doi:10.1111/j.1558-5646.2009.00610.x

EVOLUTIONARY AND BIOGEOGRAPHIC ORIGINS OF HIGH TROPICAL DIVERSITY IN OLD WORLD FROGS (RANIDAE)

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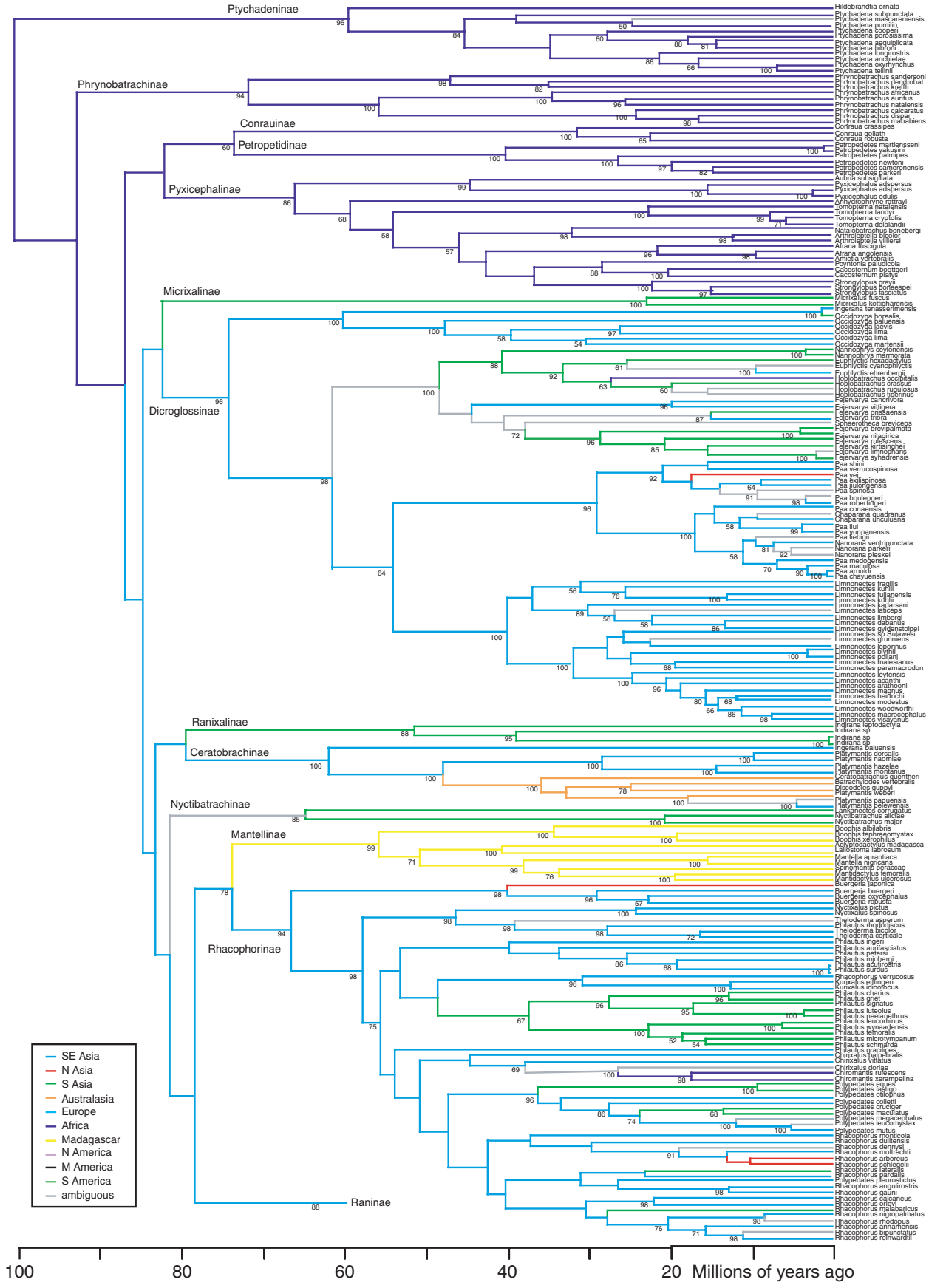
Received May 24, 2008
Accepted November 17, 2008

