

Evolutionary and Ecological Causes of the Latitudinal Diversity Gradient in Hylid Frogs: Treefrog Trees Unearth the Roots of High Tropical Diversity

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ABSTRACT: Why are there more species in the tropics than in temperate regions? In recent years, this long-standing question has been addressed primarily by seeking environmental correlates of diversity. But to understand the ultimate causes of diversity patterns, we must also examine the evolutionary and biogeographic processes that directly change species numbers (i.e., speciation, extinction, and dispersal). With this perspective, we dissect the latitudinal diversity gradient in hylid frogs. We reconstruct a phylogeny for 124 hylid species, estimate divergence times and diversification rates for major clades, reconstruct biogeographic changes, and use ecological niche modeling to identify climatic variables that potentially limit dispersal. We find that hylids originated in tropical South America and spread to temperate regions only recently (leaving limited time for speciation). There is a strong relationship between the species richness of each region and when that region was colonized but not between the latitudinal positions of clades and their rates of diversification. Temperature seasonality seemingly limits dispersal of many tropical clades into temperate regions and shows significant phylogenetic conservatism. Overall, our study illustrates how two general principles (niche conservatism and the time-for-speciation effect) may help explain the latitudinal diversity gradient as well as many other diversity patterns across taxa and regions.

Keywords: amphibians, biogeography, latitudinal gradient, niche conservatism, phylogeny, species richness.

The tendency for most groups of organisms to have more species in tropical regions than in temperate regions is one of the oldest known patterns in ecology and biogeography (Brown and Lomolino 1998). It also remains poorly understood. At least 100 hypotheses have been proposed to explain this pattern (e.g., Pianka 1966; Rahbek and Graves 2001; Willig et al. 2003), and there is little consensus as to which hypothesis (or combination of hypotheses) is the most likely explanation. Many hypotheses address how ecological processes might allow larger numbers of species to coexist in the tropics (e.g., productivity, energy, stability, spatial heterogeneity, predation, and competition hypotheses; Pianka 1966; Willig et al. 2003). Several other hypotheses focus (explicitly or implicitly) on potential differences in rates of speciation and extinction between temperate and tropical regions (e.g., evolutionary rates hypothesis; Willig et al. 2003). Explaining these large-scale patterns of species richness has become a pressing problem as global diversity is increasingly threatened, particularly by destruction of tropical rain forests (Wilson 1992, 2002).

In recent years, much of the research on the latitudinal diversity gradient has focused on seeking environmental variables that correlate with patterns of richness and testing the associated ecological hypotheses (e.g., energy and productivity hypotheses; Francis and Currie 2003; Hawkins et al. 2003; Willig et al. 2003). In some ways, this approach has been highly successful, in that environmental variables do seem to be strongly correlated with diversity patterns in many cases. At the same time, this ecological approach has important limitations because it does not directly address the processes that ultimately change species numbers (Ricklefs 2004; Wiens and Donoghue 2004). An environmental variable cannot by itself change the number of species in a region or community. Instead, the factors that directly influence species numbers are speciation, extinction, and dispersal of taxa into or out of a

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region. To fully explain species richness patterns, we must determine how ecological factors (e.g., climate) interact with the evolutionary and biogeographic processes of speciation, extinction, and dispersal to create geographic gradients in species numbers.

In the 1990s, several evolutionary ecologists independently converged on a similar explanation for how the interplay of ecological and evolutionary processes might create the latitudinal diversity gradient (Farrell et al. 1992; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998). Wiens and Donoghue (2004) pointed out this convergence among authors and dubbed the explanation the “tropical conservatism hypothesis.” This hypothesis has three main components, which are described below. It is important to note that the tropical conservatism hypothesis is not an entirely new hypothesis, given that all three components have direct or indirect antecedents in the earlier literature. Instead, we see this hypothesis as one promising synthesis of evolutionary and ecological perspectives.

First, groups with high tropical species richness originated in the tropics and have dispersed to temperate regions either recently or not at all, leaving less time for species richness to accumulate in temperate regions. This aspect is clearly related to the evolutionary time hypothesis (Willis 1922; Stebbins 1974) or time-for-speciation effect (Stephens and Wiens 2003), the idea that there will tend to be more species in the area where a given group originated.

Second, dispersal of tropical groups into temperate regions is limited by their inability to adapt to freezing temperatures in winter. The idea that freezing temperatures are harmful to tropical organisms and might limit their poleward dispersal is highly intuitive and supported by some empirical studies (Sakai and Larcher 1987; Woodward 1987; Fine 2001). However, relatively little evidence was provided to support this idea by the authors who proposed the hypothesis (Farrell et al. 1992; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998).

Third, a large number of extant groups originated in the tropics because the tropics were more extensive until recently (~30–40 million years ago [mya]), when the temperate regions expanded (Behrensmeyer et al. 1992; Morley 2000). This aspect of the hypothesis is related to the idea that species richness is positively correlated with area, a long-standing theory in ecology and biogeography (MacArthur and Wilson 1967; Rosenzweig 1995).

So far, the tropical conservatism hypothesis has not been thoroughly tested in any group of organisms. Nevertheless, some studies have addressed certain aspects of the hypothesis, such as the tendency of temperate regions to have phylogenetically younger lineages (e.g., Ricklefs and Schlu-

ter 1993; Gaston and Blackburn 1996; Hawkins et al. 2006).

In this article, we attempt to uncover the evolutionary and ecological causes of the latitudinal diversity gradient and to test the major predictions of the tropical conservatism hypothesis. We combine a diversity of analytical approaches (e.g., phylogenetics, ancestral area reconstruction, divergence date estimation, analysis of diversification rates, ecological niche modeling) and focus on New World hylid frogs (treefrogs) as our empirical system. Hylid frogs are distributed widely (all major continental regions except sub-Saharan Africa and Antarctica), but most species and genera occur in the New World (AmphibiaWeb 2005). Within the New World, hylids show the typical latitudinal diversity gradient that characterizes many higher taxa; Hylidae has few species in temperate North America ($n = 28$; United States and Canada), many in tropical Middle America ($n = 162$; Mexico to Panama) and tropical South America ($n = 456$; $\leq 30^\circ\text{S}$), and few in temperate South America ($n = 22$; $\geq 30^\circ\text{S}$; IUCN et al. 2004; AmphibiaWeb 2005). Hylid frogs are a promising study system because they have been the recent subject of intensive phylogenetic study and systematic revision (e.g., Faivovich et al. 2005; Smith et al. 2005; Wiens et al. 2005), because updated range maps are available for all species (Global Amphibian Assessment; IUCN et al. 2004), and because the hylid fauna at the interface between temperate and tropical regions in the Northern Hemisphere has been especially well studied (Duellman 2001). On the negative side, available phylogenies do not yet include all hylid species, and new species continue to be described. However, these problems may be common to most species-rich clades in the tropics, and new hylid phylogenies now allow >95% of all described hylid species to be assigned to major clades within the group (Faivovich et al. 2005; Wiens et al. 2005).

Predictions of the Tropical Conservatism Hypothesis

An important criticism that has been made of evolutionary explanations for diversity patterns is that they make “few strong predictions about expected patterns of richness” (Francis and Currie 2004, p. 782). In this article, we develop explicit predictions based on the tropical conservatism hypothesis and then test them in hylid frogs.

The first part of the tropical conservatism hypothesis predicts that groups with high tropical species richness originated in the tropics and have spread to temperate regions more recently. Thus, we predict that ancestral area reconstruction will show that hylids originated in tropical South America. An ancillary prediction is that there is a general relationship between how long a clade has been present in a given region and how many species are in that region, regardless of whether regions are tropical or

temperate (the evolutionary time hypothesis or time-for-speciation effect; reviewed and tested by Stephens and Wiens [2003]). If this prediction is not supported, it might suggest that the timing of colonization is not important and that differences in diversification rate between tropical and temperate regions might explain the latitudinal diversity gradient instead (Cardillo 1999; Cardillo et al. 2005). Thus, a second ancillary prediction is that there is no general relationship between where clades occur (i.e., their latitudinal midpoint) and their rate of diversification. It is also possible that hylid frogs spread to temperate regions only recently but that their rate of diversification is nonetheless higher in the tropics. This pattern would suggest that low temperate diversity might be explained by a combination of recent dispersal and lower diversification rates.

