePC 3	Size	Bill Shape	Wing Shape	Leg Shape	Tail Shape
Synallaxis Clade 1	17	6.75	0.288	4.706	2.262	2.138	1.85E-04	2.15E-04	2.51E-04	2.72E-04	1.09E-03
Synallaxis Clade 2	10	6.802	0.184	1.092	0.664	1.317	6.40E-05	1.01E-04	2.12E-04	1.58E-04	2.91E-04
Synallaxis Clade 3	5	4.639	0.163	1.397	0.373	1.951	1.32E-04	2.36E-04	5.59E-05	1.95E-04	3.29E-04
Cranioleuca	28	4.604	0.481	15.167	4.885	3.333	7.25E-04	1.40E-03	3.46E-04	5.74E-04	5.07E-04
Asthenes Clade 1	13	4.417	0.352	2.088	0.827	1.251	1.08E-04	2.14E-04	3.10E-04	9.37E-04	4.80E-03
Asthenes Clade 2	10	4.506	0.255	1.692	3.136	0.405	2.53E-04	1.94E-04	2.14E-04	5.60E-04	1.43E-03
Phacellodomus	10	5.635	0.279	3.752	2.962	1.301	8.88E-04	4.26E-04	2.75E-04	2.03E-04	1.77E-04
Leptasthenura	5	5.304	0.144	1.275	4.807	0.141	1.95E-04	7.24E-05	7.72E-05	1.08E-05	4.86E-04

Automolus	5	5.3 86	0.15 8	2.46 4	0.52 4	2.8 06	9.64E- 05	8.65E- 05	3.71E- 04	2.32E- 04	1.29E- 04
Syndactyla	8	5.5 52	0.21 6	3.44 1	0.36 1	1.3 64	2.51E- 04	2.15E- 04	1.52E- 04	2.40E- 04	1.58E- 04
Anabacerthia	5	6.4 85	0.11 4	0.49 7	0.59 0.59	0.4 9	7.39E- 05	9.14E- 05	1.62E- 04	6.62E- 05	8.62E- 05
Cinclodes	15	5.8 95	0.35 6	6.64 1	12.2 63	2.6 76	7.10E- 04	1.06E- 03	1.41E- 04	7.64E- 04	9.88E- 04
Upucerthia	5	6.1 66	0.01 9	2.30 3	8.49 8.49	0.3 96	1.61E- 04	2.16E- 04	2.23E- 04	2.67E- 04	2.34E- 04
Lepidocolaptes	8	5.1 51	0.20 2	2.74 3	0.75 2	0.7 23	9.14E- 05	4.23E- 04	7.85E- 05	1.60E- 04	1.09E- 04
Xiphorhynchus Clade 1	8	6.7 77	0.16 5	2.23 3	0.32 9	0.6 34	2.61E- 04	2.70E- 04	1.21E- 04	3.70E- 05	1.26E- 04
Xiphorhynchus Clade 2	6	6.7 39	0.13 7	0.45 9	0.31 2	1.0 28	2.65E- 04	1.12E- 04	3.78E- 05	1.63E- 04	3.80E- 05

Table 3. Results of model selection and model adequacy tests for niche axes across the entire tree. Left of dashed line: Brownian motion (BM) is a poor fit relative to alternative models Ornstein-Uhlenbeck (OU), delta, and kappa for all traits by bill shape as indicated by AIC<sub>c</sub> scores and weights (wtAIC<sub>c</sub>). Right of dashed line: P-values for each niche axis-by-model test representing the probability that the observed summary statistic deviates from the expectations of the model (based on 1000 simulations). The lower the p-value the more likely that the model is inadequate. P-values less than 0.05 are in bold. See Methods and Pennell et al. (2015) for details on the summary statistics.

Niche Axis	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	wtAIC <sub>c</sub>	$M_{SIG}$	$C_{VAR}$	$S_{VAR}$	$S_{ASR}$	$S_{HGT}$	$D_{CDF}$
ePC1	BM	1785.003	128.09	0	0.89 1	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	0.099
	OU	1712.632	55.719	0	0.89 1	< <b>0.001</b>	< <b>0.001</b>	0.317	< <b>0.001</b>	0.158
	delta	1745.107	88.194	0	0.97	< <b>0.001</b>	< <b>0.001</b>	0.079	< <b>0.001</b>	0.277
	kappa	<b>1656.913</b>	<b>0</b>	<b>1</b>	0.95	0.733	< <b>0.001</b>	0.079	<b>0.04</b>	0.832