Differences in species richness between regions are ultimately explained by patterns of speciation, extinction, and biogeographic dispersal. Yet, few studies have considered the role of all three processes in generating the high biodiversity of tropical regions. A recent study of a speciose group of predominately New World frogs (Hylidae) showed that their low diversity in temperate regions was associated with relatively recent colonization of these regions, rather than latitudinal differences in diversification rates (rates of speciation–extinction). Here, we perform parallel analyses on the most species-rich group of Old World frogs (Ranidae; ~1300 species) to determine if similar processes drive the latitudinal diversity gradient. We estimate a time-calibrated phylogeny for 390 ranid species and use this phylogeny to analyze patterns of biogeography and diversification rates. As in hylids, we find a strong relationship between the timing of colonization of each region and its current diversity, with recent colonization of temperate regions from tropical regions. Diversification rates are similar in tropical and temperate clades, suggesting that neither accelerated tropical speciation rates nor greater temperate extinction rates explain high tropical diversity in this group. Instead, these results show the importance of historical biogeography in explaining high species richness in both the New World and Old World tropics.

KEY WORDS: **Amphibians, biogeography, phylogeny, speciation, species richness.**

Why are there more species in tropical regions than in temperate regions? This question has perplexed evolutionary biologists and ecologists for hundreds of years, and dozens of hypotheses have been proposed to answer it (e.g., Pianka 1966; Rosenzweig 1995; Rahbek and Graves 2001; Willig et al. 2003; Mittelbach et al. 2007). In recent years, there has been growing appreciation for the idea that any reasonably complete explanation for the latitudinal diversity gradient must incorporate the three processes that directly change the number of species within and between regions: speciation, extinction, and biogeographic dispersal (e.g., Ricklefs 2004; Wiens and Donoghue 2004; Mittelbach et al. 2007; Special Issue of *American Naturalist* in 2007). For example, the latitudinal diversity gradient might arise because of higher rates of speciation in the tropics, higher rates of extinction in the temperate zone, or a tendency for groups that originate in the tropics to disperse only recently and rarely to the temperate zone.

Surprisingly few studies have attempted to address the role of these processes in creating the latitudinal diversity gradient. For example, many ecological studies have sought correlations between species richness and environmental variables (e.g., Francis and Currie 2003; Hawkins et al. 2003; Willig et al. 2003; Buckley and Jetz 2007), without addressing any of these