A second major component of the tropical conservatism hypothesis posits that dispersal of species from tropical to temperate regions is limited by their inability to tolerate cold winter temperatures (Farrell et al. 1992; Ricklefs and Schluter 1993; Futuyma 1998). Thus, we predict that diverse lineages of tropical hylids will independently converge on similar northern range limits adjacent to temperate regions and that ecological niche modeling will show that the distribution of cold winter temperatures predicts the poleward range limits of these taxa. An ancillary prediction is that tolerances to the climatic factors that limit dispersal into temperate regions (e.g., extreme cold) will generally be conserved across the evolutionary history of the group (phylogenetic niche conservatism; Ricklefs and Latham 1992; Peterson et al. 1999; Wiens and Graham 2005).

We consider the third part of the tropical conservatism hypothesis (i.e., the idea that many clades originated in the tropics because the tropics were formerly more extensive than they are today) to be the most difficult to test, particularly for a single clade of organisms. Minimally, we predict that hylids originated before expansion of the temperate regions 30–40 mya, and that their major clades arose before this period as well. However, we acknowledge that this is not a particularly compelling test of this aspect of the hypothesis.

We test these three sets of predictions using a battery of approaches including phylogenetic analysis, ancestral area reconstruction, molecular dating methods, and ecological niche modeling. In order to test the first set of predictions, we first reconstruct a phylogeny for hylid species based on combined nuclear and mitochondrial DNA sequence data. We then use ancestral area reconstruction to address the biogeographic relationships between the tropical and temperate hylid faunas. We estimate the divergence times of the major clades of hylids by combining molecular branch length information and fossil calibration

points, using penalized likelihood analysis (Sanderson 2002). We combine these estimated divergence dates and ancestral area reconstructions to determine the relationship between the timing of colonization of each region and the number of species there (Stephens and Wiens 2003). We then use these divergence dates to estimate absolute rates of diversification (e.g., Magallón and Sanderson 2001) and to examine the relationship between the diversification rates of clades and their latitudinal positions (e.g., Cardillo et al. 2005). To address the second part of the tropical conservatism hypothesis, we use ecological niche modeling to determine whether the distribution of coldest winter temperatures predicts the poleward range limits of major hylid clades adjacent to temperate regions. We also test for significant phylogenetic conservatism in the most limiting climatic variable across the phylogeny of hylid frogs (e.g., Smith et al. 2005). Finally, to address the third part of the hypothesis, we estimate divergence dates to address whether hylids originated and diversified before or after the expansion of temperate regions ~30–40 mya.

In the following paragraphs, we provide a highly abbreviated version of our methods. A more detailed description is provided in the appendix in the online edition of the *American Naturalist*.

Material and Methods

Taxonomy

Throughout this article, we follow the new hylid taxonomy proposed by Faivovich et al. (2005), which was generally corroborated by Wiens et al. (2005). However, we continue to recognize the genus *Phrynohyas*, given that relationships within the larger clade containing this genus (*Lophiohyli*) are poorly supported.

Phylogenetic Analysis

We reconstructed hylid relationships primarily using a combined, partitioned Bayesian analysis of up to 10 genes (four mitochondrial, six nuclear; 7,390 base pairs combined) for each of 140 species (124 hylids, 16 outgroup taxa). An analysis including 325 taxa was also performed to confirm placement of species in major clades. Sequence data were compiled from several literature sources (e.g., Faivovich et al. 2005; Smith et al. 2005; Wiens et al. 2005), and 46 new sequences were also generated. Molecular and phylogenetic methods generally follow Wiens et al. (2005) and are explained in detail in the appendix, including results for 325 taxa and GenBank numbers.

Reconstructing Biogeographic Changes

Major dispersal events between biogeographic regions were estimated using parsimony and likelihood reconstructions of ancestral areas on the trees for 325 and 140 taxa, respectively. We followed the general method of Ronquist (1994), and details are described in the appendix. In brief, this involved treating different biogeographic regions as character states, coding each species with a given state, and then reconstructing ancestral character states (and changes between states) on the phylogenies. We also performed similar analyses using dispersal-vicariance analyses (Ronquist 1997) implemented with DIVA, version 1.1 (Ronquist 1996).

Estimating Ages of Clades

Estimates of the absolute ages of clades were used in order to determine (1) the relationship between regional species richness and the time when a given region was colonized, (2) absolute diversification rates of clades, and (3) the age of major hylid lineages relative to the Cenozoic expansion of the temperate regions. We used penalized likelihood (Sanderson 2002) as implemented in r8s (ver. 1.6 for Unix; Sanderson 2003) to estimate these ages, using a combination of molecular branch length information and estimates of absolute clade age based on fossils and other geological criteria. Methods generally followed Smith et al. (2005) and are described in the appendix.

Regional Species Richness versus Time of Colonization

The tropical conservatism hypothesis implicitly assumes a general relationship between how long a group has been present in a region and how many species currently occur in that region. We performed linear regression of the estimated minimum age of the first colonization of hylids in a region (independent variable, in millions of years) versus the natural log of the number of hylid species in that region (dependent variable), generally following Stephens and Wiens (2003).

We took advantage of three recent Web-based summaries to estimate the number of species in each region: the Global Amphibian Assessment Web site (<http://www.globalamphibians.org>; IUCN et al. 2004); Amphibian Species of the World, version 3.0 (checked September 5, 2005; Frost 2004); and the AmphibiaWeb database (<http://amphibiaweb.org/>). Methods are described further in the appendix, and estimates of species richness and dates of first colonization for each region are provided in table 1.

Table 1: Species richness and estimated minimum dates of colonization for hylid frogs in seven major continental regions, using two different root ages for Neobatrachia

Region	Species	Time colonized (mya)	
		Using 100-mya root age	Using 160-mya root age
South America	458	63.43	90.50
Australia	166	42.37	60.40
Middle America	162	44.72	60.65
North America	28	35.61	48.10
Asia	11	18.47	23.65
West Indies	9	21.91	29.53
Europe	5	21.93	28.34

Latitudinal Variation in Rates of Diversification

The tropical conservatism hypothesis implicitly assumes that there is no relationship between the rate of diversification of a clade and its geographic location (i.e., temperate or tropical) or at least that differences in diversification rate between regions are not the major cause of the latitudinal gradient. We divided Hylidae into 11 clades and then performed linear regression of the diversification rate of each clade and the latitudinal midpoint of the geographic range of that clade. We initially estimated the absolute diversification rate of each clade using the maximum likelihood estimator under a pure birth model and utilizing the crown group age (where the crown group is the least inclusive monophyletic group that includes all the extant members of a clade):

$$\hat{r} = \frac{\log(n) - \log(2)}{t}, \quad (1)$$

where n is the number of species in the clade and t is the estimated age of the crown group (from Magallón and Sanderson 2001). A set of analyses was also performed using the method-of-moments estimators for crown and stem groups (eqq. [6] and [7] in Magallón and Sanderson 2001) and assuming high relative extinction rates ($\epsilon = 0.90$).

We performed linear regression analyses using raw data on diversification rate and latitudinal midpoint for these 11 clades. We also performed an analysis using independent contrasts (Felsenstein 1985*b*) of diversification rate and latitudinal midpoint to account for the shared histories of these clades, using equal branch lengths (all branches set to 1), branch lengths based on the combined partitioned molecular data, and branch lengths based on the penalized likelihood analysis. Summaries of estimated

Table 2: Summary of estimated age, species richness, diversification rate (\hat{r}), and absolute value of latitudinal midpoint for each of 11 clades of hylid frogs, with ages and diversification rates estimated using two different root ages for Neobatrachia

Clade	Age (mya)		Species	\hat{r}		Latitudinal midpoint (°) ^a	Northern/southern latitudinal limits (°)
	Using 100-mya root age	Using 160-mya root age		Using 100-mya root age	Using 160-mya root age		
Pelodyadinae	42.37	60.40	166	.045	.032	19.68	4.49/−43.85
Phyllomedusinae	34.39	49.76	52	.041	.028	3.86	27.15/−34.87
Cophomantini	51.67	73.55	145	.036	.025	12.90	12.54/−38.35
<i>Dendropsophus</i> clade	50.18	70.78	87	.033	.023	6.87	21.82/−35.57
<i>Scinax</i> clade	53.77	75.95	102	.032	.022	6.76	23.23/−36.75
Lophiohylini	35.90	48.59	62	.042	.031	2.78	26.66/−32.22
<i>Acris-Pseudacris</i> clade	35.61	48.10	16	.025	.019	42.90	62.50/23.30
<i>Plectrohyla</i> clade	32.00	41.97	50	.044	.033	18.78	23.55/14.00
<i>Ptychohyla</i> clade	40.18	54.14	40	.032	.024	17.00	24.45/8.55
<i>Smilisca</i> clade	33.49	44.77	29	.035	.026	15.88	31.93/−.18
Holarctic <i>Hyla</i>	31.85	41.65	32	.038	.029	33.20	51.01/15.39

Note: Estimates of error for divergence dates are provided in the appendix.