ePC2	BM	1610.311	151.194	0	0.97	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>
	OU	<b>1459.117</b>	<b>0</b>	<b>1</b>	0.832	< <b>0.001</b>	< <b>0.001</b>	<b>0.04</b>	<b>0.02</b>	< <b>0.001</b>
	delta	1561.673	102.556	0	0.673	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>
	kappa	1487.998	28.881	0	0.851	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	<b>0.04</b>	0.079
ePC3	BM	1438.324	199.18	0	0.97	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>
	OU	<b>1239.144</b>	<b>0</b>	<b>1</b>	0.812	0.238	< <b>0.001</b>	< <b>0.001</b>	0.535	0.634
	delta	1386.194	147.05	0	0.95	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>
	kappa	1307.122	67.978	0	0.851	<b>0.02</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	0.257
size	BM	-923.034	5.499	0.056	0.871	< <b>0.001</b>	0.059	0.95	0.614	< <b>0.001</b>
	OU	-921.835	6.698	0.031	0.832	< <b>0.001</b>	0.079	0.95	0.832	< <b>0.001</b>
	delta	-921.727	6.806	0.029	0.95	< <b>0.001</b>	0.139	0.931	0.871	< <b>0.001</b>
	kappa	<b>-928.533</b>	<b>0</b>	<b>0.883</b>	0.851	< <b>0.001</b>	0.97	0.95	0.257	< <b>0.001</b>
bill shape	BM	-780.779	2.73	0.161	0.97	< <b>0.001</b>	0.139	< <b>0.001</b>	0.495	0.079
	OU	-779.69	3.819	0.093	0.99	< <b>0.001</b>	0.475	<b>0.02</b>	0.733	0.178
	delta	-780.144	3.365	0.117	0.851	< <b>0.001</b>	0.257	< <b>0.001</b>	0.891	0.059
	kappa	<b>-783.509</b>	<b>0</b>	<b>0.629</b>	0.97	< <b>0.001</b>	0.95	< <b>0.001</b>	0.495	0.099
wing shape	BM	-1074.571	9.594	0.008	0.97	<b>0.02</b>	0.099	0.515	0.317	0.634
	OU	-	10.342	0.006	0.75	<	0.238	0.832	0.931	0.158

		1073.823			2	<b>0.001</b>					
	delta	-1073.282	10.883	0.004	0.911	<b>0.02</b>	0.158	0.614	0.812	0.317	
	<b>kappa</b>	-1084.165	<b>0</b>	<b>0.982</b>	0.891	0.059	0.356	0.772	0.634	0.515	
leg shape	BM	-976.108	23.34	0	0.99	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	<b>0.02</b>	<b>0.04</b>	
	OU	-980.007	19.441	0	0.891	< <b>0.001</b>	< <b>0.001</b>	<b>0.04</b>	0.218	< <b>0.001</b>	
	delta	-976.719	22.729	0	0.851	< <b>0.001</b>	< <b>0.001</b>	<b>0.04</b>	<b>0.04</b>	<b>0.02</b>	
	<b>kappa</b>	-999.448	<b>0</b>	<b>1</b>	0.871	<b>0.02</b>	0.317	< <b>0.001</b>	0.099	<0.001	
tail shape	BM	-770.348	47.135	0	0.891	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	
	OU	-817.206	0.277	0.465	0.97	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	0.02	
	delta	-801.166	16.317	0	0.812	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	
	<b>kappa</b>	-817.483	<b>0</b>	<b>0.534</b>	0.911	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	0.02	

Table 4. Results of model selection and model adequacy tests for niche axes across 16 phylogenetically non-overlapping subclades from the MCC tree. In each cell, the best fit model for the clade-by-niche axis pairing is followed by the proportion of the six summary statistics for which the observed data did not deviate significantly ( $p\text{-value} > 0.05$ ) from the expectations of BM (based on 1000 simulations). See Methods, Table 2 and Pennell et al. (2015) for information about the summary statistics and significance tests. Larger values of the proportion indicate an overall better fit of the BM model given the niche data and tree of the subclade.