Ptychadeninae
Phrynobatrachinae
Conrauinae
Petropetidinae
Pyxicephalinae
Micrixalinae
Dicroglossinae
Ranixalinae
Ceratobrachinae
Nyctibatrachinae
Mantellinae
Rhacophorinae
Raninae
Hildebrandtia ornata
Ptychadena subpunctata
Ptychadena mascareniensis
Ptychadena pumilio
Ptychadena cooperi
Ptychadena porosissima
Ptychadena aequiplicata
Ptychadena bibroni
Ptychadena longirostris
Ptychadena anchietae
Ptychadena oxyrhynchus
Ptychadena tellinii
Phrynobatrachus sandersoni
Phrynobatrachus dendrobat
Phrynobatrachus reniti
Phrynobatrachus africanus
Phrynobatrachus auritus
Phrynobatrachus natalensis
Phrynobatrachus calcaratus
Phrynobatrachus dispar
Phrynobatrachus mababiens
Conraua crassipes
Conraua goliath
Conraua robusta
Petropedetes martiensseni
Petropedetes vakujini
Petropedetes palmipes
Petropedetes newtoni
Petropedetes cameronensis
Petropedetes parkeri
Aubria subsigillata
Pyxicephalus adspersus
Pyxicephalus adspersus
Pyxicephalus edulis
Amnirana galamensis
Amietia vertebralis
Poyntonia paludicola
Cacosternum boettgeri
Cacosternum platys
Strongylopus grayii
Strongylopus bonaespei
Strongylopus fasciatus
Micrixalus fuscus
Micrixalus kottigharensis
Ingerana tenasserimensis
Occidozyga borealis
Occidozyga baluensis
Occidozyga laevis
Occidozyga lima
Occidozyga lima
Occidozyga martensii
Nannophrys ceylonensis
Nannophrys marmorata
Euphlyctis hexadactylus
Euphlyctis cyanophlyctis
Euphlyctis ehrenbergii
Hoplobatrachus occipitalis
Hoplobatrachus crassus
Hoplobatrachus rugulosus
Hoplobatrachus tigerinus
Fejervarya cancrivora
Fejervarya vittigera
Fejervarya orissaensis
Fejervarya limnocharis
Sphaerotheca breviceps
Fejervarya brevipalmata
Fejervarya nilagirica
Fejervarya rufescens
Fejervarya kirtisinghei
Fejervarya limnocharis
Fejervarya syhadrensis
Paa shini
Paa verrucospinosa
Paa yei
Paa exilispinosa
Paa liulongensis
Paa spinosa
Paa boulengeri
Paa robertingeri
Paa conaensis
Chaparana quadranus
Chaparana unculuana
Paa liui
Paa yunnanensis
Paa liebigii
Nanorana ventripunctata
Nanorana parkeri
Nanorana pleskei
Paa medogensis
Paa maculosa
Paa arnoldi
Paa chayuensis
Limnonectes fragilis
Limnonectes kuhlii
Limnonectes fujianensis
Limnonectes kuhlii
Limnonectes kadarsani
Limnonectes laticeps
Limnonectes limborgi
Limnonectes dabanus
Limnonectes grunniens
Limnonectes ibanorum
Limnonectes blythii
Limnonectes poilani
Limnonectes malesianus
Limnonectes paramacrodon
Limnonectes leytensis
Limnonectes acanthi
Limnonectes arathooni
Limnonectes magnus
Limnonectes heinrichi
Limnonectes modestus
Limnonectes woodworthi
Limnonectes macrocephalus
Limnonectes visayanus
Indirana leptodactyla
Indirana sp
Indirana sp
Indirana sp
Ingerana baluensis
Platymantis dorsalis
Platymantis naomiae
Platymantis hazelae
Platymantis montanus
Ceratobatrachus guentheri
Batrachylodes vertebralis
Discodeles guppyi
Platymantis weberi
Platymantis papuensis
Platymantis pelewensis
Lankanectes corrugatus
Nyctibatrachus aliciae
Nyctibatrachus major
Boophis albilabris
Boophis tephraeomystax
Boophis xerophilus
Aglyptodactylus madagasca
Latidactylus labrosum
Mantella aurantiaca
Mantella nigricans
Spinomantis peraccae
Mantidactylus femoralis
Mantidactylus ulcerosus
Buergeria japonica
Buergeria buergeri
Buergeria oxycephalus
Buergeria robusta
Nyctixalus pictus
Nyctixalus spinosus
Theloderma asperum
Philautus rhododiscus
Theloderma bicolor
Theloderma corticale
Philautus ingeri
Philautus aurifasciatus
Philautus petersi
Philautus mjobergi
Philautus adutocritis
Philautus surdus
Rhacophorus verrucosus
Kurixalus eiffingeri
Kurixalus idiootocus
Philautus charius
Philautus gret
Philautus signatus
Philautus luteolus
Philautus neelanethrus
Philautus leucorhinus
Philautus wynaadensis
Philautus femoralis
Philautus microtympanum
Philautus schmarda
Philautus gracilipes
Chirixalus palpebralis
Chirixalus vittatus
Chirixalus doriae
Chiromantis rufescens
Chiromantis xerampelina
Polypedates leucomystax
Polypedates taeniatus
Polypedates otilophus
Polypedates colletti
Polypedates cruciger
Polypedates maculatus
Polypedates megacephalus
Polypedates leucomystax
Polypedates mutus
Rhacophorus moltrechti
Rhacophorus dulitensis
Rhacophorus dennysi
Rhacophorus moltrechti
Rhacophorus arboreus
Rhacophorus schlegelii
Rhacophorus lateralis
Rhacophorus pardalis
Polypedates pleurostictus
Rhacophorus angulirostris
Rhacophorus gauni
Rhacophorus calcaneus
Rhacophorus orlovi
Rhacophorus malabaricus
Rhacophorus nigropalmatus
Rhacophorus rhodopus
Rhacophorus annamensis
Rhacophorus bipunctatus
Rhacophorus reinwardtii
SE Asia
N Asia
S Asia
Australasia
Europe
Africa
Madagascar
N America
M America
S America
ambiguous
100
80
60
40
20
Millions of years ago

processes. Even though climatic variation almost certainly plays an essential role in generating the latitudinal diversity gradient, climatic variables do not directly change the number of species in a region without acting through the processes of speciation, extinction, or dispersal.