^a Analyses were based on the absolute value of each latitudinal midpoint; that is, we did not distinguish between Northern and Southern Hemispheres.

clade age, species numbers, diversification rates, and latitudinal midpoints are provided in table 2. Additional details of methods are provided in the appendix.

Ecological Niche Modeling

We performed ecological niche modeling to test the prediction that cold winter temperatures limit dispersal of tropical lineages into temperate regions. We first used biogeographic analyses to identify clades that occur adjacent to temperate regions and to address qualitatively whether clades have converged on similar poleward range limits. Based on the availability of adequate locality data, our analyses focused primarily on the northern range limits of six representative species from four primarily tropical clades in eastern Mexico. These species are *Scinax staufferi* (*Scinax* clade), *Agalychnis callidryas* and *Agalychnis moreletii* (Phyllomedusinae), *Dendropsophus ebraccatus* and *Dendropsophus microcephalus* (*Dendropsophus* clade), and *Phrynohyas venulosa* (Lophiohylini). We obtained presence and absence localities for a given species from museum locality records, obtained data on 19 climatic variables (table 3) for each locality (from Hijmans et al. 2004, 2005), and then determined how well different climatic variables (either alone or in combination) were able to predict the presence or absence of the species at its northern range limits, using logistic regression and similar approaches. Methods are described in the appendix.

Testing for Phylogenetic Conservatism in a Climatic Niche Variable

The tropical conservatism hypothesis predicts that dispersal of lineages between tropical and temperate climatic regimes is relatively uncommon. As one way to address this hypothesis, we tested for phylogenetic conservatism in the climatic variable (Bio4; see “Results”) that seemingly limits dispersal of tropical clades into temperate regions, as identified from the ecological niche modeling described above (following Smith et al. 2005). We first obtained georeferenced locality data for the 124 hylid species included in the primary phylogeny. We then obtained climatic data for each locality (from Hijmans et al. 2004, 2005), determined mean climatic values for each species, and tested for significant association of this variable with the phylogeny, using the measure of phylogenetic correlation (λ) introduced by Pagel (1999a). Additional information on methods is provided in the appendix.

Results

Phylogenetic Analysis

Phylogenetic analyses of the combined data for 325 and 140 taxa support the same major clades found by Faivovich et al. (2005) and Wiens et al. (2005). The Bayesian phylogeny for 124 ingroup taxa is shown in figure 1. Hylid frogs are strongly supported as monophyletic, as are the three subfamilies (Hylinae, Pelodyadinae, and Phyllomedusinae). Pelodyadinae and Phyllomedusinae are strongly supported as sister taxa. Cophomantini is the sis-

Table 3: Summary of environmental variables from the WORLDCLIM data set (Hijmans et al. 2004, 2005)

Abbreviation	Environmental variable
Bio1	Annual mean temperature
Bio2 ^a	Mean diurnal temperature range (mean of monthly [maximum temperature – minimum temperature])
Bio3	Isothermality (Bio2/Bio7 × 100)
Bio4 ^a	Temperature seasonality (standard deviation of monthly temperature)
Bio5 ^a	Minimum temperature of coldest month
Bio6 ^a	Maximum temperature of warmest month
Bio7 ^a	Temperature range (maximum temperature of the warmest month – minimum temperature of the coldest month)
Bio8	Mean temperature of wettest quarter (i.e., mean temperature of the four consecutive wettest months)
Bio9	Mean temperature of driest quarter
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of wettest month
Bio14	Precipitation of driest month
Bio15 ^a	Precipitation seasonality (standard deviation of monthly precipitation)
Bio16 ^a	Precipitation of driest quarter
Bio17 ^a	Precipitation of wettest quarter
Bio18 ^a	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter

^a Variables selected for use in ecological niche modeling.

ter group to all other Hylinae. The remaining species fall into four strongly supported clades: the *Dendropsophus* clade, the *Scinax* clade, the Lophiohyliini or *Phrynohyas* clade, and the Middle American clade of Wiens et al. (2005) or Hylini of Faivovich et al. (2005).

Biogeographic Reconstruction

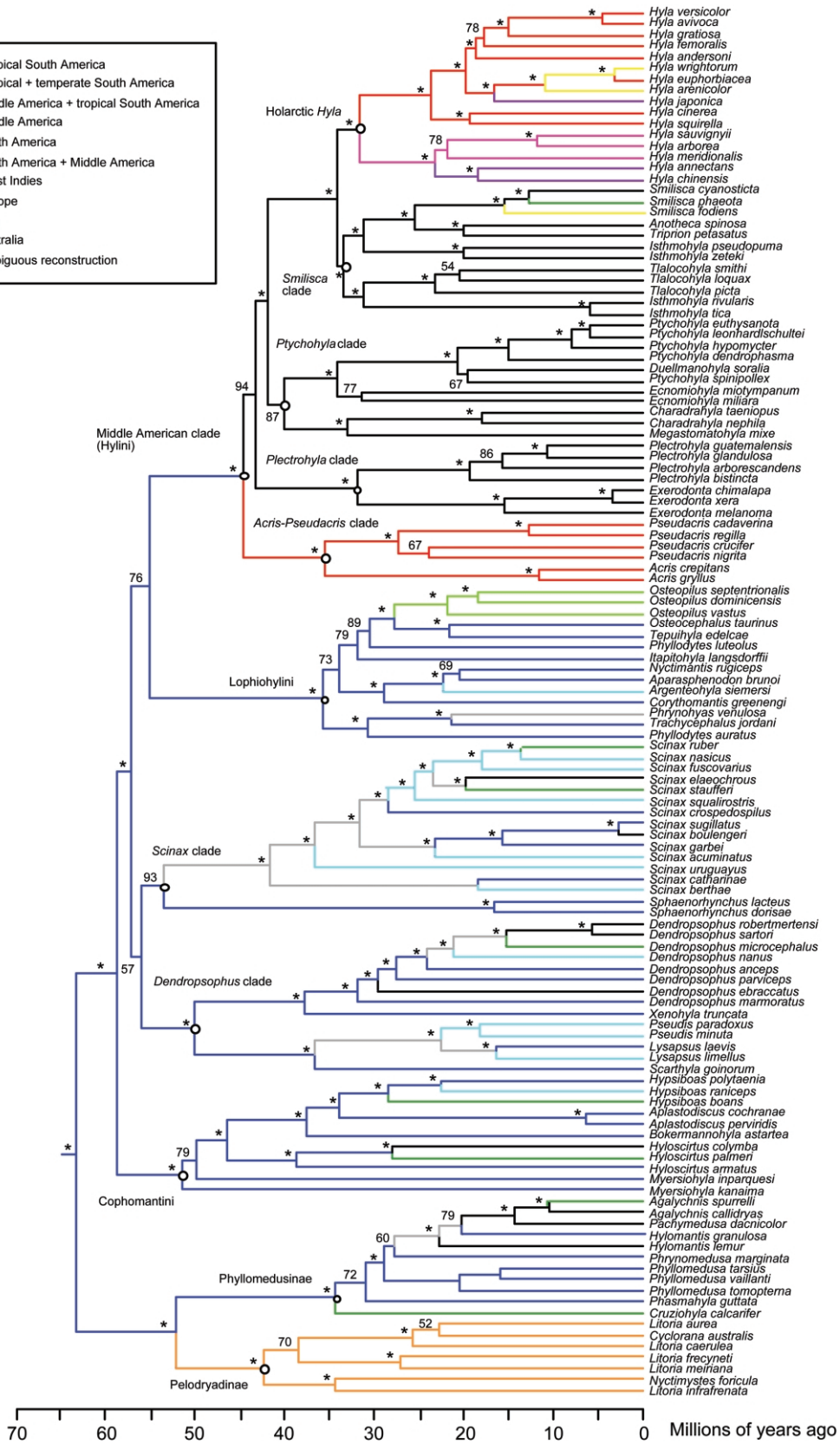
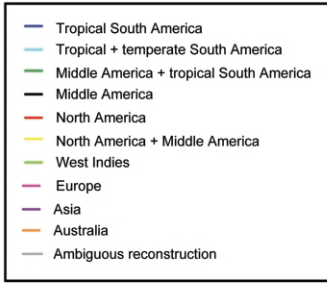
Parsimony and likelihood reconstructions of ancestral areas on the trees for 325 and 140 taxa all gave similar results. To illustrate the general results, the likelihood reconstruction for 140 taxa (124 ingroup) is shown in figure 1, using a root age of 100 mya for Neobatrachia to estimate branch lengths. Dispersal-vicariance analysis gave similar results (not shown). The analyses all agree that the ancestral area for Hylidae is tropical South America. This is also the ancestral area for most of the clades within Hylidae, including the Phyllomedusinae, Cophomantini, *Dendropsophus* clade, *Scinax* clade, and *Phrynohyas* clade (Lophiohyliini). However, the pelodyadines are confined to

