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Reviewed work(s):

Source: *The American Naturalist*, Vol. 179, No. 5 (May 2012), pp. 649-666

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/664998>

Accessed: 15/07/2012 17:25

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# Ecological Opportunity and Diversification in a Continental Radiation of Birds: Climbing Adaptations and Cladogenesis in the Furnariidae

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Submitted September 1, 2011; Accepted January 9, 2012; Electronically published March 29, 2012

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.832k336g>.

**ABSTRACT:** Ecological theories of adaptive radiation predict that ecological opportunity stimulates cladogenesis through its effects on competitive release and niche expansion. Given that key innovations may confer ecological opportunity, we investigated the effect of the acquisition of climbing adaptations on rates of cladogenesis in a major avian radiation, the Neotropical bird family Furnariidae, using a species-level phylogeny. Morphological specializations for vertical climbing originated in the woodcreepers ~23 million years ago, well before that adaptation occurred in woodpeckers (Picidae) or in other potential competitors in South America. This suggests that the acquisition of climbing adaptations conferred ample ecological opportunity to early woodcreepers. Nonetheless, we found that increases in speciation rates in Furnariidae did not coincide with the acquisition of climbing adaptations and that the relationship between the accumulation of climbing adaptations and rates of speciation was negative. In addition, we did not detect a diversity-dependent decline in woodcreeper diversification rates consistent with saturation of the trunk-climbing niche. These findings do not support the hypothesis that ecological opportunity related to trunk foraging stimulated cladogenesis in this radiation. The negative effect of climbing on diversification may be mediated by an indirect positive effect of climbing on dispersal ability, which may reduce speciation rates over evolutionary timescales.

**Keywords:** key innovation, macroevolution, specialization, speciation, woodcreepers, Neotropics.

## Introduction

According to ecological theories of adaptive radiation, diversification is stimulated by ecological opportunity (Simpson 1953; Schluter 2000; Yoder et al. 2010). For example, the presence of “empty niches” due to low accessibility by continental organisms may catalyze rapid di-

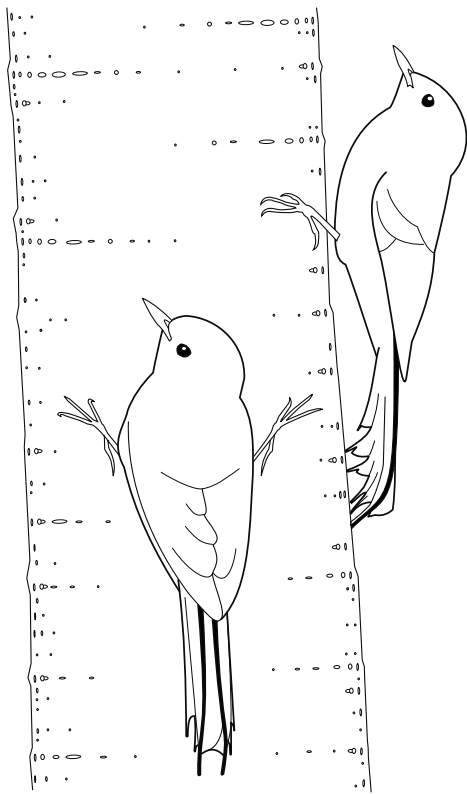
versification on oceanic islands (Rosenzweig 1995; Grant 1999; Gillespie 2004). Ecological opportunity may also arise as a result of phenotypic changes that enhance the ecological performance of lineages (Simpson 1953; Schluter 2000; Yoder et al. 2010). These changes, usually called “key innovations,” are considered a cause of high rates of diversification in many groups (Hunter 1998). Examples of putative key innovations are the specialized toepads of *Anolis* lizards (Losos 2009) and the decoupling of pharyngeal and oral jaws in cichlids (Liem 1973; Hulsey et al. 2006). Key innovations may be particularly important for diversification on continents. In contrast to oceanic islands, empty niches are almost certainly relatively few on the much older and more biologically diverse continents. Although geologic and climatic changes on continents may create ecological opportunities, competition for occupation of those new niches may be intense. Key innovations can create new niche space for particular lineages or can determine which of the existing clades will exploit the ecological opportunities created by external forces.

We investigated the evolution of climbing adaptations in the passerine family Furnariidae (ovenbirds and woodcreepers) and its effects on rates of cladogenesis to test whether evolutionary innovations that created ecological opportunities stimulated diversification in these birds. The Furnariidae represents an impressive case of a continental radiation (Fitzpatrick 1982; Fjeldså et al. 2005; Claramunt 2010), with high species richness (293 species) and lineages adapted to a remarkable variety of habitats and feeding strategies (Skutch 1996; Stotz et al. 1996; Remsen 2003). Among those strategies is foraging on trunks and major branches. Not unique among passerines but rare outside the Furnariidae is the use of the tail as a prop during climbing (fig. 1), a character that has evolved elsewhere only in woodpeckers (Picidae) and treecreepers (Certhiidae; Richardson 1942). Within Furnariidae, tail-assisted climbing is found in several clades, which show various

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Am. Nat. 2012. Vol. 179, pp. 649–666. © 2012 by The University of Chicago. 0003-0147/2012/17905-53301\$15.00. All rights reserved.

DOI: 10.1086/664998



**Figure 1:** Olivaceous woodcreeper *Sittasomus griseicapillus* showing typical specialized climbing adaptations. Rachises of the central tail feathers are shown in black to highlight their shape. Note also the position of the feet and the elongated outer toe.

degrees of development of this specialization (Feduccia 1970; Remsen 2003; Fjeldså et al. 2005). Some lineages, such as the *Margarornis* group and, to a lesser extent, *Berlepschia* and *Cranioleuca*, show tapered tail feather tips with slightly stiffened rachises and moderately scansorial feet (Feduccia 1970; Remsen 2003; Areta 2007). At the most specialized end of the spectrum are the woodcreepers (subfamily Dendrocolaptinae), which show a degree of climbing specialization rivaling that of woodpeckers (Richardson 1942; Raikow and Bledsoe 2000; Marantz et al. 2003). Many aspects of woodcreeper anatomy are modified for climbing, including hindlimb proportions, relative toe length, claw curvature, tail feather structure, and many components of the hindlimb-tail musculoskeletal apparatus (Richardson 1942; Feduccia 1973; Bledsoe et al. 1993; Raikow 1993, 1994; Tubaro et al. 2002; Marantz et al. 2003). Although several hypotheses have been proposed for the evolution of scansoriality in Furnariidae (Feduccia

1973; Willis 1974; Fjeldså et al. 2005), none have been tested in a phylogenetic framework.

Adaptations for climbing in the Furnariidae are a clear example of evolutionary innovations that launched lineages into a new adaptive zone (Raikow and Bledsoe 2000): a suite of functionally related morphological changes allowed some lineages to forage effectively on trunks and branches. That there are no other passerines in the Neotropics that forage regularly on trunks or vertical branches suggests that tree-trunk insectivory was an empty niche when the first furnariids acquired climbing adaptations. Most woodpeckers—the other large radiation of tree-trunk-climbing birds—specialize on drilling into the bark and wood for insect larvae and seldom glean insects from the trunk surface or epiphytes; therefore, competition with climbing furnariids is not immediately expected. However, given that some woodpeckers do glean insects from surfaces and fly catch (Winkler and Christie 2002) and that many woodcreepers prey on insects hidden in wood crevices, under the bark, or in dead wood (Feduccia 1970; Marantz et al. 2003), the potential for competition should not be ruled out.

We tested the key innovation hypothesis by assessing whether evolutionary innovations for climbing are associated with shifts in rates of speciation and extinction (Hunter 1998; de Queiroz 2002; Alfaro et al. 2009a). Using detailed morphological data for all furnariid species together with a species-level molecular phylogeny and a wide variety of methods, we investigated patterns of evolution of climbing adaptations and their effect on rates of cladogenesis. We also assessed whether climbing furnariids and woodpeckers coexisted by comparing the time of origin of climbing adaptations in Furnariidae with the time of origin of woodpeckers and their arrival in South America. We provide a novel historical framework for the evolution of scansoriality in suboscine birds and the first test of whether climbing adaptations stimulated diversification. Moreover, because of the clear-cut relationship between climbing innovations and the use of a new feeding niche, we provide insights into whether ecological opportunity stimulated diversification in a hyperdiverse continental radiation.