On the other hand, many evolutionary studies have looked for latitudinal variation in rates of speciation and extinction, but without considering the potential role of historical biogeography. For example, several recent papers have tested for latitudinal variation in the rates of diversification (speciation rate – extinction rate) in clades in different regions (e.g., Cardillo 1999; Cardillo et al. 2005; Ricklefs 2006; Weir and Schluter 2007; Svennig et al. 2008). These papers focused specifically on diversification rate given that this rate is relatively straightforward to estimate and should reflect major latitudinal variation in speciation and extinction rates, whereas directly estimating speciation and extinction rates or disentangling their contribution to the overall diversification rate is more difficult (e.g., Ricklefs 2006). Similarly, some papers have indirectly addressed historical biogeography, but without addressing rates of diversification (e.g., studies showing that younger clades tend to occur in more temperate climates; Ricklefs and Schluter 1993; Gaston and Blackburn 1996; Stevens 2006; Hawkins et al. 2007).

A few studies have begun to explicitly consider both biogeography and diversification rates. Jablonski et al. (2006) analyzed extensive distributional data on fossil marine bivalve distributions over the past 11 million years (MY), but examined genera rather than species richness per se. Two recent studies used innovative simulation-based approaches to address the causes of species richness patterns in New World birds in terms of biogeography and speciation (Diniz-Filho et al. 2007; Rangel et al. 2007), but without directly analyzing the biogeographic history of clades or their diversification rates.

A recent study addressed the potential roles of biogeography and diversification rates in creating the latitudinal diversity gradient in a species-rich group of frogs (hylid treefrogs) with a center of diversity in the New World tropics (Wiens et al. 2006). These authors found that the timing of biogeographic dispersal was critical in explaining high tropical diversity in this group, and that latitudinal differences in rates of speciation and extinction were not. Specifically, they found that the low species richness of hylids in temperate North America, Europe, and Asia was seemingly explained by their relatively recent dispersal to those regions (i.e., leaving limited time for speciation to build up diversity in those regions), given a general relationship between how long hylids have been present in each region and the number of species there today (the time-for-speciation effect; Stephens and Wiens 2003). They found no evidence for latitudinal differences in rates of diversification, suggesting that rates of speciation and extinction are generally similar across different latitudes. However, that study was criticized because hylids offer only a limited number of temperate clades for these comparisons (Mittelbach et al. 2007). In addition, it is possible that an analysis of a single group in a given region may reflect the outcome of a unique set of historical events (e.g., separation of South America from North and Middle America), rather than general processes that might drive the latitudinal diversity gradient in many groups.

Here, rather than focusing on a completely different set of organisms, we conduct a similar set of analyses on a group of frogs of similar age and diversity but which occurs predominately in the Old World. The family Ranidae (sensu Bossuyt et al. 2006) is the dominant clade of frogs in the Old World tropics in terms of species richness (Amphibiaweb 2008). Ranids are generally similar in age and diversity to hylids (e.g., hylids ~50 MY, ranids ~60 MY in fig. 1 of Wiens [2007]; hylids = 852 species, ranids = 1284 species; Amphibiaweb 2008), but have their highest diversity in different regions. Both groups are distributed almost globally, but whereas hylids are most diverse in South America, Middle America, and Australia, ranids are most diverse in Asia, Africa, Madagascar, and Europe (Amphibiaweb 2008). Ranids show the expected latitudinal gradient in species richness in the Old World (IUCN et al. 2006), with many species in tropical southeastern Asia ($n = 457$), south Asia ($n = 236$), sub-Saharan Africa ($n = 214$), and Madagascar ($n = 158$), but relatively few in temperate Europe ($n = 34$) and northern Asia ($n = 74$; see Table 1).

We address the underlying causes of the latitudinal diversity gradient in ranid frogs with a set of analyses designed to address the relative importance of diversification rates (speciation–extinction) and large-scale biogeographic dispersal. First, we generate an extensive species-level molecular phylogeny for ranid

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Figure 1. Phylogeny of ranid frogs based on combined maximum likelihood analysis of five genes (two mitochondrial, three nuclear), showing branch support, estimated ages of clades, and biogeographic patterns. The likelihood of the tree is –216,114.7573. Numbers adjacent to nodes are bootstrap support values. Branch lengths indicate estimated ages of lineages based on Bayesian divergence-time estimation using a root date for ranids of 111.3 MY. Colors of branches indicate generalized geographic ranges of extant taxa and inferred ancestors (based on maximum-likelihood reconstruction, treating geographic regions as character states). Polymorphic states and ambiguous reconstructions are shown in gray. Only reconstructions supported by a likelihood-ratio test are considered unambiguous. Outgroup taxa are not shown. The phylogeny of ranid frogs continues in Figure 2.