Australasia. Within the Middle American clade (Hylini), the ancestral area is seemingly Middle America, and there have been two independent colonizations of North America (by the *Acris-Pseudacris* clade and *Hyla*), two colonizations of Asia (*Hyla*), one colonization of Europe (*Hyla*), and a recolonization of montane Middle America from North America (*Hyla*; see also Smith et al. 2005). There are also several species that occur in tropical South America but extend their ranges into parts of temperate South America. Overall, the results support the prediction that hylids originated in tropical regions and have spread to temperate regions more recently. Furthermore, given that most major clades originated in tropical South America, this result is robust to uncertainty regarding the relationships among these clades.

Ages of Clades, Richness versus Time, and Latitudinal Variation in Diversification Rates

A chronogram estimated from the penalized likelihood analysis is shown in figure 1. Although the estimated ages

Figure 1: Phylogeny of 124 species of hylid frogs based on combined, partitioned Bayesian analysis of 10 genes, showing branch support, divergence date estimates, and ancestral area reconstructions. Numbers adjacent to nodes indicate Bayesian posterior probabilities (× 100); asterisks indicate strongly supported clades with posterior probabilities ≥ 0.95. Open circles indicate named clades used in analyses of diversification rates. Branch lengths indicate the estimated ages of lineages based on penalized likelihood analysis with nine fossil calibration points and a root age for Neobatrachia of 100 mya (see table 2 for estimated ages of major clades using a root age of 160 mya). Colors of branches indicate generalized geographic ranges of extant taxa and inferred ancestors (based on maximum likelihood reconstruction, treating different regions as different character states). Only reconstructions supported by a likelihood ratio test are shown as unambiguous. The phylogeny, chronogram, and reconstructions are all based on a tree that also includes 16 nonhylid outgroup taxa; these taxa were deleted from this figure for clarity.



of major clades differ depending on the root age assumed for Neobatrachia (table 2; fig. 1), the major clades of tropical hylids appear to have split from each other before the expansion of the temperate regions (~30–40 mya).

Our results show a very strong relationship between hylid species richness in a region and the time when that region was first colonized by hylids (fig. 2; table 1), regardless of the root age used for neobatrachians in the penalized likelihood estimate of dates ($r^2 = 0.905$, $P = .001$ for 100 mya; $r^2 = 0.908$, $P = .001$ for 160 mya). Hylids have relatively low species richness in areas that have been colonized more recently, regardless of whether those regions are temperate (e.g., North America, Europe, Asia) or tropical (e.g., West Indies).

Nonphylogenetic analyses show that there is no relationship between the latitudinal midpoint of a clade and the absolute rate of diversification of that clade, regardless of the root age used for neobatrachians in the penalized likelihood estimate of dates ($r^2 = 0.133$, $P = .270$ for 100 mya; $r^2 = 0.063$, $P = .455$ for 160 mya). Results are similar and also nonsignificant when the data are analyzed using independent contrasts to account for shared phylogenetic history (fig. 3), regardless of whether the branch lengths are assumed to be equal ($r^2 = 0.180$, $P = .194$ for 100 mya; $r^2 = 0.114$, $P = .311$ for 160 mya), are estimated from the combined molecular data ($r^2 = 0.012$, $P = .751$ for 100 mya; $r^2 < 0.001$, $P = .957$ for 160 mya), or are based on the estimated divergence dates from penalized likelihood ($r^2 < 0.001$, $P = .966$ for 100 mya; $r^2 = 0.009$, $P = .784$ for 160 mya). Analyses assuming a high relative extinction rate ($\epsilon = 0.90$) to estimate diversification rates also show no relationship between diversification rate and latitude, for both root ages and using both stem and crown groups (results not shown).

Northern Range Limits of Tropical Clades in Middle America

We found convergence in the northern range limits of many tropical clades of hylid frogs in Middle America (fig. 4). The highest regional species diversity of hylids occurs in tropical South America, where up to five species-rich clades of hylids occur together (Cophomantini, *Dendropsophus* clade, *Phrynohyas* clade, Phyllomedusinae, *Scinax* clade), and the only clades absent are the Australasian pelodryadines and the Middle American clade. In contrast, in temperate North America, only members of the Middle American clade are present. Thus, the low species richness of temperate North America may be explained (at least in part) by the absence of the many species-rich clades that occur in tropical regions.

Most major clades of hylid frogs occur in Middle America as well as in South America (all but the Australian

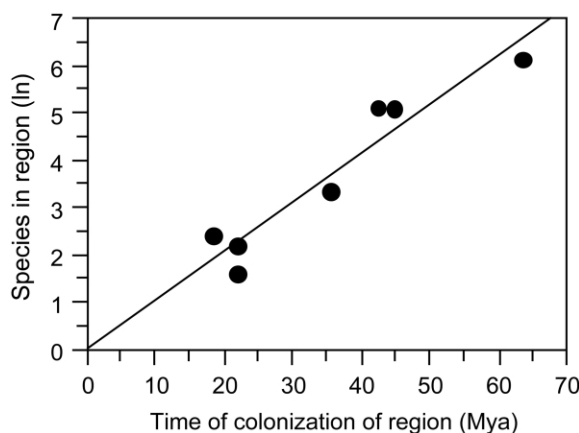


Figure 2: Linear regression analysis shows a strong relationship between the number of hylid species in different regions and the time when each region was colonized (in mya). Results are based on the chronogram with a root of age of 100 mya for Neobatrachia (fig. 1); results are very similar using a root age of 160 mya.

Pelodryadinae). One of these clades (Cophomantini) is confined to lower Middle America (Nicaragua to Panama). The other four major clades (*Dendropsophus*, *Scinax*, *Phrynohyas*, and Phyllomedusinae) are distributed widely in tropical Middle America and reach their northern range limits in Mexico. These four clades show different northern range limits along the Pacific Coast of Mexico (fig. 4), but many of the relevant species are sparsely and patchily distributed in this area (e.g., *Scinax staufferi*, *Phrynohyas venulosa*). They show similar northern range limits along the Gulf Coast of Mexico. For example, the distantly related *P. venulosa* and *S. staufferi* show very similar northern range limits in central Tamaulipas. *Dendropsophus ebracatus* and *Dendropsophus microcephalus* show very similar range limits in central Veracruz. These two species are only distantly related within the genus *Dendropsophus* (fig. 1). Similarly, the two species of *Agalychnis* that occur in Mexico (*Agalychnis callidryas* and *Agalychnis moreleti*) have northern range limits that are similar to each other and to those of the two *Dendropsophus* species in central Veracruz.