## Material and Methods

### *Morphology*

We examined morphological traits associated with tree trunk climbing in study skins of 290 of the 293 currently recognized species of Furnariidae. Most specimens were examined at the Louisiana State University Museum of Natural Science, but additional specimens from other institutions were examined (see “Acknowledgments”). For

each specimen, we recorded the morphology of seven characters of the tail and one character of the foot that have functional significance for tail-assisted climbing (table 1; fig. 2). For each character, states were coded such that 0 represents no specialization for climbing (the predominant state in passerines) and other states represent increasing degrees of specialization (table 1). In addition to discrete characters, we measured the length of one of the central tail feathers and the depth of its rachis at the midpoint using digital calipers. The relationship between the length and thickness of the rachis controls buckling failure when the tail is supporting the body weight (Tubaro et al. 2002); therefore, we expressed rachis thickness as a percentage of the total length of the rachis. Claw curvature, which is greater in climbing birds and has a clear functional role in climbing (Richardson 1942; Feduccia 1993; Pike and Maitland 2004), was not considered in this analysis because it is not associated exclusively with tail-assisted climbing (Richardson 1942). Character state data for all species were deposited in Dryad.

#### *Phylogeny*

We used a recently published species-level molecular phylogeny of the Furnariidae (Derryberry et al. 2011). The tree was calibrated using (1) the age of the split between tyrannoids and furnarioids (Barker et al. 2004) and (2) multiple biogeographic calibration nodes based on the last rapid uplift of the northern Andes, which separates multiple lineages, and the formation of the Isthmus of Panama, which allowed multiple furnariid lineages to colonize Central America. The phylogenetic tree is deposited in TreeBASE (study S11550). For further details on phylogenetic reconstruction and calibration, see Derryberry et al. (2011). We computed a maximum clade credibility tree from a sample of trees derived from a Bayesian analysis in BEAST (ver. 1.5.2; Drummond and Rambaut 2007) and pruned taxa used only for calibration.

#### *Shifts in Diversification Rates*

As a first step in addressing the potential relationship between the evolution of climbing adaptations and rates of cladogenesis, we investigated whether rates of speciation and extinction changed during the evolution of the Furnariidae. We used the MEDUSA (modeling evolutionary diversification using stepwise Akaike Information Criterion [AIC]; Alfaro et al. 2009b) approach. MEDUSA fits birth-death models of cladogenesis to different parts of a calibrated phylogeny and then uses the AIC to select the model that represents an optimum balance between fit (maximized likelihood) and complexity (number of shifts). In this way, MEDUSA identifies the branches in

which a significant shift in diversification rates has occurred. We ran MEDUSA in R language for statistical computing (R Development Core Team 2009) using functions of the GEIGER library (Harmon et al. 2008a). We used the second-order estimator of the AIC (AICc) throughout this study.

#### *Climbing and Diversification: Discrete Traits*

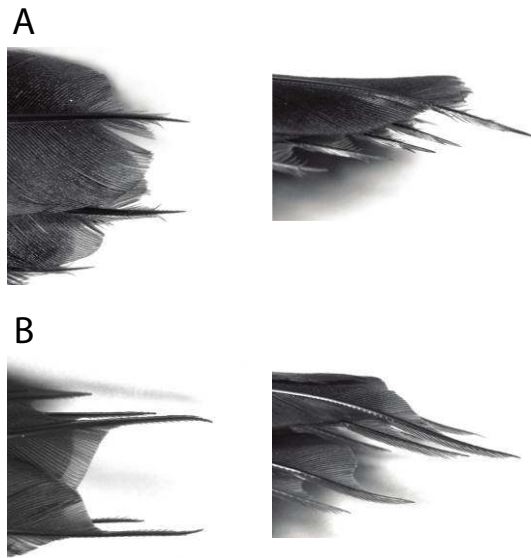
We performed analyses of character evolution and their effect on diversification using two approaches: (1) a discrete-traits approach in which we analyzed discrete traits individually and (2) a continuous-trait approach in which we combined discrete traits in a composite index to study the accumulation of climbing adaptations. For the discrete-traits approach, we reconstructed ancestral states for individual traits using parsimony and likelihood methods in Mesquite (ver. 2.74; Maddison and Maddison 2009). Multistate characters were treated as ordered for parsimony reconstructions. Ancestral reconstructions were performed, including a diverse array of outgroup taxa (Derryberry et al. 2011) to inform ancestral states at the base of the Furnariidae tree. Because multiple equally parsimonious reconstructions are typical, we examined all maximum parsimony reconstructions for relevant branches. Maximum likelihood reconstructions were performed using the Markov  $k$ -state model with a single rate of change (Schluter et al. 1997; Maddison and Maddison 2009). We examined character transitions not only at branches in which a shift in diversification was inferred by MEDUSA but also at the two closest ancestral branches. Finally, to detect a signal of concentration of changes near branches that experienced a shift in diversification, we inferred the number of state changes along each branch of the phylogeny by estimating branch lengths using both accelerated and delayed transformation algorithms under the parsimony criterion in PAUP\* (Swofford 2003).

As a more direct test of the effect of climbing on diversification, we used the BiSSE (binary-state speciation and extinction; Maddison et al. 2007) approach, in which the state of a discrete binary trait is associated with discrete changes in rates of speciation. Instead of performing the test for individual traits, we divided species into two main categories. We considered a species a climber if it regularly uses climbing as a foraging strategy (Remsen 2003) and if it possesses a number of morphological adaptations for doing so. We then used functions in the DIVERSITREE library in R to fit BiSSE models assuming no extinction and a symmetric model of trait evolution (equal rate for transition to climbing and the reversal). We tested the hypothesis of an effect of climbing on diversification by fitting a null model with a single speciation rate and comparing it with the alternative model in which the speciation

**Table 1:** External characters that represent adaptations for tail-supported trunk climbing in Furnariidae

Character	Character states	Functional significance
Tail rachis curvature	<ul style="list-style-type: none"> <li>0 = straight</li> <li>1 = uniformly decurved</li> <li>2 = decurved distally</li> <li>3 = logistic</li> </ul>	<p>Rachis curvature increases the angle with which the tip touches the substrate (Richardson 1942). A uniformly decurved rachis is the most basic way of attaining this. Decurving only the tip has the advantage of maintaining a flat, streamlined tail for flight (fig. 2A). A logistic shape (fig. 2B) is considered here the most specialized because it involves an additional inflection in the rachis. The logistic shape is associated with the presence of short, stiff barbs, and the shape of the rachis increases the contact of these barbs with the substrate (fig. 2B).</p>
Alignment of rachises	<ul style="list-style-type: none"> <li>0 = parallel</li> <li>1 = divergent laterally</li> </ul>	<p>In all woodcreepers and a few other scansorial furnariids, the rachises of the central feathers of the tail are not completely parallel but diverge distally (fig. 1). We hypothesize that this provides a more stable support because these rachises can absorb lateral forces that otherwise would produce bending stresses.</p>
Rachis stiffness	<ul style="list-style-type: none"> <li>0 = soft</li> <li>1 = semirigid (flexible to the touch)</li> <li>2 = rigid</li> </ul>	<p>Stiff rachises tips provide a stronger and more stable support for the tail, especially when the tip plays a major role in support.</p>
Barbs in rachis tip	<ul style="list-style-type: none"> <li>0 = present</li> <li>1 = absent</li> </ul>	<p>When the tip of the rachis plays a major role in support, a reduction in density of barbs toward the tip enhances contact of the tip with the substrate (fig. 2A). It also prevents barb abrasion if distal barbs are soft.</p>
Rectrix apex shape	<ul style="list-style-type: none"> <li>0 = rounded or obtuse</li> <li>1 = moderately pointed (acute, acuminate, short attenuate, short cuspidate, or bilobate)</li> <li>2 = highly pointed (long attenuate, long cuspidate, or asymmetrical forms)</li> </ul>	<p>Decreasing barb length toward the tip maximizes rachis exposure and minimizes barb abrasion (Richardson 1942). We divided a more detailed classification of rectrix tip shapes in Furnariidae (fig. A1, available online) into three categories representing an increasing degree of tapering of the vanes. Asymmetrical forms are considered highly specialized because they show a considerable reduction in barb length in the lateral side of the vane, which is more exposed to abrasion.</p>
Barb specializations	<ul style="list-style-type: none"> <li>0 = unspecialized</li> <li>1 = long, semistiff barbs</li> <li>2 = short, stiff barbs</li> </ul>	<p>Stiff barbs near the tip can contribute to mechanical support and are more resistant to abrasion (Richardson 1942). Stiffened barbs can be long and still flexible, as in woodpeckers, or short and rigid, as in several woodcreepers (fig. 2).</p>
Barb orientation	<ul style="list-style-type: none"> <li>0 = lateral</li> <li>1 = lateroventral</li> </ul>	<p>A lateroventral orientation of the barbs facilitates the contact of stiffened barbs with the substrate.</p>
Relative length of toe 4	<ul style="list-style-type: none"> <li>0 = equal to toe 2</li> <li>1 = slightly longer than toe 2</li> <li>2 = slightly shorter than toe 3</li> <li>3 = equal to toe 3</li> </ul>	<p>Elongation of the outer toe improves the ability to grasp around trunks and branches (Richardson 1942; Bock and Miller 1959; fig. 1), which counteracts the forces that tend to pull the bird away from the trunk (Norberg 1986).</p>

Note: All tail traits refer to the characteristics of the two central feathers.