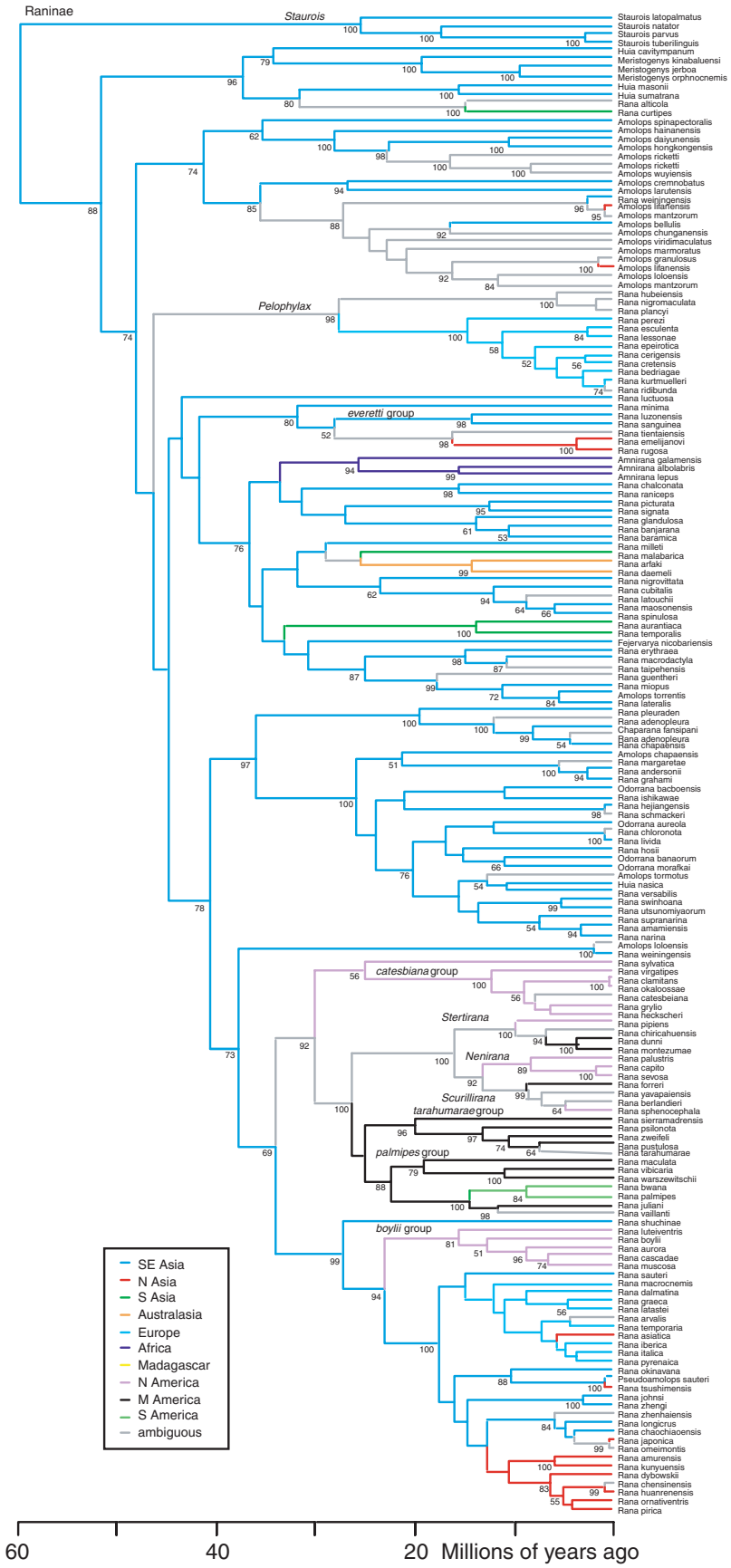

Figure 2. Phylogeny of ranid frogs, continued from Figure 1.

Table 1. Summary of ranid species richness and timing of colonization in each region.

Region	Species	Age of first colonization	Summed ages of colonization events
Africa	214	101.10	101.10
SE Asia	457	87.40	87.40
S Asia	236	64.12	282.10
N Asia	74	22.73	68.55
Australia	53	36.00	50.02
Europe	34	14.54	26.68
Madagascar	158	55.94	55.94
North America	28	25.15	45.91
Middle America	32	25.23	25.23
South America	3	8.61	8.61

frogs, and use the phylogeny and branch lengths to estimate the ages of clades. We next estimate the species richness of ranids in different regions throughout their range (e.g., Africa, Europe, Southeast Asia). We then reconstruct the relative timing of biogeographic colonization of each region and test for a relationship between how long ranids have been present in each region and their current diversity. We then divide ranids into several clades of relatively well-known monophyly and species diversity, estimate the latitudinal position of these clades, estimate the diversification rates of clades (given their age and species diversity), and test for a relationship between latitude and diversification rate.