Most hylid species in Middle America belong to the Middle American clade (132 of 162 species). Within the Middle American clade, there are five major subclades. Two of these subclades occur in temperate North America (*Acris-Pseudacris* and *Hyla*), although one (*Hyla*) has reinvaded parts of montane Middle America and occurs in Asia and Europe (Faivovich et al. 2005; Smith et al. 2005). The other three subclades of the Middle American clade are largely confined to tropical regions and contain most of the species (table 2). Two clades are almost entirely

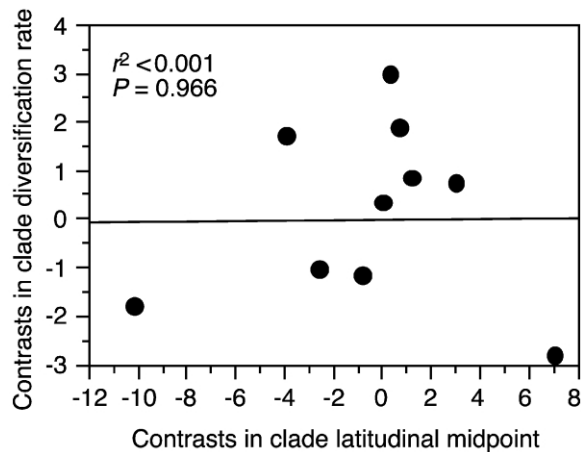


Figure 3: Linear regression analysis shows no relationship between independent contrasts in the diversification rate and latitudinal midpoint of the geographic range for 11 hylid clades. Diversification rates (\hat{r}) and branch lengths (for calculating independent contrasts) were estimated using the chronogram with a root age of 100 mya for Neobatrachia (fig. 1); results are very similar using a root age of 160 mya. Results are also similar and nonsignificant analyzing the raw data (i.e., not contrasts) and using the Bayesian branch lengths to calculate independent contrasts rather than branch lengths estimated from the chronogram.

montane (based on data in Duellman 2001). One montane clade (*Plectrohyla* clade) does not closely approach temperate North America. The other montane clade (*Ptychohyla* clade) approaches temperate North America in southern Nuevo Leon (*Ecnomiohyla miotympanum*). The third subclade (*Smilisca* clade) contains two lowland subclades, which also approach or enter temperate North America. One of these extends as far north as southeastern Arizona (*Smilisca fodiens*) and southern Texas (*Smilisca baudinii*). The other extends as far north as northern Sinaloa (*Tlalocohyla smithii*) and northern Veracruz (*Tlalocohyla picta*). Thus, we performed ecological niche analyses to address the range limits of these five species of the Middle American clade.

Ecological Niche Modeling

Analyses of ecological niche modeling for six species strongly suggests that temperature seasonality (Bio4) is the most important climatic variable that potentially limits the spread of four major hylid clades into temperate North America along the Gulf Coast of Mexico. Table 4 shows the final backward model for each species. In general, we could fit a reasonable model for each species such that each model had a low Akaike Information Criterion (AIC) and a high r^2 . Bio4 was chosen by the backward algorithm in every model. Most of the other nine variables were

present in one or more models, with the exception of Bio17 (precipitation of the wettest quarter), which was not present in any model. Bio4 was consistently one of the most important contributors to the models based on deviance in AIC (results not shown). Similarly, Bio4 was the best predictor of absence localities for all six species (table 5) and correctly predicted all absence localities for five of the six species and predicted 88% of them for one species.

Extending these analyses to six other species also showed that temperature seasonality was a consistent predictor of northern range limits at the interface between the tropical and temperate regions. The variables with climatic niche envelopes that most closely matched the northern range limits of each species were *Ecnomiohyla miotympanum* (in Nuevo Leon; Bio4, Bio7), *Pachymedusa dacnicolor* (Sonora; Bio4), *Smilisca baudinii* (Texas; Bio4), *Smilisca fodiens* (Arizona; Bio4, Bio7, Bio15, Bio16, Bio18), *Tlalocohyla picta* (Veracruz; Bio4, Bio7, Bio16), and *Tlalocohyla smithii* (Sinaloa; Bio4, Bio6, Bio7). For all these species, Bio4 alone closely predicted the northern range limits, except for *T. picta*, for which all the climatic variables overpredicted the northern range limit somewhat.

Phylogenetic Conservatism in a Climatic Niche Trait

Analyses of mean species values for temperature seasonality (Bio4) suggest that tolerances of individual species for extreme seasonality are generally conserved across the phylogeny. Using branch lengths estimated from the combined molecular data, the estimated maximum likelihood value for phylogenetic correlation (λ) is 0.8545. The log likelihood under the null hypothesis of no phylogenetic conservatism ($\lambda = 0$) is $-1,106.37$, whereas the log likelihood under the alternate hypothesis (where λ takes the estimated value of 0.8545) is $-1,092.65$. The likelihood ratio test statistic is 27.44 ($P < .001$), which is consistent with the idea that this climatic niche variable is phylogenetically associated. Results are very similar using maximum and minimum values of Bio4 within a species instead of the mean.

Discussion

Testing the Tropical Conservatism Hypothesis

In recent years, much of the research on the latitudinal gradient in species richness has focused primarily on correlations between environmental variables and species richness. Yet all large-scale patterns of species richness must ultimately be explained by the evolutionary and biogeographic processes of dispersal, extinction, and speciation. Several authors have independently converged on a similar explanation for the latitudinal diversity gradient