**Figure 2:** Climbing specializations at the tip of the tail feathers. *A*, Decurved and seminude rachis tip (*Dendrocincla tyrannina*; Louisiana State University Museum of Natural Science [LSUMZ] 128400). *B*, Logistic rachis tip with short, stiff barbs (*Deconychura longicauda*; LSUMZ 108272).

rate depends on the value of the variable using a likelihood ratio test.

#### *Climbing and Diversification: Index of Climbing Adaptations*

To investigate the accumulation of climbing adaptations and its effect on diversification as a continuous process, we calculated a composite index of climbing adaptations for each species as the sum of the eight discrete characters (table 1) plus relative rachis thickness. By dividing this sum by 16 we obtained an index that varied approximately from 0 (complete absence of climbing adaptations) to 1 (presence of the full set of advanced climbing adaptations). The index was most influenced by the seven discrete traits of the tail, but relative rachis thickness and length of toe 4 were also correlated with the index and among each other (fig. A2, available online), suggesting that most characters share a common signal and contributed to the composite index of climbing adaptations. Values of the index for each species were deposited in Dryad.

We investigated the mode of evolution of this index by evaluating the maximum likelihood fit of simple models of continuous-trait evolution: a random walk model (Brownian motion; Felsenstein 1973), a speciational model in which trait changes take place at speciation events ( $\kappa$

model; Pagel 1999), a model in which phenotypic change can accelerate or decelerate ( $\delta$  model; Pagel 1999), and a constrained random walk (Ornstein-Uhlenbeck process with a single central optimum; Butler and King 2004; Harmon et al. 2010). We used the function `fitContinuous` in the GEIGER library (Harmon et al. 2008a) to fit models and to obtain the corresponding parameters. We then transformed the branch lengths of the phylogenetic tree according to the best model by the `tree-transformation` function in the GEIGER library and used the transformed tree to estimate ancestral states using maximum likelihood methods (Schluter et al. 1997).

To test for a correlation between the index of climbing adaptations and diversification, we used a Yule model with covariates approach (Paradis 2005). The Yule model with covariates represents the relationship between diversification rates and species traits as a linear model; specifically, the logit transformation of the speciation rate is modeled as a linear function of the values of one or more predictor variables. The parameters of the model are estimated by nonlinear minimization of the deviance (Paradis 2005). The great advantage of the Yule model with covariates is that the flexibility of the linear function allows the evaluation of a variety of models using conventional statistical modeling and model selection techniques. Because the effect of a trait on diversification can be nonmonotonic or vary from clade to clade (de Queiroz 2002; Donoghue 2005; Paradis 2005), we considered the following alternative models:

1. Models with a differential effect for woodcreepers versus other furnariids. Only the first lineage that enters a new niche may experience the stimulating effect of ecological opportunities (Losos et al. 1998), and the Dendrocolaptinae was the first clade that acquired climbing adaptations. Lineages that acquired climbing adaptations later presumably found a niche already occupied and faced competition with woodcreepers. We modeled this scenario by including a categorical variable for whether a species or an internal node belongs to the Dendrocolaptinae. We evaluated a model with a main “clade” effect only and a model that included an interaction with the climb index, thus allowing for the relationship between the climb index and diversification to differ between woodcreepers and other furnariids.

2. Models incorporating rate shifts identified by MEDUSA. With these models, we investigated whether the climb index affects diversification after accounting for major rate shifts that could have been the result of other factors, such as other key innovations or extrinsic events. As before, we evaluated a model with a main “clade” effect only and a model with an interaction term.

3. A model with a quadratic term, allowing for a non-monotonic relationship between the speciation rate and

the climb index. This model represents a case in which lineages with intermediate climbing capabilities cannot take full advantage of the new niche, yet they have lost an optimal generalized perching morphology; only unspecialized or highly specialized lineages experience higher speciation rates.

We obtained maximum likelihood values for each model and calculated the AIC and Akaike weights ( $w$ ) to guide model selection (Burnham and Anderson 2002). Akaike weights sum to 1 and represent the probability that a certain model is the best model among the set under consideration (Burnham and Anderson 2002). We evaluated the statistical significance of particular parameters by comparing models with and without the parameter using a likelihood ratio test (Paradis 2005). We used the function `yule.cov`, part of the APE library (Paradis et al. 2004), to fit the models. The Yule model with covariates represents diversification as a pure-birth process, and even low levels of extinction can decrease the power of the method to detect an effect (Paradis 2005). However, although extinction has certainly occurred in the Furnariidae (e.g., Claramunt and Rinderknecht 2005), the signal of extinction is not present in the phylogeny (Derryberry et al. 2011). In any case, because low levels of extinction make the analysis more conservative, we abstained from interpreting nonsignificant results.

#### *Lineage Accumulation through Time in the Dendrocolaptinae*

Because the Dendrocolaptinae is the most diverse and specialized clade of climbing furnariids, we performed additional tests focused on this group. We analyzed the accumulation of lineages through time in woodcreepers to investigate whether the acquisition of climbing adaptations produced patterns predicted by the ecological theory of adaptive radiation. According to this theory, speciation rates are highest when a lineage enters a new adaptive zone and starts to radiate, but subsequently, as the new niches are filled, ecological opportunity is reduced and speciation rates decrease (Simpson 1953; Schluter 2000; Gavrillets and Vose 2005; McPeck 2008). This predicts that lineages accumulate rapidly early in the history of a clade, but then the rate of accumulation decreases and the number of lineages may reach a plateau. We investigated this pattern by using lineage-through-time plots (Nee et al. 1992) and by fitting likelihood models of time-dependent speciation and extinction (Rabosky 2006b; Rabosky and Lovette 2008) implemented in functions of the LASER library in R (Rabosky 2006a). We examined eight models of time-dependent speciation. Four were pure-birth models (no extinction): (1) a Yule model of constant speciation, (2) a Yule model with a shift in the speciation rate occurring

at a certain moment in time (both the two rates and the time of the shift were estimated), (3) a diversity-dependent model (i.e., a model in which the speciation rate depends on the number of extant lineages at a given time) with an exponential change of speciation rates, and (4) a diversity-dependent model with a logistic change in speciation rates. The remaining four models were birth-death models (i.e., they included extinction): (1) a uniform birth-death model, (2) a model with declining speciation rates (SPVAR of Rabosky and Lovette 2008), (3) a model with increasing extinction rates (EXVAR), and (4) a model in which both speciation and extinction rates vary (BOTHVAR). As before, we used model selection techniques to compare models (Burnham and Anderson 2002).

## Results

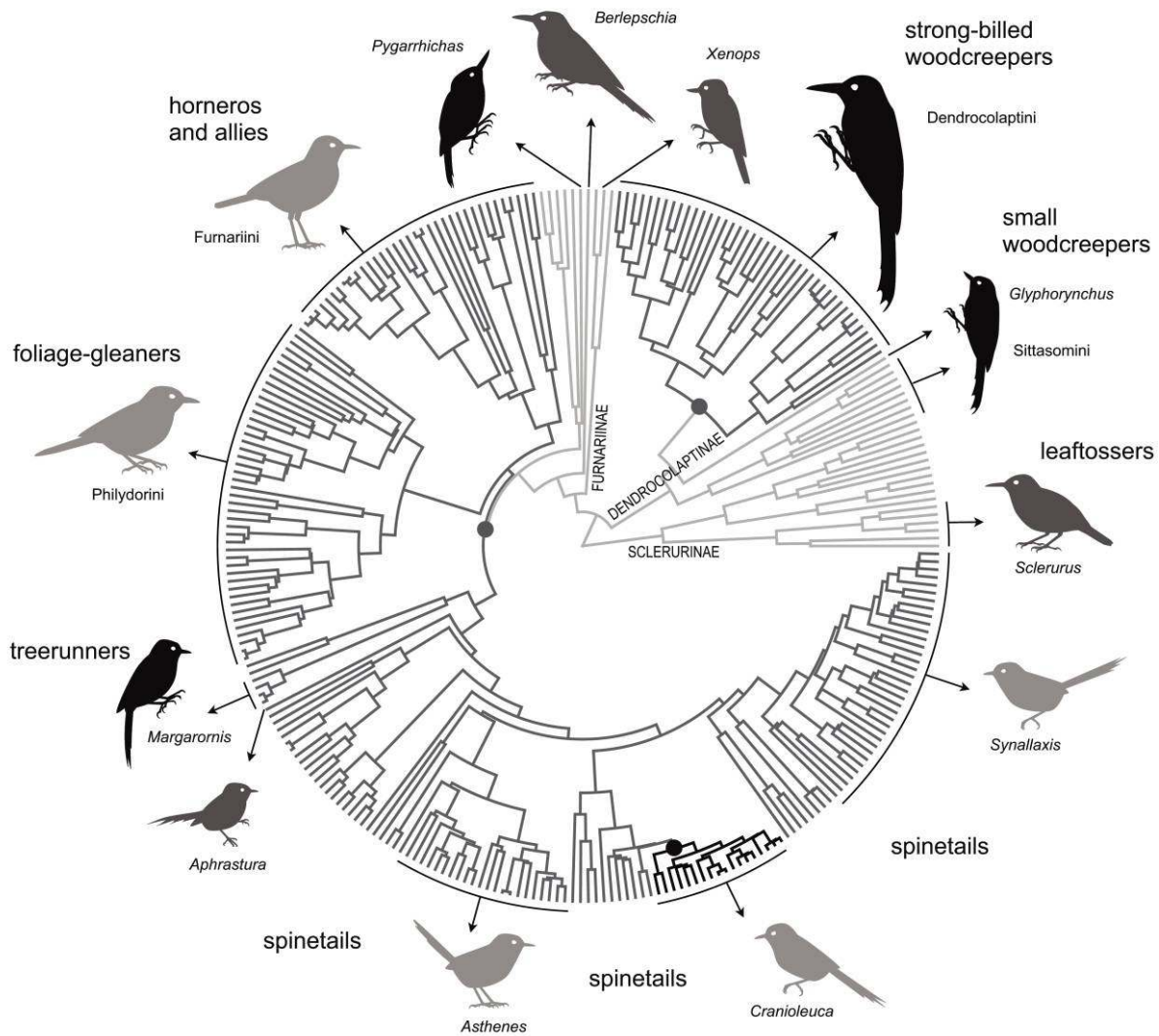
### *Major Shifts in Diversification Rates in the Furnariidae*