Clade	s	Anabacerthia	Niche Axes							
			ePC1	ePC2	ePC3	size	bill shape	wing shape	leg shape	tail shape
			BM, 0.8	BM, 1.0	BM, 0.8	BM, 1.0	BM, 1.0	BM, 1.0	BM, 0.8	BM, 0.7

Asthenes Clade 1	BM, 1.0	BM, 0.3	BM, 0.8	BM, 0.8	BM, 0.5	BM, 0.7	BM, 0.7	BM, 1.0
Asthenes Clade 2	BM, 1.0	BM, 0.8	BM, 0.5	BM, 0.8	BM, 0.8	BM, 0.7	BM, 0.8	BM, 1.0
Automolus	BM, 1.0	BM, 0.8	BM, 0.3	BM, 0.3	BM, 0.5	BM, 1.0	BM, 0.5	BM, 0.8
Cinclodes	BM, 1.0	BM, 0.5	BM, 0.7	BM, 1.0	BM, 0.7	BM, 0.8	BM, 0.8	BM, 0.3
Cranioleuca	BM, 0.5	BM, 0.8	BM, 0.7	kappa, 0.5	BM, 0.7	kappa, 0.7	BM, 0.8	BM, 0.7
Lepidocolaptes	BM, 0.8	BM, 0.7	BM, 0.8	BM, 0.8	BM, 0.8	BM, 0.8	BM, 0.8	BM, 0.8
Leptasthenura	BM, 0.7	BM, 0.3	BM, 0.8	BM, 0.3	BM, 0.7	BM, 1.0	BM, 0.8	BM, 0.3
Phacellodomus	BM, 0.5	BM, 0.5	BM, 1.0	BM, 1.0	BM, 0.5	BM, 0.7	BM, 0.5	BM, 0.7
Synallaxis Clade 1	BM, 1.0	BM, 1.0	BM, 0.8	BM, 0.8	BM, 1.0	BM, 0.8	BM, 0.8	BM, 0.5
Synallaxis Clade 2	BM, 0.8	BM, 1.0	BM, 0.8	BM, 0.8	BM, 1.0	BM, 0.8	BM, 1.0	BM, 0.7
Synallaxis Clade 3	BM, 0.8	BM, 1.0	BM, 0.8	BM, 0.8	BM, 0.5	BM, 0.8	BM, 0.8	BM, 0.7
Syndactyla	BM, 0.8	BM, 0.7	BM, 1.0	BM, 0.8	BM, 0.7	BM, 0.5	BM, 1.0	BM, 0.5
Upucerthia	BM, 0.8	BM, 0.8	BM, 1.0	BM, 0.5	BM, 1.0	BM, 0.8	BM, 1.0	BM, 0.8
Xiphorhynchus Clade 1	BM, 0.8	BM, 1.0	BM, 0.5	BM, 0.7	BM, 0.7	BM, 0.8	BM, 0.8	BM, 0.7
Xiphorhynchus Clade 2	BM, 0.8	BM, 1.0	BM, 0.7	BM, 0.7	BM, 0.8	BM, 1.0	BM, 0.3	BM, 1.0

Table 5. Modeled-averaged parameter estimates from phylogenetic generalized least squares regressions to examine univariate and multivariate relationships between rates of niche evolution and lineage diversification across independent furnariid clades; a) birth-death rate, b) log species richness. Note  $wtAIC_c^*$  values are the summed  $wtAIC_c$  values for each model containing the predictor variable, as such, they will not sum to one. Top models are in bold.

	Reponse	Predictor	$\beta$ +/- SE	wtAIC <sub>c</sub> *
A.	div. rate (bd)	crown age	43.276 +/- 9.487	0.165
	<b>div. rate (bd)</b>	<b>ePC1 rate</b>	<b>0.005 +/- 0.011</b>	<b>0.719</b>
	div. rate (bd)	ePC2 rate	0.032 +/- 0.005	0.235
	div. rate (bd)	ePC3 rate	0.062 +/- 0.004	0.15
	div. rate (bd)	size rate	55.805 +/- 2.2	0.399
	div. rate (bd)	bill shape rate	68.727 +/- 16.69	0.29
	div. rate (bd)	leg shape rate	80.201 +/- 18.56	0.377
	div. rate (bd)	tail shape rate	77.813 +/- 33.701	0.604
	div. rate (bd)	wing shape rate	42.091 +/- 5.749	0.135
B.	log richness	crown age	248.957 +/- 67.796	0.192
	<b>log richness</b>	<b>ePC1 rate</b>	<b>0.029 +/- 0.072</b>	<b>0.828</b>
	log richness	ePC2 rate	0.023 +/- 0.002	0.152
	log richness	ePC3 rate	0.087 +/- 0.005	0.154
	log richness	size rate	165.366 +/- 6.33	0.172
	log richness	bill shape rate	307.294 +/- 68.499	0.247
	log richness	leg shape rate	468.609 +/- 74.862	0.401
	log richness	tail shape rate	323.703 +/- 116.111	0.486
	log richness	wing shape rate	230.316 +/- 16.336	0.147