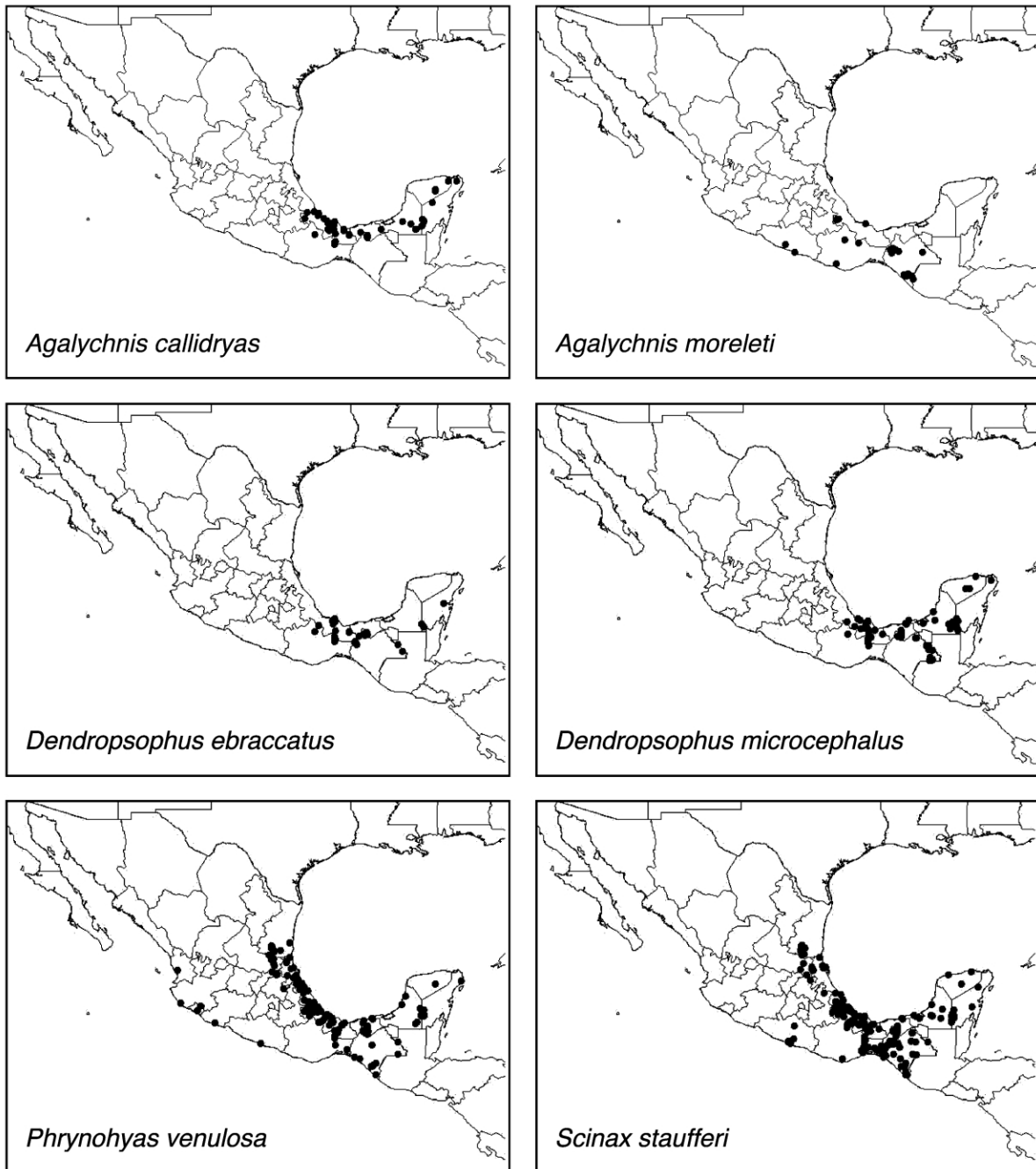


Figure 4: Northern range limits of four major clades of primarily tropical hylids in Mexico, showing that separate lineages that have invaded from South America (fig. 1) have converged independently on similar range limits near the interface between the tropics and temperate regions along the Gulf Coast of Mexico. Note that only localities in Mexico are shown. Species have their northern range limits in central Veracruz or southern Tamaulipas. The four major clades are the Phyllomedusinae (*Agalychnis*), *Dendropsophus* clade (*Dendropsophus*), Lophiohylini (*Phrynohyas*), and *Scinax* clade (*Scinax*). The two species of *Dendropsophus* are not closely related and probably represent separate invasions from South America (fig. 1; Faivovich et al. 2005; Wiens et al. 2005). Relationships within *Agalychnis* are currently uncertain, but available data (Duellman 2001) suggest that these two species are not sister taxa.

Table 4: Results of ecological niche modeling for the northern range limits of six hylid species in Mexico

Species	Absence	Presence	Preferred model	AIC	r^2
<i>Agalychnis callidryas</i>	56	54	Bio2 + Bio4 + Bio5 + Bio7	13.8	.73
<i>Agalychnis moreletii</i>	96	31	Bio4 + Bio5	6.0	.67
<i>Dendropsophus ebraccatus</i>	77	36	Bio2 + Bio4 + Bio7 + Bio18	34.8	.39
<i>Dendropsophus microcephalus</i>	50	82	Bio4 + Bio5 + Bio15 + Bio16 + Bio18	18.3	.72
<i>Phrynohyas venulosa</i>	39	149	Bio4 + Bio6	6.0	.64
<i>Scinax staufferi</i>	42	226	Bio4 + Bio5 + Bio16	8.0	.58

Note: Data shown are the numbers of presence and absence localities used for each species; the variables included in the final model, using general additive models run with backward selection; the Akaike Information Criterion (AIC) fit for each model; and r^2 based on logistic regression.

(the tropical conservatism hypothesis) that explains how climate might interact with these processes to create the latitudinal gradient (e.g., Farrell et al. 1992; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998). In this article, we have provided the first test of many of the predictions of this hypothesis, using treefrogs as a model system. Our analyses support many of the major predictions of the tropical conservatism hypothesis, although some parts are more strongly supported than others.

Time and Species Richness

We found strong support for the prediction that species-rich clades of hylids originated in the tropics and spread to temperate regions more recently. Other studies have also found that older clades tend to be present in tropical regions, whereas temperate faunas are dominated by younger clades, particularly in birds (e.g., Ricklefs and Schluter 1993; Gaston and Blackburn 1996; Hawkins et al. 2006). This topic has been discussed by some authors as a debate over whether the tropics are a “museum” of ancient clades that have had millions of years to develop high species richness (e.g., Gaston and Blackburn 1996) or are instead a “cradle of diversity” where many new lineages have speciated rapidly (e.g., Richardson et al. 2001).

We also found a strong relationship between the time when a region was colonized and how many species are present there today, regardless of whether the region is tropical or temperate. Thus, the limited species richness in temperate regions may be explained by the fact that these regions have been colonized more recently and that there has been too little time for species to accumulate (through in-situ speciation) to the same levels seen in tropical regions (Willis 1922; Stebbins 1974; Stephens and Wiens 2003).

We found no significant relationship between the diversification rate of individual clades and the latitudinal midpoint of those clades. Thus, there is no evidence from hylids that tropical clades speciate faster than temperate clades and/or that temperate clades experience more ex-

inction. Instead, these results imply that diversification occurs at similar overall rates in tropical and temperate regions. Coupled with the strong relationship between regional species richness and time since colonization, these results suggest that relative time since colonization is the primary factor driving higher species richness of hylids in tropical regions. It is important to note that some studies have found evidence that diversification rates may be higher in tropical regions (e.g., Cardillo 1999; Cardillo et al. 2005). The time-for-speciation effect and high diversification rates may both be important in explaining tropical species richness in general. However, our results suggest that a high diversification rate in tropical regions is not necessary to explain high tropical species richness in every group.

Why More Clades in the Tropics?

Our results imply that there are more species in the tropics because more clades have originated there and have spread to temperate regions only recently. But why did more clades arise in the tropics in the first place? One might argue that if the only explanation posited for high tropical species richness is that more clades originated in the tropics, then the tropical conservatism hypothesis merely pushes the question of why there are more species in the tropics backward in time and does not really answer it at all. According to the tropical conservatism hypothesis, more clades have originated in tropical regions because these areas were much more extensive until roughly 30–40 mya, when the temperate regions expanded (Behrensmeyer et al. 1992; Morley 2000). This aspect of the hypothesis is the most difficult to test and has few obvious predictions. However, if the species-rich tropical clades are younger than 30–40 million years old, then the shrinking of tropical regions during this period is irrelevant to their high species richness. In support of the idea that many tropical clades arose before the Cenozoic expansion of temperate regions, our analyses of divergence dates using penalized likelihood analysis suggest that most major hylid lineages originated more than 30 mya (fig. 1; table 2).

Table 5: Percentage of absence points for which a species is incorrectly predicted to be present based on the ecological niche model for a given climatic variable

Species and variable	Incorrect prediction (%)
<i>Agalychnis callidryas:</i>	
Bio2	48
Bio4	0
Bio5	30
Bio7	13
<i>Agalychnis moreletii:</i>	
Bio4	0
Bio5	20
<i>Dendropsophus ebraccatus:</i>	
Bio2	31
Bio4	12
Bio7	30
Bio18	34
<i>Dendropsophus microcephalus:</i>	
Bio4	0
Bio6	32
Bio15	36
Bio16	18
Bio18	46
<i>Phrynohyas venulosa:</i>	
Bio4	0
Bio6	0
<i>Scinax staufferi:</i>	
Bio4	0
Bio5	24
Bio16	5

Note: Temperature seasonality (Bio4) provides the most accurate prediction for each variable and correctly predicts all of the absence localities for five of the six species.

However, we acknowledge that this is not a particularly compelling test of the hypothesis and that better tests should be developed. For example, Fine and Ree (2006) recently showed that the reconstructed geographic area of different biomes in the early to mid-Cenozoic is a strong predictor of the current species richness of these biomes (for trees), whereas the present geographic extent of these biomes is not.

The fossil record is obviously relevant to this hypothesis. For example, we might expect to see paleontological evidence that tropical clades occurred where temperate regions are today. There is a fossil record for hylids in North America, but these data show that the only clades present in North America are closely related to those present today and that these hylids were not present for long periods (if they were present at all) before the region became temperate (Holman 2003).

We also note that the tropical conservatism hypothesis may not apply universally to all timescales. We suspect

that it applies primarily to groups that are moderately recent (i.e., tens of mya, not hundreds) and that diversified when the tropics were extensive. However, it may not apply to older groups and timescales. For example, the common ancestor of living frogs was presumably temperate, given that the most basal lineages of frogs are confined to temperate regions (e.g., leiopelmatids, discoglossids, pelobatids), as are the basal lineages of the sister group of anurans, the caudates (Zug et al. 2001). The earliest fossil anurans are known from the Triassic period, more than 200 mya (Zug et al. 2001). Thus, although hylids originated in the tropics, it seems likely that frogs in general did not, even though anuran species richness is higher in tropical regions on all continents (IUCN et al. 2004).