We identified several shifts in diversification rates in the Furnariidae (fig. 3). The single shift with the largest improvement in AICc over the single rate model (difference in AICc = 16.5) was an increase in the diversification rate ( $r = 0.58$  million years [myr]<sup>-1</sup>) at the base of *Cranioleuca* spinetails (a monophyletic *Cranioleuca* including *Thriophaga berlepschi* but not *Cranioleuca gutturata* or *Cranioleuca sulphurifera*). A second shift, at the base of a clade composed of most members of the Furnariinae, improved the fit compared with the one-shift model ( $r = 0.16$  myr<sup>-1</sup>, difference in AICc = 6.7). Excluded from this group are *Xenops*, *Berlepschia*, and the Pygarrhichini (sensu Moyle et al. 2009), which diversified at the estimated basal rate of 0.073 myr<sup>-1</sup>. A third increase improved the AICc only moderately compared with the two-shifts model (difference in AICc = 3.1), but we found additional support for it in the Yule with covariates analysis; it occurred at the base of the “strong-billed” woodcreepers (sensu Feduccia 1973), which diversified at a rate of 0.15 myr<sup>-1</sup>. The addition of a fourth shift did not improve the model significantly (difference in AICc < 2). Estimates of relative extinction were negligible (extinction rate/speciation rate < 0.001), suggesting that the estimated diversification rates can be interpreted as speciation rates.

### *Discrete Traits*

The acquisition of climbing adaptations was not associated with increases in diversification rates (fig. 4). Ancestral reconstructions indicated that climbing specializations evolved first in the most recent common ancestor of the Dendrocolaptinae. This ancestor would have had the majority of the most advanced states for all traits (fig. 5), suggesting that it was a highly specialized climber. Parsi-



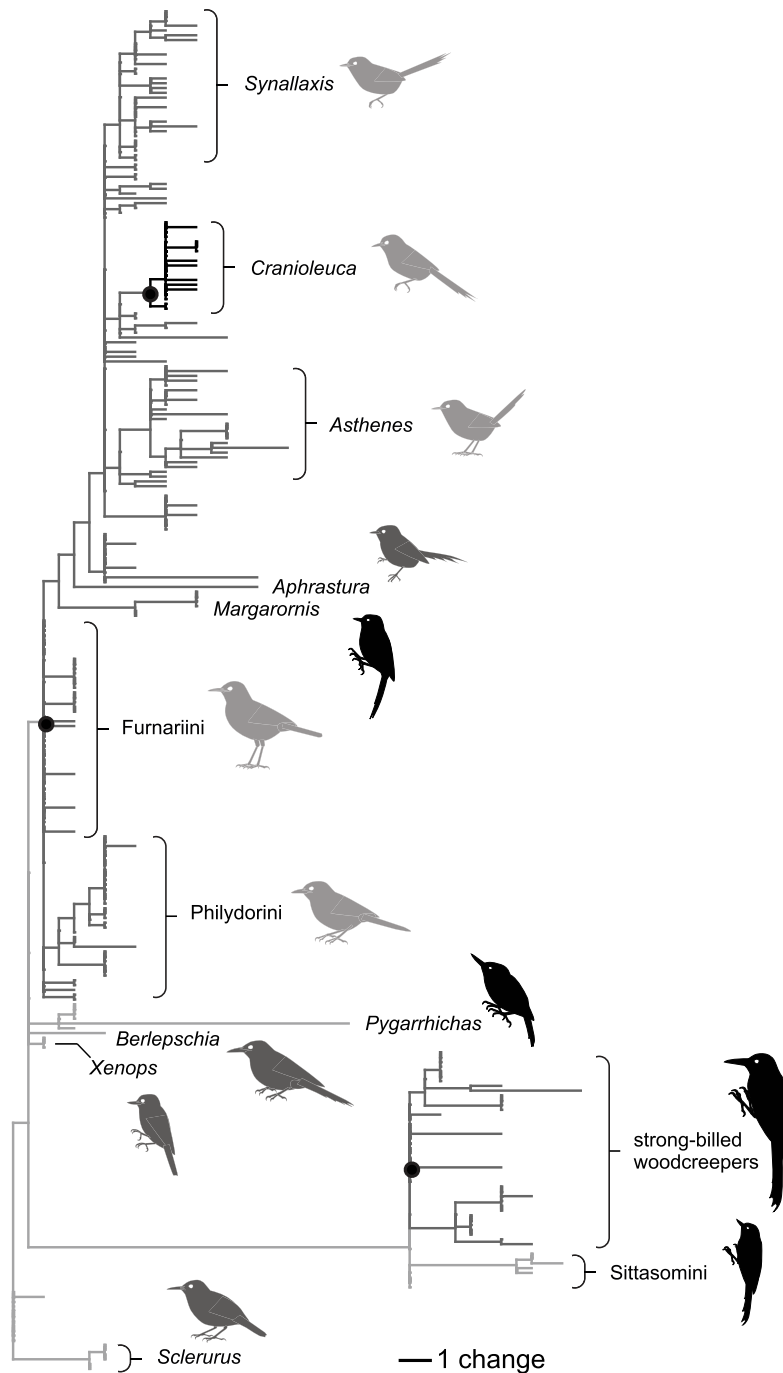


**Figure 3:** Calibrated species-level phylogeny of the Furnariidae from a Bayesian analysis (maximum-clade-credibility tree). Dots on nodes indicate three shifts in diversification rates from the MEDUSA analysis. Shades of gray on branches are proportional to the estimated net rate of diversification: light gray = 0.073 million years ( $\text{myr}^{-1}$ ), dark gray = 0.15–0.16  $\text{myr}^{-1}$ , and black = 0.58  $\text{myr}^{-1}$ . Bird silhouettes illustrate relevant taxa mentioned in the text as well as the diversity in morphology and locomotion behavior shown by the Furnariidae: terrestrial or perching birds (light gray), perching birds that occasionally engage in climbing behavior or show few climbing adaptations (dark gray), and specialized trunk and branch climbers (black).