If we find a relationship between time and richness but no relationship between latitude and diversification rates, this pattern would suggest that historical biogeography (i.e., the time-for-speciation effect; Stephens and Wiens 2003) drives the pattern of high tropical diversity in ranids, as in hylids. Alternately, if there is no relationship between time and richness, and if diversification rates are higher in tropical clades, this would suggest that higher rates of speciation in the tropics (or higher rates of extinction in temperate regions) may drive the pattern. A combination of patterns is also possible. Our analyses reveal that, as in hylids, the timing of biogeographic dispersal seems to explain the latitudinal diversity gradient in ranid frogs, rather than differences in speciation or extinction rates.

Materials and Methods

TAXONOMY

Various competing taxonomies of ranid frogs have been proposed recently, making it necessary to clarify which we follow here. We follow the classification of Bossuyt et al. (2006) for the classification of ranid subfamilies, which was derived from a rigorous phylogenetic analysis. Although other authors (e.g., Frost et al. 2006; Roelants et al. 2007) have recognized many of these subfamilies as separate families (e.g., Mantellinae, Rhacophorinae), there seems to be generally broad agreement between authors as to which genera and species should be assigned to each one. We follow the classification of Amphibiaweb (2008) for generic-level taxonomy, but without necessarily assuming the monophyly of these genera. When data were derived from different sources for a given species (e.g., Bossuyt et al. 2006; Frost et al. 2006; IUCN et al. 2006; Che et al. 2007; Frost 2007; Amphibiaweb 2008) information was carefully checked to make sure that all data pertained to the same species, regardless of which genus the species was assigned to by a given set of authors.

PHYLOGENY ESTIMATION

We reconstructed ranid phylogeny by combining molecular datasets for ranid frogs from several sources, including Hillis and Wilcox (2005), Bossuyt et al. (2006), Frost et al. (2006), Che et al. (2007), and many others. In most cases, sequences were obtained directly from GenBank (ncbi.nlm.nih.gov/Genbank/index.html), and we searched GenBank repeatedly for new ranid sequences (stopping in January 2008). Following Bossuyt et al. (2006), we used available data from one mitochondrial gene region (12S-16S and adjacent transfer RNAs; up to ~2400 base pairs) and three nuclear protein-coding genes—recombinase activating gene 1 (RAG-1, up to ~1200 bp), rhodopsin (parts of exons 1 and 4; ~500 bp), and tyrosinase (part of exon 1; ~500 bp). The dataset of Bossuyt et al. (2006) provides a backbone of > 100 species that includes all the major ranid taxa and outgroups for these genes. Other taxa were added that had some subset of these data available. All included species had data from at least part of the 12S-16S fragment. Although some taxa are relatively incomplete and have extensive missing data, recent simulations and empirical analyses suggest that highly incomplete taxa can be accurately placed in phylogenetic analyses if the overall number of characters in the analysis is large (e.g., Wiens 2003; Philippe et al. 2004; Wiens et al. 2005; Wiens and Moen 2008). A listing of GenBank numbers and sources for the sequences used is provided in Supporting Appendix S1. Given the large number of different sources used (> 60), most of these sources are cited only in the Appendix.

Whenever possible, sequences for different genes were obtained from the same individual specimen. In some cases, data for different genes for the same species were only available from different individuals used in different studies. In these cases, data were combined so that each species was represented by a single terminal taxon that included as many of the genes as possible (rather than having many terminal taxa representing the same species, each with many missing data cells). In the final matrix, most species were represented by a single individual. However, sequences were obtained for multiple individuals for the same

gene (usually 12S-16S) in some cases. Preliminary phylogenetic analyses were performed on each gene using parsimony (as implemented in PAUP* ver. 4.0b10; Swofford 2002). When putatively conspecific individuals formed a monophyletic group, all individuals but one were eliminated. When individuals did not cluster together, they were retained as separate taxa in the phylogenetic analysis, given the possibility that they may represent distinct but unrecognized species. In several cases, we replaced the RAG-1 sequences from Bossuyt et al. (2006) with those from other studies for the same species, so that a much longer fragment of this gene could be included (~500 bp vs. ~1200 bp).