Climate and Niche Conservatism

A critical component of the tropical conservatism hypothesis is that phylogenetic niche conservatism maintains the disparity in species richness between tropical and temperate regions over long evolutionary timescales (Wiens and Donoghue 2004). Specifically, various authors have hypothesized that most tropical clades fail to disperse into temperate regions because they lack the necessary ecological and physiological adaptations to survive cold winter temperatures (e.g., Ricklefs and Schluter 1993; Futuyma 1998). This is an essential aspect of the hypothesis because it potentially explains why so many clades that arose in the tropics have not spread into temperate regions. Furthermore, this part of the hypothesis links the evolutionary and biogeographic processes (i.e., speciation and dispersal) that directly change species numbers with the climatic variables that are strongly correlated with species richness in many ecological studies of the latitudinal gradient. It is also an aspect of the hypothesis that has not been tested in previous studies.

Our results partially support this aspect of the hypothesis. They show that many tropical hylid clades converge on similar northern range limits in eastern Mexico, that the northern range limits of many tropical clades can be predicted by climatic data, that temperature seasonality is the specific climatic variable that may limit the northern dispersal of tropical clades in this region, and that temperature seasonality shows significant nonrandom conservatism across the phylogeny.

There are several caveats that should be noted. The first is that extreme winter temperatures seemingly are not the critical limiting factor, contrary to the prediction by Ricklefs and Schluter (1993), Futuyma (1998), Wiens and Donoghue (2004), and others. Instead, it is the variability in temperature over the course of the year that seems to be most important. Examination of climatic niche envelopes suggests that extremely high summer temperatures (Bio5

in table 3) probably do not limit northward dispersal in this region either (not shown) and that addition of a cool winter season to the yearly climatic cycle may be the most critical factor. Thus, it appears that it is the seasonality of temperate regions that limits dispersal of tropical clades (i.e., cool winters) but not extreme cold temperatures per se.

Second, the patterns found in these four clades are less clear on the Pacific Coast, where fewer localities are known for these taxa and these lineages appear not to have converged on similar northern range limits. Nevertheless, our analyses of lowland tropical species on the Pacific Coast (e.g., *Pachymedusa dacnicolor*, *Smilisca fodiens*, *Tlalocohyla smithii*) support the idea that temperature seasonality is potentially an important factor limiting the dispersal of tropical clades into temperate regions along the Pacific Coast as well.

Another caveat is that we have not proven that climate alone limits the northward dispersal of these lineages. We have shown that climate alone can predict their northern range limits (table 5), but we cannot rule out other factors, given the available evidence. Furthermore, we have not identified the specific ecological or physiological mechanisms that limit dispersal. Range limits may be set by complex interactions between biotic and abiotic factors (e.g., climate, food availability, and competition; Gross and Price 2000), and more detailed study will be needed to tease apart these factors in hylids. However, some additional observations, listed below, seem to support the importance of climate as the primary limiting factor.

First, competition with temperate hylids seems unlikely to be the primary explanation for the northern range limits of these tropical lineages. The southernmost range limits of the North American *Acris-Pseudacris* clade and Holarctic *Hyla* on the Gulf Coast are along the Rio Grande in extreme northern Tamaulipas (Duellman 2001), far north of the northernmost range limits of the four tropical clades (fig. 4). Obviously, competitive interactions between the temperate and tropical clades are unlikely to be important if the relevant species are completely allopatric and separated by hundreds of kilometers. Hylids are the only arboreal anurans in North America, and we are unaware of other North American organisms that might compete with hylids apart from other hylids.

Second, the fact that these hylid lineages share similar northern range limits despite their ecological differences suggests that there may be a common cause that is related to abiotic and not biotic factors. For example, among the hylids with northern range limits in southern Tamaulipas, *Phrynohyas venulosa* is very large (maximum snout-vent length 114 mm) and *Scinax staufferi* is small (up to 32 mm; Duellman 2001). In central Veracruz, *Dendropsophus ebraccatus* and *Dendropsophus microcephalus* are small (up

to 36 and 28 mm, respectively), whereas *Agalychnis callidryas* and *Agalychnis moreleti* are large (up to 71 and 83 mm, respectively; Duellman 2001). These large- and small-bodied species presumably have somewhat different sets of predators, prey, parasites, and competitors, yet they share similar northern range limits.

Similarly, both zoologists and botanists have long recognized that a major shift in plant and animal distributions occurs between southern and northern Mexico; this general region corresponds to the transition zone between the Neotropical and Nearctic zoogeographic realms (Wallace 1876; Good 1947). For many groups, this transition zone seems to correspond to the convergent northern range limits of many widespread tropical clades, as it does in hylids. These clades include caecilian amphibians, centro-lid frogs, boine snakes (Zug et al. 2001), atelid monkeys, ramphastid and tinamid birds (toucans and tinamous), and *Amazona* parrots (NatureServe 2004). Given the diversity of species that have their northern range limits in this region, it seems likely that a common cause (e.g., climate) may explain this pattern. Ours may be the first study to address the specific ecological (climatic) factors that underlie this transition zone.

Other Biogeographic Patterns Underlying the Latitudinal Gradient

In this article, we have emphasized the northern range limits of four major tropical hylid clades in Mexico (*Scinax* clade, *Dendropsophus* clade, Phyllomedusinae, and *Phrynohyas* clade [Lophiohylini]). However, other biogeographic factors also contribute to the latitudinal gradient in hylid species richness in the Northern Hemisphere.

First, these four clades represent only a small fraction of the hylid diversity in Middle America (18.5%, or 30 of 162 species). In Middle America, most hylid species belong to a large endemic radiation (the Middle American clade, Hylini). Our climatic niche analyses have addressed why the northernmost Middle American members of this clade have not dispersed into temperate North America (*Ecnomiohyala*, *Smilisca*, *Tlalocohyla*), and they support temperature seasonality as a potentially important limiting factor. However, it is clear that the largely montane *Plectrohyla* and *Ptychohyla* clades (91 species total) contribute substantially to the high diversity of tropical Middle America relative to that of temperate North America. Our results (table 2) do not show dramatically higher diversification rates in these two montane clades relative to those of lower-elevation or temperate clades (although the *Plectrohyla* clade did diversify more rapidly than the *Acris-Pseudacris* clade). Furthermore, temperature seasonality also seems to limit the northward dispersal of the northernmost member of the montane *Ptychohyla* clade (i.e.,

Ecnomiohyla miotympanum). We merely emphasize here that tropical montane endemism may also contribute to the diversity gradient in hylids, not only to limitations on the distribution of tropical lowland clades.

Second, many tropical hylid lineages in Middle America have their northern range limits in lower Central America and do not enter tropical Mexico or approach temperate North America. For example, of the 30 species in Middle America that do not belong to the Middle American clade, only nine reach as far north as Mexico. Mapping biogeographic patterns onto the tree for 325 taxa suggests that many of these lineages have independently entered lower Middle America from South America but failed to disperse further northward (i.e., *Hyloscirtus colymbus*, *Hyloscirtus palmeri*, *Hypsiboas crepitans*–*Hypsiboas rosenbergi*, *Hypsiboas rufitela*, *Scinax boulengeri*). Many other vertebrate clades also reach their northern range limits in lower Central America (e.g., dendrobatid frogs and gymnophthalmid lizards [Zug et al. 2001]; ageneiosid, callichthyid, auchenipterid, loricariid, and trichomycterid catfishes [Brown and Lomolino 1998]; aotid, callitrichid, and cebid primates [NatureServe 2004]). We suspect that many of these clades have entered Middle America only recently across the Panamanian landbridge (~3.5 mya; Brown and Lomolino 1998) and have simply had too little time to disperse further northward, but this is a topic in need of further study.