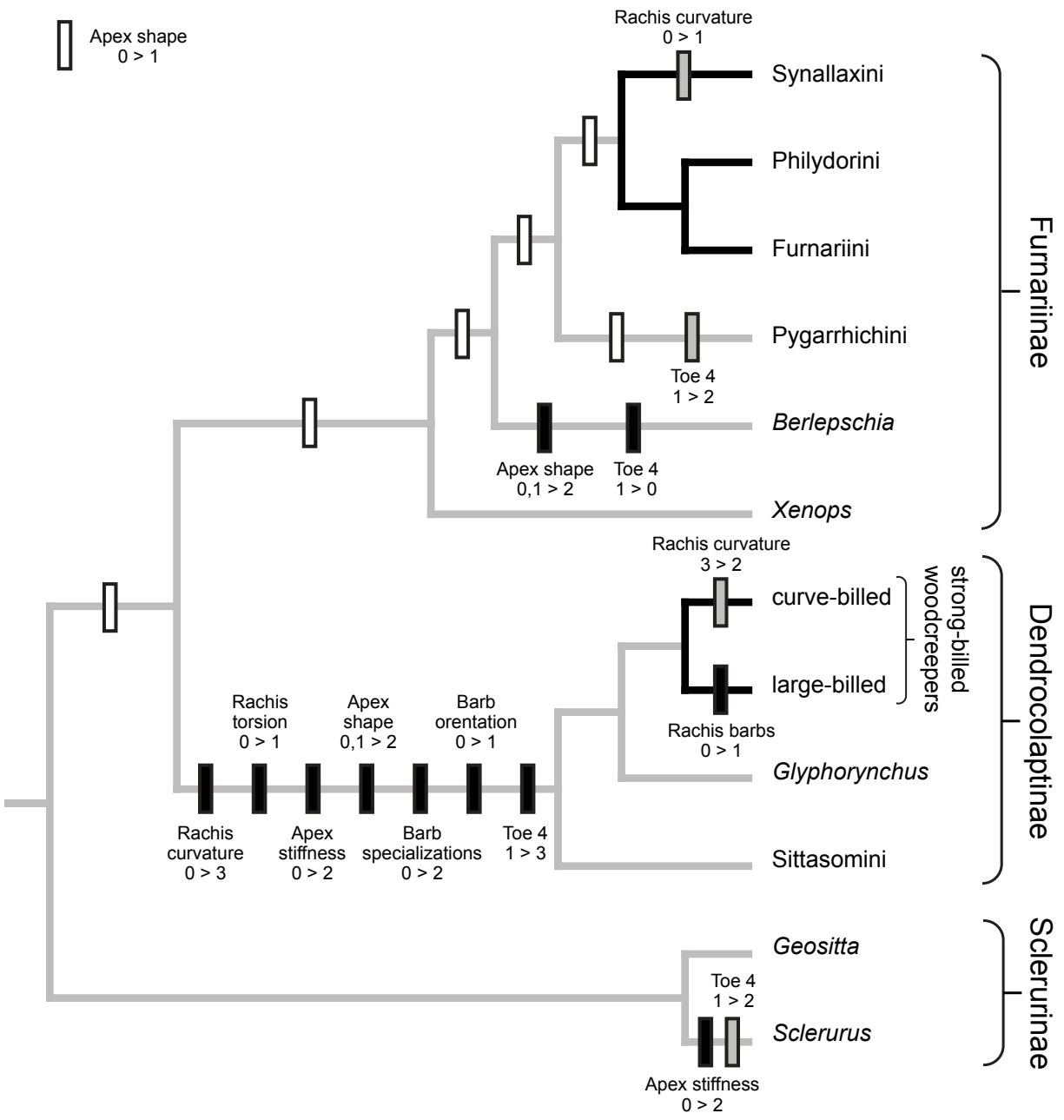
many reconstructions suggest a transition in tail apex shape (from rounded to moderately pointed) at the base of the Furnariinae clade that experienced an increase in diversification. However, the position of this change is highly ambiguous (fig. 5), and maximum likelihood indicated only slight changes in state probabilities. Contrary to prediction, a reduction in toe 4 length (reducing climbing ability), from slightly longer to equal to toe 3, occurred

at the base of *Cranioleuca* (fig. A3, available online). A change in rectrix apex shape is also implied for those branches, but its position is ambiguous in parsimony reconstructions, and almost no change is implied in maximum likelihood reconstructions. Finally, the two branches that precede the increase in diversification in woodcreepers do not show any morphological transition; the great majority of adaptations for climbing evolved earlier, in the





**Figure 4:** Phylogeny of the Furnariidae with branch lengths proportional to the number of character changes that represent climbing adaptations. Branch lengths are averages of values obtained by accelerated and delayed parsimony optimization methods. Black dots mark an increase in diversification rates as identified by the MEDUSA procedure. Shades of gray on branches are proportional to diversification rates, as in figure 3. Bird silhouettes are as in figure 3.



**Figure 5:** Morphological changes associated with climbing at the base of the Furnariidae tree. All most parsimonious reconstructions were considered. Black boxes indicate unambiguous changes. Gray boxes indicate ambiguous changes. White boxes indicate the highly ambiguous position of a transition from rounded to moderately pointed tail feather tips (apex shape in table 1). Black branches indicate clades with higher diversification rates as identified by MEDUSA. The basal node was reconstructed as having state 0 for all tail characters but state 1 for length of toe 4 (table 1).

branch that leads to the most recent common ancestor of all woodcreepers (fig. 5).

For the BiSSE analysis, we considered “climbers” those species that climb regularly and possess an index of climbing adaptations greater than 40: all woodcreepers (*Dendrocolaptinae*) and the genera *Pygarrhichas* and *Margarornis*. We did not find a significant effect of climbing on rates of speciation ( $\chi^2 = 1.5$ ,  $df = 1$ ,  $P = .2$ ).

### *Index of Climbing Adaptations*

The index of climbing adaptations ranged from 0.02 to 0.97. Woodcreepers ranked highest, with values above 0.73, except for the semiterrestrial *Drymornis* (0.54). Within woodcreepers, species of *Dendrocolaptes* and *Dendroplex* reached the highest values (more than 0.93), whereas most species of *Dendrocincla*, *Dendrexetastes*, and *Drymornis* had the lowest values. The only Furnariinae that attained comparable values was *Pygarrhichas* (0.71), which is well known for its scansorial habits (Remsen 2003). Other clades in which tail-assisted climbing is a regular locomotion strategy had intermediate values: the *Margarornis* group (0.34–0.46), *Aphrastura* (0.57), and *Roraimia* (0.47). Most perching and terrestrial species had values less than 0.25. Exceptions were some spintails in the genera *Sylviorthorhynchus* (0.50), *Acrobatornis* (0.27), *Asthenes* (3–36), and *Leptasthenura* (21–27), as well as *Sclerurus* leaf-tossers (0.26–0.30).

The evolution of the climb index was best described by a  $\delta$  model (table 2). The estimated value of the  $\delta$  parameter (0.11), being less than 1, suggests that evolution of the climb index was rapid early in the history of furnariids but then decelerated. Ancestral reconstructions based on the  $\delta$  transformation of the tree showed no pronounced changes coinciding with shifts in diversification rates (fig. 6).

The best models for a relationship between the climb index and diversification (table 3; fig. 7A, 7B) included an overall negative effect of climbing on speciation rates but with different parameters for strong-billed woodcreepers. The best model included a negative slope for all clades ( $\beta = -1.7$ ,  $\chi^2 = 13.6$ ,  $df = 1$ ,  $P < .001$ ; fig. 7A) but with a different intercept for strong-billed woodcreepers ( $\chi^2 = 12.7$ ,  $df = 1$ ,  $P < .001$ ). The second model, which received considerable support, included an interaction term that produced a positive relationship between the climb index and speciation among strong-billed woodcreepers (table 3; fig. 7B). However, the interaction term was not statistically significant ( $\chi^2 = 1.2$ ,  $df = 1$ ,  $P = .28$ ). Models with different rates for woodcreepers versus other furnariids and with a quadratic relationship (to account for potentially lower competitive ability of moderate

**Table 2:** Model selection parameters for the evolution of the index of climbing adaptations

Models	Log-lik	$k$	AICc	$\Delta$ AICc	$w$
$\delta$	374	3	-742	0	1.0
Brownian motion	359	2	-713	29	.0
$\kappa$	359	3	-711	31	.0
Ornstein-Uhlenbeck	359	3	-711	31	.0

Note: Log-lik is the maximized log likelihood of the model,  $k$  is the number of parameters, AICc is the second-order estimator of the Akaike Information Criterion,  $\Delta$ AICc is the difference between a model and the best model, and  $w$  is the model probability, or Akaike weight.