Initially, we included in our phylogenetic analyses 390 ingroup taxa (all within Ranidae), 70 outgroup species representing other ranoid families (e.g., Breviciptidae, Hemisotidae, Hyperoliidae, Microhylidae), and six species from outside Ranoidea, for use as distant outgroups. Only the 390 ranid taxa were included in the analyses of biogeography and diversification rates.

Alignment of protein-coding genes was straightforward and was done by eye, but was aided by performing amino acid translations of the sequences using MacClade version 4.0 (Maddison and Maddison 2000). The 12S-16S fragment was somewhat more difficult to align. Alignments were performed using MUSCLE (Edgar 2004) with some adjustments made by eye, and regions of uncertain alignment were excluded.

Phylogenies were constructed using maximum likelihood, as implemented in RAxML 6.0.0 (Stamatakis 2006). RAxML 6.0 uses only the GTR model (general time reversible), and so analyses of model fitting were not performed, given that all other substitution models represent special cases of GTR. A parameter for variation in rates among sites (Γ) was also included. Although an additional parameter for invariant sites can be included in some phylogenetic software packages, this was not available on the version of RAxML used. However, this parameter should be adequately accounted for in RAxML by Γ, given the large number of rate categories used to estimate among-site rate variation (25 or more; Stamatakis 2006). RAxML analyses were conducted on LifeMapper and Phyllomedusa, the 256-node and 16-node computer clusters at the University of Kansas Biodiversity Institute.

Before conducting the final analyses, analyses were performed on each gene and the 12S-16S region to test if different partitions within each gene were supported by the data (i.e., allowing for different model parameters in each partition). Partitions within each gene were tested by conducting maximum-likelihood analyses of each gene both with and without partitions and then comparing likelihood scores for the partitioned and unpartitioned data using the Akaike Information Criterion (AIC; Akaike 1973). Protein-coding genes were partitioned into three sets of characters each based on codon positions. The 12S-16S fragment was divided into two partitions, corresponding to inferred stem and loop regions. Stems and loops were identified based on models provided in the European ribosomal database (http://bioinformatics.psb.ugent.be/webtools/rRNA/) for *Hyla arenicolor* and *Rana catesbiana*. Previous studies suggest that the assignment of nucleotide positions to stems and loops is generally conserved across anuran clades (e.g., Wiens et al. 2005). For each analysis of each gene, 250 independent searches were conducted using the GTRMIX setting. The MIX setting conducts initial searches using the CAT approximation of the GTR + Γ model to rapidly find the ML estimate of the tree and branch lengths, and then maximizes the final likelihood by optimizing the tree using the full GTR + Γ model. These analyses strongly supported the use of partitions within each gene (results not shown), and all subsequent analyses were based on the combined, partitioned data.

To find the optimal likelihood tree, we ran 250 independent tree searches on the combined matrix using the GTRMIX substitution model applied independently to 11 partitions of the data (12S-16S stems; 12S-16S loops; and first, second, and third positions of RAG-1, rhodopsin, and tyrosinase separately). The overall best tree from the 250 independent RAxML searches was then optimized in RAxML using the "−f" option. The support for individual branches was evaluated using nonparametric bootstrapping (Felsenstein 1985a), using 200 replicates, each using the GTRMIX model.

DIVERGENCE-TIME ESTIMATION

We performed Bayesian divergence-time estimation using BEAST version 1.4.7 (Drummond and Rambaut 2007). To avoid repeating the time-intensive search for the best topology, we used the topology of the maximum-likelihood tree as a constraint in the dating analyses (although we acknowledge that it would be preferable to estimate dates by integrating across many possible topologies, given fewer taxa). As for the likelihood analysis, we used separate partitions within and between genes, and we here used the GTR + I + Γ model for each partition. Divergence times were estimated under the uncorrelated relaxed-clock tree model (Drummond et al. 2006) with a Yule process speciation prior and Jeffrey's priors on the substitution model parameters. Lognormal date priors were placed on the root of the tree, with a broad prior distribution (lognormal standard deviation of 0.25) to allow for the possibility of substantial rate variance.