Temperate South America

We have not addressed the transition in hylid faunas between tropical and temperate South America, but preliminary analyses suggest intriguing differences with the patterns at the interface between temperate North America and tropical Middle America. In temperate North America, the fauna is dominated by two temperate subclades within the larger Middle American clade. Each of these clades has undergone a small temperate radiation. In contrast, in temperate South America, most of the same major clades that are present in the megadiverse tropical rain forests (Duellman 1978, 2005) are present in temperate regions of Uruguay and Argentina (e.g., *Scinax* clade, *Dendropsophus* clade, *Hypsiboas*, phyllomedusines, *Phrynohyas* clade), but the species richness of these clades is greatly diminished such that each clade is represented by only a few species (Cei 1980; Núñez et al. 2004). Another difference is that many of the species that occur in temperate South America also range into tropical or subtropical regions. Thus, although there are 22 hylid species that occur south of 30°S in South America, only two species are endemic to these temperate regions (IUCN et al. 2004; AmphibiaWeb 2005).

Furthermore, hylids range much farther poleward in temperate North America than they do in temperate South

America (table 2). For example, in temperate North America, the northernmost range of the *Acris-Pseudacris* clade is 62.50°N, and that of the Holarctic *Hyla* clade is 51.01°N. In temperate South America, the southernmost range limits for major clades are 38.35°S (*Hypsiboas*), 36.75°S (*Scinax*), 35.57°S (*Dendropsophus*), 34.87°S (phyllomedusines), and 32.22°S (*Phrynohyas*). These clades are confined to lower, more tropical latitudes in Middle America than in South America (table 2).

We speculate that these four major clades range into temperate regions in South America because they have been adjacent to temperate climate regimes for tens of millions of years and thus may have had considerable time to adapt to these conditions. In contrast, in the Northern Hemisphere, these same clades may have entered Middle America quite recently (across the Isthmus of Panama) and may have had only a few million years (or less) to adapt to temperate climates. Why, then, have these clades not radiated more extensively in temperate South America, as some hylid clades have done in temperate North America? We suspect that species occurring in both temperate and tropical climates may have limited ability to adapt to cold climate regimes and disperse further poleward relative to species that occur entirely in temperate regimes. Specifically, adaptation of these species to cooler climates in temperate populations may be limited by ongoing gene flow with populations in tropical regions. The tendency of gene flow to limit adaptation is generally thought to be an important factor limiting range expansion in the theoretical literature (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997). These patterns and hypotheses will require further study.

Elevational Patterns of Diversity

Elevational patterns of species richness are an important component of global biodiversity but are somewhat beyond the scope of this study. Nevertheless, our studies of elevational patterns in hylid frogs in Middle America (S. A. Smith, A. Nieto, T. W. Reeder, and J. J. Wiens, unpublished manuscript) suggest some intriguing parallels with latitudinal diversity patterns. Like many organisms, Middle American hylids show their highest species richness at intermediate elevations (i.e., 1,000–2,000 m above sea level). This pattern seemingly is associated not with higher diversification rates at middle elevations (see above and table 2) but rather with the early colonization of these elevations and more recent colonization of lower and higher elevations. In other words, there appears to be an elevational time-for-speciation effect. In one clade of montane hylids (genus *Hyla*), climatic tolerances may limit dispersal into lowland tropical regions, and the climatic distribution of the clade appears to be phylogenetically

conserved (Smith et al. 2005). Thus, the same two principles that are critical in explaining latitudinal diversity patterns in hylids may also explain their elevational species richness patterns. These patterns should be tested more widely, as specific patterns of elevational colonization and diversity may differ somewhat across montane regions and clades, even within hylids. However, there is no evidence or reason to expect that the same specific climatic variable is important in explaining both elevational and latitudinal gradients (e.g., temperature seasonality shows major variation latitudinally but not elevationally; Janzen 1967).

Conclusions

The tropical conservatism hypothesis has been proposed as a general explanation for the latitudinal diversity gradient that links the ecological factors correlated with species richness patterns (e.g., climate) to the evolutionary and biogeographic processes that ultimately cause these patterns (e.g., speciation, continental-scale dispersal). In this study, we provide the first empirical test of the major predictions of this hypothesis. Our results for treefrogs generally support the tropical conservatism hypothesis, but with two major caveats. First, temperature seasonality seems to limit the dispersal of tropical clades (rather than extreme winter temperatures per se, as had previously been hypothesized). Second, our study offers only a weak test of the role of the Cenozoic expansion of temperate regions in generating the latitudinal gradient.

Many of the hypotheses proposed to explain the latitudinal diversity gradient focus either on ecological mechanisms allowing coexistence of large numbers of species in the tropics or on differences in rates of diversification between climatic regimes. Our results suggest instead that the patterns and timing of large-scale biogeographic dispersal (and the ecological and evolutionary limitations on that dispersal) may be just as important.

In theory, the tropical conservatism hypothesis should apply to most groups of organisms with high tropical species richness. However, we anticipate that not every group will support its predictions as well as hylid frogs seem to. Instead, we suggest that the tropical conservatism hypothesis reflects the combined effects of two general factors, the time-for-speciation effect (i.e., more species accumulate in regions where a group has been present longer; review in Stephens and Wiens 2003) and niche conservatism (i.e., the tendency for climatic specialization of clades to limit their dispersal between different climatic regimes; review in Wiens and Graham 2005). The time-for-speciation effect and niche conservatism can be thought of as two important elements of a conceptual toolbox for understanding large-scale patterns of species richness in an integrated evolutionary and ecological

framework. The importance of these two factors may vary from group to group, and other factors will doubtless prove to be important as well. Our studies of hylids so far suggest that these two elements may explain high tropical species richness in hylids as a whole, the tendency for some hylid clades to show high species richness at midtemperate latitudes in Europe, Asia, and North America (Smith et al. 2005), and possibly elevational patterns of diversity as well.

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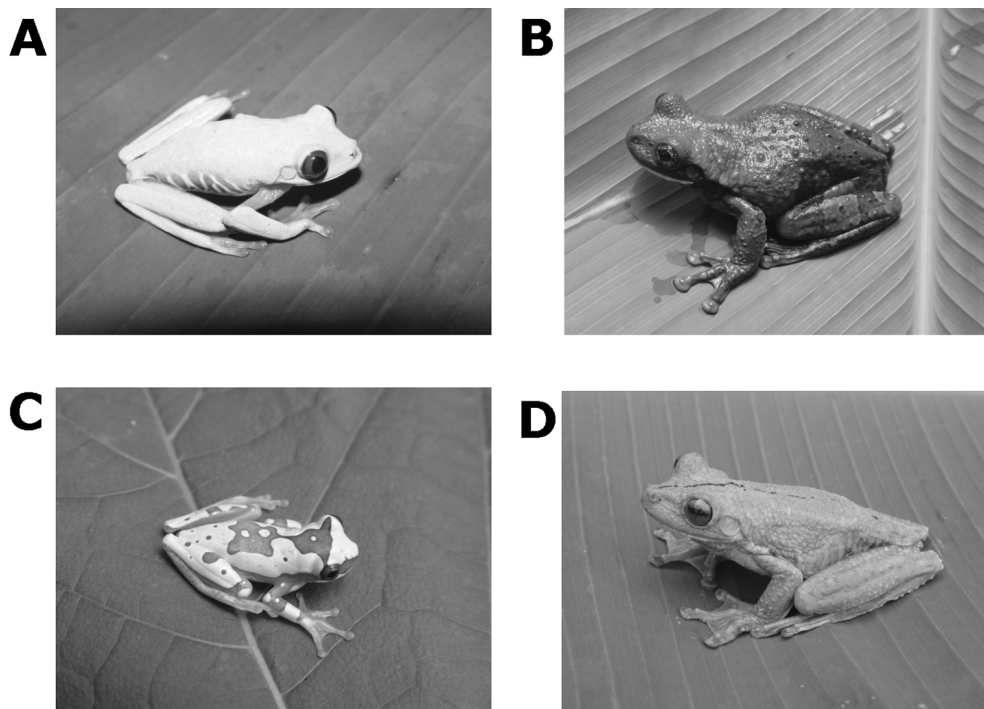
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A, Red-eyed treefrog (*Agalychnis callidryas*); B, marbled treefrog (*Phrynohyas venulosa*); C, hourglass treefrog (*Dendropsophus ebraccatus*); D, Rosenbergs treefrog (*Hypsiboas rosenbergi*). Photographs by John Wiens.