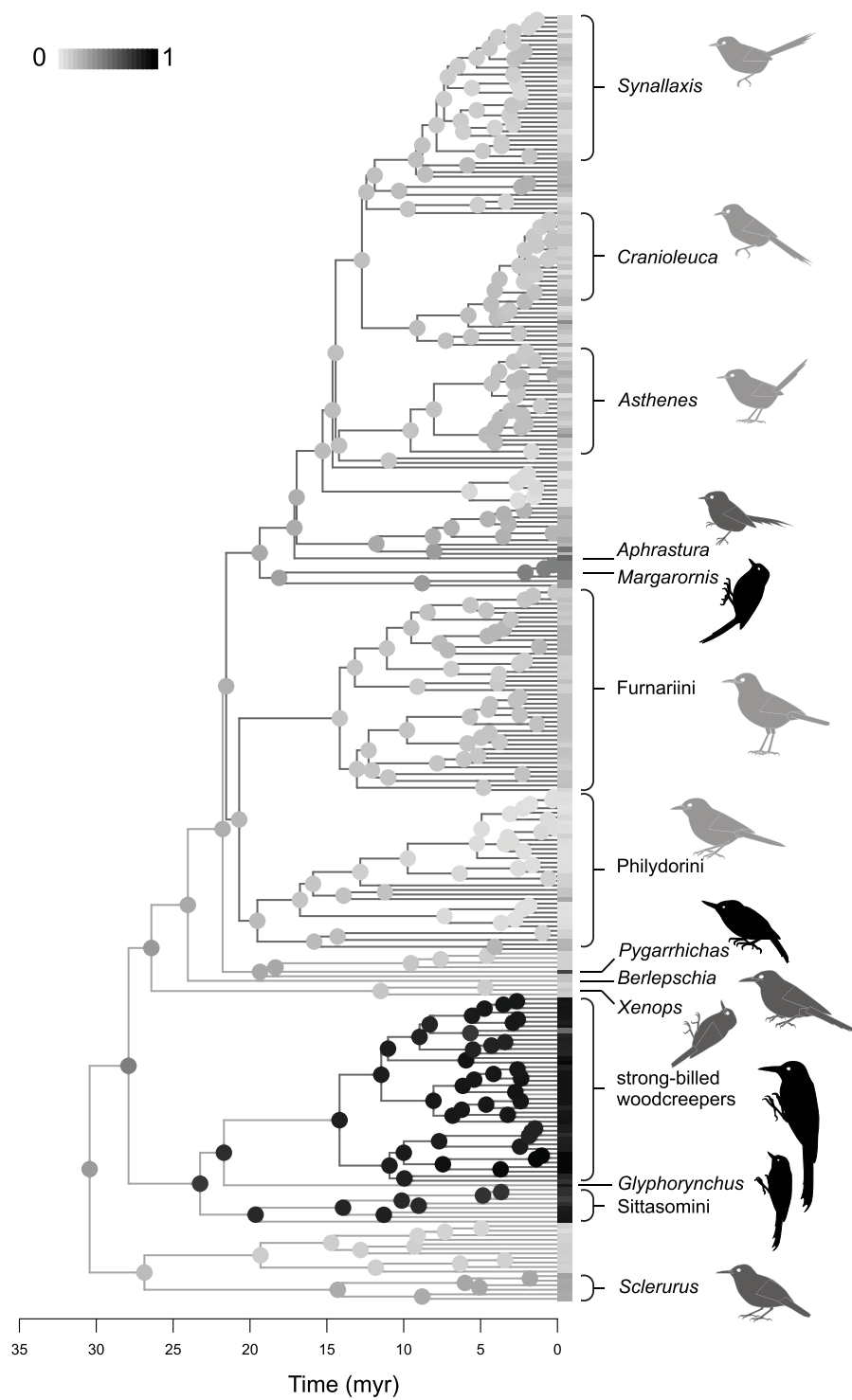
climbers) received low support compared with the previous models (table 3; fig. 7).

### *Lineage Accumulation through Time in the Dendrocolaptinae*

The pattern of lineage accumulation through time in the *Dendrocolaptinae* does not suggest diversity-dependent changes in diversification (fig. 8). The best likelihood model of lineage accumulation was a pure-birth model with a discrete decrease in the speciation rate from 0.18 to 0.04  $\text{myr}^{-1}$  that occurred 2.4  $\text{myr}$  ago (table 4). None of the diversity-dependent models consistent with niche-filling processes received significant support (table 4).

## Discussion

The acquisition of climbing adaptations in Furnariidae is a clear example of an evolutionary innovation that placed lineages in a new adaptive zone (Raikow and Bledsoe 2000). The first furnariids to acquire climbing adaptations, the woodcreepers, likely experienced significant ecological opportunity. Nonetheless, we did not find evidence supporting a link between the evolution of climbing and increased lineage diversification in woodcreepers or in the broader group of Furnariidae. This result is at odds with theories of adaptive radiation regarding the effect of ecological opportunity on cladogenesis (Simpson 1953; Schluter 2000; Yoder et al. 2010). Although there is evidence for the influence of adaptation and interspecific competition in the speciation process (Schluter 2000; Coyne and Orr 2004; Price 2008; Schluter 2009), the mechanisms by which ecological opportunities increase speciation rates are not well established (Losos 2010; Yoder et al. 2010), and many species-rich groups do not show signs of adaptive radiation (Kozak and Wiens 2006; Moore and Donoghue 2007; Harmon et al. 2008b; Price 2010). Instead, factors related to the distribution and dispersal abilities of lineages may influence speciation rates more directly through their influence on levels of gene flow and opportunities for geographic isolation (Mayr 1963; Rosenzweig 1995; Coyne



**Figure 6:** Phylogeny of the Furnariidae with ancestral reconstructions of the composite index of climbing adaptations. Ancestral states were estimated using maximum likelihood methods in a  $\delta$ -transformed tree. Shades of gray indicate the value of the index of climbing adaptations for tips and nodes. Bird silhouettes are as in figure 3. myr = million years.

**Table 3:** Yule models with covariates fit and model selection parameters

Model	Log-lik	<i>k</i>	AICc	ΔAICc	<i>w</i>
$\text{logit}(\lambda) = \alpha + \beta_1\text{Ic} + \beta_2\text{Cs}$	513.7	3	-1,021.3	.0	.57
$\text{logit}(\lambda) = \alpha + \beta_1\text{Ic} + \beta_2\text{Cs} + \beta_3\text{IcCs}$	514.3	4	-1,020.5	.8	.38
$\text{logit}(\lambda) = \alpha + \beta_1\text{Ic} + \beta_2\text{Cd} + \beta_3\text{IcCd}$	511.5	4	-1,014.9	6.4	.02
$\text{logit}(\lambda) = \alpha + \beta_1\text{Ic} + \beta_2\text{Ic}^2$	510.4	3	-1,014.8	6.5	.02
$\text{logit}(\lambda) = \alpha + \beta\text{Ic}$	508.0	2	-1,011.9	9.4	.00

Note: Model parameters are the constant ( $\alpha$ ) and coefficients ( $\beta$ ) of the linear model, the index of climbing adaptations (Ic), and variables indicating whether a clade belongs to the strong-billed woodcreepers (Cs) or to the Dendrocolaptinae (Cd). Model selection parameters are the maximized log likelihood (log-lik) of the model, the number of parameters (*k*), the second-order estimator of the Akaike Information Criterion (AICc), the difference between a model and the best model (ΔAICc), and the model probability (*w*), or Akaike weight.

and Orr 2004; Losos and Parent 2009). Below, we discuss these topics in more detail and provide a dispersal-based hypothesis for reduced speciation rates in scansorial birds.

#### *Origin of Climbing Specializations in Furnariidae*

We investigated the evolution of climbing specializations in the Furnariidae using the most complete phylogeny for any major continental avian family. We found that climbing adaptations evolved to varying degrees in different furnariid lineages. The most specialized clade, the Dendrocolaptinae, is also the oldest and most diverse among climbing furnariids. Several hypotheses have been proposed for the origin of climbing in Furnariidae. Feduccia (1973) proposed that the highly specialized woodcreepers arose from foliage-gleaner ovenbirds and that *Dendrocincla* and other small woodcreepers represent intermediate stages of an “evolutionary trend” toward climbing specialization. This hypothesis was falsified on the basis of relationships revealed by molecular phylogenies (Irestedt et al. 2002; Chesser 2004; Fjeldså et al. 2005; Moyle et al. 2009).

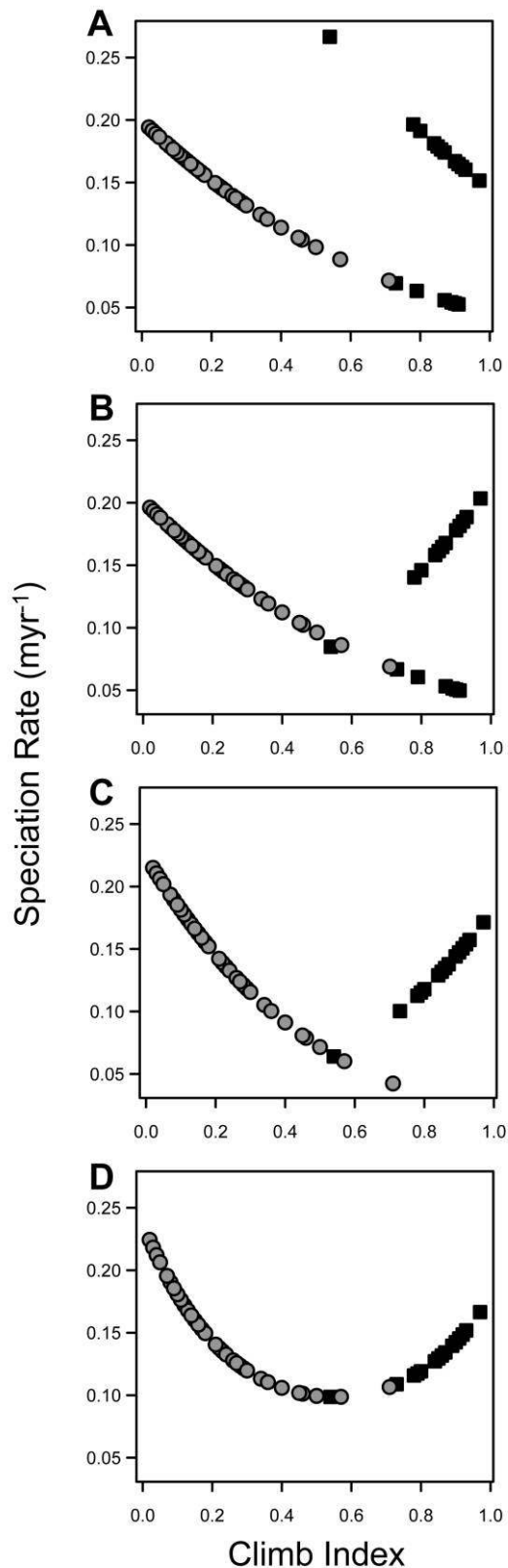
Willis (1974) proposed the alternative hypothesis that woodcreepers evolved from ground-dwelling ancestors, on the basis of morphological similarities between *Dendrocincla* and *Sclerurus* leaf-tossers. Indeed, although *Sclerurus* leaf-tossers feed primarily on the ground, they have stiffened tail rachises and elongated outer toes, two traits clearly associated with climbing. Whether these traits are useful during forceful leaf-tossing maneuvers remains to be studied, but *Sclerurus* species do sometimes cling to vertical trunks when flushed and have been reported roosting in this posture (Willis 1974; Remsen 2003; van Els and Whitney 2011). The position of *Sclerurus* in the evolutionary tree of the Furnariidae (Irestedt et al. 2002; Chesser 2004) was interpreted as providing some support for the hypothesis that woodcreepers evolved from ground-dwelling ancestors (Fjeldså et al. 2005). However, our ancestral

character reconstructions suggest that rachis stiffness and elongated outer toes were acquired independently in *Sclerurus* and woodcreepers and that the most recent common ancestor of all furnariids did not have obvious adaptations for tail-assisted climbing (figs. 5, 6). A phylogeny based on morphological characters suggested that the intermediate development of climbing adaptations in *Drymornis* were ancestral conditions (Raikow 1994), suggesting again a terrestrial ancestor. However, molecular data clearly indicated that *Drymornis* represents a case of adaptation to terrestrial habits from climbing ancestors (Irestedt et al. 2004).

Finally, Willis (1974) proposed that woodcreepers arose from ancestors like *Xenops* or *Berlepschia* that, although primarily perching, occasionally hitch up branches and leaves using their soft tails. Our reconstructions are consistent with this hypothesis and suggest that the ancestor of the woodcreeper/ovenbird clade did not have adaptations for climbing (contra Fjeldså et al. 2005) except for a slight modification in tail feather shape (fig. 5). We found that the transition from a generalized ancestor to a highly specialized climber in the lineage leading to woodcreepers was rather abrupt.

#### *Climbing Specializations and Ecological Opportunity*

Current ecological opportunity is extremely difficult to measure directly, not to mention past ecological opportunity (Losos 2010; Yoder et al. 2010). For this reason, most studies of the historical effect of ecological opportunity on diversification have been conducted on oceanic islands, where available niche space is inferred on the basis of the absence of potential competitors (Grant 1999; Gillespie 2004; Harmon et al. 2008b). Even recent developments in the quantification of historical ecological opportunity are based on the absence or the number of coexisting potential competitors on islands (Mahler et al. 2010). The evolution of climbing adaptations in Furnariidae

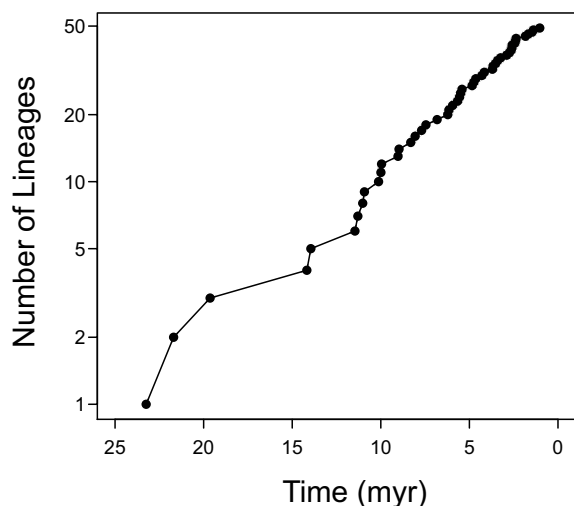


riidae provides one of the few cases in which the effects of historical ecological opportunity on cladogenesis can be examined in a continental radiation because evidence suggests that trunk insectivory was likely a relatively empty niche in South America when furnariids first acquired climbing adaptations.

Our analysis revealed that the most recent common ancestor of the Dendrocolaptinae that lived ~23 myr ago (95% confidence interval: 26–19 myr ago) was a highly specialized climber. This predates the evolution of tail-assisted climbing in woodpeckers by ~10 myr (cf. the most recent common ancestor of Picinae in Fuchs et al. [2007]). Furthermore, there is no evidence that woodpeckers occurred in South America until 5–8 myr ago (Fuchs et al. 2007). Thus, scansorial furnariids may have been the only climbing birds on the South American continent for at least 15 myr. Although these analyses depend heavily on the calibration points and methodologies utilized, a non-calibrated analysis of Dendrocolaptinae and Picinae still shows that the first woodcreepers evolved before woodpeckers arrived in South America (appendix, available online). Ultimately, the degree to which woodpeckers interact ecologically with woodcreepers is not known. It is necessary to assess not only competition but also other ecological interactions between these two groups of birds. For example, woodpeckers may benefit woodcreepers by excavating tree cavities that can be used for nesting. Because hole-nesting bird populations are often limited by the availability of adequate cavities (Newton 1994), the arrival of woodpeckers to South America may have produced a positive impact on woodcreeper populations.

Other Neotropical vertebrates are known to feed on insects from trunk surfaces. Several medium- to large-sized lizard species specialize in trunk insectivory (Pianka and Vitt 2003; Losos 2009). However, because woodcreepers can prey on small or juvenile lizards (Hayes and Argaña 1990; Chapman and Rosenberg 1991; Poulin et al. 2001), it is not clear whether trunk-foraging lizards decrease or increase resources for woodcreepers. Trunk-surface insectivory is also known among Neotropical callitrichid monkeys (marmosets and tamarins; Garber 1992), although the degree of niche overlap and competition between callitrichids and woodcreepers is not known. In any case, because callitrichids originated sometime between 14

**Figure 7:** Predicted speciation rate as a function of the climb index from the Yule model with covariates approach. *A*, Model with a different intercept for strong-billed woodcreepers (support:  $w = 0.57$ ). *B*, Model with a different intercept and slope for strong-billed woodcreepers ( $w = 0.38$ ). *C*, Model with a different intercept and slope for all woodcreepers ( $w = 0.02$ ). *D*, Model with a quadratic relationship ( $w = 0.02$ ). Gray circles indicate Furnariinae and Sclerurinae; black squares indicate Dendrocolaptinae. myr = million years.



**Figure 8:** Number of lineages through time in the Dendrocolaptinae. myr = million years.

and 20 myr ago (Fabre et al. 2009; Perelman et al. 2011), evidence points to an earlier origin of trunk foraging in woodcreepers, suggesting that woodcreeper ancestors encountered a relatively unoccupied ecological space in the forests of South America.

#### *Climbing Specializations and Cladogenesis*

Despite the apparent clear-cut case of ecological opportunity, we found no evidence that climbing adaptations stimulated lineage diversification in the Furnariidae. This was true whether we modeled character evolution and changes in diversification as discrete processes or as continuous processes. Moreover, our results are not caused by lack of power to detect tendencies in the data; we found significant shifts in diversification rates that do not coincide with innovations for climbing as well as evidence for a negative effect of climbing on diversification.

No discrete shifts in speciation rates were found to be associated with the origin of morphological innovations related to climbing. An increase in speciation rates in woodcreepers occurred well after the evolution of advanced climbing adaptations, affecting only strong-billed woodcreepers (fig. 3). This result is not an effect of small woodcreepers being intermediate in their climbing abilities. Some woodcreepers evolving at the background rate, such as *Dendrocincla* (Sittasomini), show a lesser degree of development of climbing adaptations in both external traits (climbing index: 0.73–0.87) and myological traits (Bledsoe et al. 1997), in agreement with a less active scan-sorial behavior (Skutch 1969; Willis 1972). However, other

small woodcreepers in the genera *Sittasomus*, *Glyphorynchus*, and *Deconychura* (Sittasomini) are professional trunk foragers (Marantz et al. 2003) and show climbing index values well within the range of the strong-billed woodcreepers (0.89–0.91). Other increases in diversification rates in the Furnariidae were not associated with acquisition of climbing adaptations.

When we modeled traits and diversification rates on a continuous scale, we found an overall negative effect of climbing specialization on lineage diversification across the Furnariidae. Yule models with covariates indicated that climbing adaptations had a negative effect on the diversification rate for all furnariids, with the possible exception of strong-billed woodcreepers. Models with a differential effect for all woodcreepers or with a nonmonotonic relationship did not provide a good fit to the data. The two most supported models differ on whether the relationship between climbing and speciation rates is negative or positive among strong-billed woodcreepers. Given that levels of support were similar for these two models, whether climbing is positively or negatively correlated with speciation rates among strong-billed woodcreepers remains an open question. Even assuming a positive effect, it occurred almost 10 myr after the first woodcreeper entered the new climbing niche. Therefore, the evidence for a stimulating effect consistent with the ecological theory of adaptive radiation is tenuous at best. Other aspects of the strong-billed woodcreeper phenotype, such as the reinforced skull (Feduccia 1973), may be related to the increase in cladogenesis. Further investigation of the relationship between phenotypic traits and cladogenesis in woodcreepers is warranted.

The ecological opportunity hypothesis does not provide a satisfactory explanation for the negative relationship between climbing adaptations and diversification. Under the ecological theory of adaptive radiation, a decrease in speciation rates is produced when ecological opportunity becomes scarce (Simpson 1953; Schluter 2000; Yoder 2010). Perhaps earlier woodcreepers did experience an increase in speciation, but the rate decreased toward the present as niches filled and extant lineages experienced low speciation rates due to saturation of ecological space (Simpson 1953; Gavrillets and Vose 2005; McPeck 2008). Considering the high degree of sympatry among woodcreepers, the potential for competition and saturation of the trunk-climbing niche is high. The geographic ranges of all woodcreeper species overlap in part with the distribution of at least one other woodcreeper species. About 30 of the 50 species of woodcreepers inhabit the Amazon basin, and between 10 and 20 species can occur at a single locality in Amazonian forests (Terborgh et al. 1990; Cohn-Haft et al. 1997; Marantz et al. 2003). However, we did not find evidence for changing extinction or speciation rates



**Table 4:** Likelihood models of lineage diversification through time in the woodcreepers (*Dendrocolaptinae*)

Model	Log-lik	<i>k</i>	AICc	$\Delta$ AICc	<i>w</i>
Pure-birth models:					
Yule (constant speciation)	.42	1	1.17	8.2	.01
Yule with a shift	6.65	3	-7.03	.0	.89
Diversity-dependent exponential	3.01	2	-1.94	5.1	.07
Diversity-dependent logistic	1.16	2	1.76	8.8	.01
Birth-death models:					
Birth-death	.42	2	3.26	10.3	.01
Decline in speciation rate	.87	3	4.52	11.6	.00
Increase in extinction rate	.39	3	5.49	12.5	.00
Speciation and extinction variable	.89	4	6.77	13.8	.00

Note: Log-lik is the maximized log likelihood of the model, *k* is the number of parameters, AICc is the second-order estimator of the Akaike Information Criterion,  $\Delta$ AICc is the difference between a model and the best model, and *w* is the model probability, or Akaike weight.

through time in a diversity-dependent fashion consistent with a niche-filling process (fig. 8; table 4). Instead, we found a discrete decrease in speciation rates 2.4 myr ago. Because a similar discrete decrease is found across climbing and nonclimbing furnariids (Derryberry et al. 2011), this slowdown seems unrelated to saturation of the climbing niche. This also suggests that the arrival of woodpeckers to South America 5–8 myr ago did not affect rates of speciation through time among woodcreepers.

Another possibility is that lineages failed to radiate because of a lack of phenotypic evolvability (Losos 2010). This may be particularly relevant for scansorial passerines. Gatesy and Dial (1996) hypothesized that functional decoupling of avian appendages into three somewhat-independent locomotor modules (wings, hind limbs, and tail) allowed high evolvability of locomotion styles among birds. However, because tail and hind limbs are used for the same function in tail-assisted climbing, they are not free to evolve independently. This constraint on the evolution of two locomotor modules may reduce evolvability among scansorial passerines relative to perching passerines. Consistent with this, woodcreepers are relatively uniform in body shape, limb proportions, and foot morphology (Raikow and Bledsoe 2000; Marantz et al. 2003). Yet woodcreeper morphometric diversity is comparatively high (Claramunt 2010). They vary extensively in body size (Claramunt 2010), bill morphology (Raikow and Bledsoe 2000), and the structure of the tail tip (fig. 2). In particular, the variety of bill morphologies is related to the diverse ways woodcreepers explore the substrate looking for prey (Feduccia 1970; Marantz et al. 2003). Therefore, although woodcreepers may be constrained in traits related to locomotion, they are not constrained in other traits, and they have evolved into a variety of sizes and ecological forms (Raikow and Bledsoe 2000; Marantz et al. 2003). Thus, reduced evolvability does not appear to explain the lack

of increased speciation rates after woodcreepers entered the new niche.

Some argue that the effect of a key trait on species proliferation may not be manifested until other changes in the phenotype or the environment take place (Jensen 1990; de Queiroz 2002; Donoghue 2005). However, in that case it is highly speculative to decide whether changes in diversification were influenced by a putative key innovation or by the other factors themselves. Ultimately, any evolutionary change may depend on innovations acquired during the evolution of ancestral lineages, but if the occurrence of a putative key innovation does not coincide with a shift in diversification, then key innovations may be impossible to test analytically (Cracraft 1990). Progress regarding the effect of species traits on diversification can be made only if hypotheses can be tested, and increasingly complex analytical tools are being developed for that purpose (Paradis 2005; Maddison et al. 2007; Alfaro et al. 2009b; FitzJohn 2010). The same considerations are valid regarding the direct effect of ecological opportunity on diversification, with the added difficulty that ecological opportunity is much more difficult to quantify (Harmon et al. 2008b; Mahler et al. 2010; Yoder et al. 2010).

Another possibility is that the negative effect of climbing on diversification might be the result of an indirect effect of a correlated phenomenon. In particular, the negative effect of climbing adaptations on speciation rates could be the indirect result of a correlation between climbing and dispersal propensity, which influences gene flow. Climbing birds typically make flights of many meters between trees during normal foraging behavior. In contrast, foliage gleaners do not have to make as many long flights to move among their more continuously distributed foraging substrate. This may be particularly true among small furnariids that inhabit dense vegetation. Therefore, trunk foraging requires the capability of making, on average,

longer flights. Although woodcreepers typically climb up trees and then take easy flights down to the base of the next tree (Marantz et al. 2003), they nonetheless typically make longer flights than most furnariids. Consequently, woodcreepers may be more likely to cross barriers such as rivers or forest gaps and thus have relatively higher dispersal rates. This is supported by experiments in which the cocoa woodcreeper (*Xiphorhynchus susurrans*) showed greater ability to fly over water than foliage insectivores (Moore et al. 2008). Higher levels of gene flow (Bates 2000) and lower levels of population genetic differentiation (Bates et al. 2004; Burney and Brumfield 2009) have been found in woodcreeper species compared with other understory arboreal insectivores. At an evolutionary time-scale, higher dispersal rates and gene flow in trunk climbers could reduce their chances of speciation by maintaining genetic cohesion among populations (Mayr 1963; Coyne and Orr 2004). That furnariids show an overall negative relationship between dispersal ability and speciation rates (Claramunt et al. 2012) is consistent with this hypothesis.

#### Acknowledgments

For granting access to specimens, we thank P. Capainolo, J. Cracraft, and P. Sweet, American Museum of Natural History, Field Museum of Natural History; I. Franke and L. Salinas, Museo de Historia Natural Universidad Nacional Mayor de San Marcos (Lima); P. Tubaro, Museo Argentino de Ciencias Naturales (Buenos Aires); N. Rice, Academy of Natural Sciences (Philadelphia); J. Cuello, Museo Nacional de Historia Natural (Montevideo); K. Zyskowski, Yale University Peabody Museum of Natural History; R. Faucett, University of Washington Burke Museum of Natural History; K. Garret, Natural History Museum of Los Angeles County; and M. Robbins, University of Kansas Natural History Museum. We thank A. Bravo for help collecting morphological data. We thank J. Aldabe, A. Bravo, G. Bravo, L. Emmons, M. Gavilanez, L. Naka, M. Pattten, K. Petren, and three anonymous reviewers for discussion, comments, and suggestions. This research was supported in part by Sigma Xi and National Science Foundation grant DEB-0543562.

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