We evaluated three different possible root dates: 79.2 MY million years before present, 111.3 MY, and 152.6 MY. The earliest and latest ages were selected based on the extremes of the accepted interval of dates for the age of the ranid crown-group age generated by Bossuyt et al. (2006; their Table 2), whereas the middle date (111.3) was based on their mean estimated date from the analysis including all of their calibration points. These three dates were used as priors in the dating analyses, but the analyses were not constrained such that these were forced to be the actual

Table 2. Raw data on the species richness, age, and latitudinal midpoint (absolute value) of selected ranid clades used in analyses of diversification rates and latitude. Clades are ordered phylogenetically.

Clade	Species	Crown-group age	Stem-group age	Latitudinal midpoint (northern/southern range limits)
Ptychadeninae	51	59.80	101.10	0.14 (32.95/−33.23)
Phrynobatrachinae	72	72.18	93.33	9.28 (15.50/−34.05)
Conrauinae	6	31.55	73.86	5.52 (15.73/−5.30)
Pyxicephalinae	61	66.49	82.49	6.73 (21.39/−34.85)
Nyctibatrachinae	13	65.03	81.85	13.00 (19.73/6.28)
Ranixalinae	10	51.71	79.95	14.32 (20.08/8.55)
Petropedetinae	10	40.38	73.86	0.11 (9.28/−9.06)
Micrixalinae	11	22.86	82.77	11.94 (15.52/8.35)
Ceratobatrachinae	74	62.30	79.95	1.20 (18.57/−16.18)
Rhacophorinae	278	66.89	74.14	15.58 (41.53/−10.36)
Mantellinae	165	55.94	74.14	18.96 (−12.32/−25.61)
Dicroglossinae	161	74.50	82.77	15.60 (40.03/−9.11)
Raninae				
Staurois	4	25.42	60.09	5.12 (12.46/−2.23)
Pelophylax	24	27.53	46.57	35.82 (60.76/10.88)
Rana boylii group	7	15.67	23.14	45.26 (59.83/30.68)
Rana catesbiana group	7	12.30	25.15	36.72 (54.06/19.39)
Rana tarahumarae group	5	20.06	25.23	23.74 (31.60/15.87)
Rana palmipes group	8	22.59	25.23	0.15 (19.32/−17.17)
Rana (subgenus *Stertirana*)	6	9.71	16.04	39.86 (61.48/18.25)
Rana (subgenus *Nenirana*)	4	8.20	13.25	37.49 (49.18/25.80)
Rana (subgenus *Scurillirana*)	20	8.65	13.25	24.95 (41.10/8.80)
Rana everetti group	5	14.40	28.04	9.26 (18.18/0.34)

root ages in the results. Note that the fossil record of ranids is meager, and that other studies of frog divergence times (which included groups having more extensive fossil records) have estimated dates that are generally similar for the ranid crown group (e.g., Roelants et al. 2007).

Analyses were run for 10 million generations, with the first five million discarded as burnin. Convergence of parameters was assumed when the effective sample size reached at least 100, which occurred prior to five million generations in all runs. Although it might have been desirable to estimate divergence times on a large number of phylogenies, the analysis of a single tree was very time-intensive given the large number of taxa (i.e., >2 weeks).

For each root age, we generated a chronogram based on the mean of the estimated dates for each node of the 390-species ranid tree, summarized from the post-burnin values. The major analyses of biogeography and diversification rates were initially conducted using all three chronograms. However, different chronograms gave virtually identical results (presumably because these analyses ultimately depend on the relative ages of clades, and not their absolute ages). Therefore, only results based on the root age of 111.3 MY are presented.

TIMING OF COLONIZATION AND REGIONAL SPECIES RICHNESS

We estimated the relationship between the approximate time when each region was first colonized by ranids and the number of species presently occurring in that region. The age of the oldest divergence of endemic species or clades within a region provides a minimum estimate of the age of colonization of that region. These divergence times were visualized by reconstructing the biogeographic history of ranids on the estimated chronogram using maximum likelihood, as implemented in Mesquite version 1.05 (Maddison and Maddison 2004). Each of the 390 ranid species was assigned a character state corresponding to a given geographic region. Although most species were endemic to a single region, some species occurred in more than one. Additional character states were defined for different combinations of regions. In total, the following character states were used: 0 = Southeast Asia, from Myanmar east to Taiwan, south to Indonesia (excluding the island of New Guinea) and north to 30°N latitude in China; 1 = North Asia including China and Japan (north of 30°N latitude), Russia (east of the Ural Mountains), Mongolia, North Korea, South Korea, Kazakhstan, Uzbekistan, Kyrgyzstan, and Turkmenistan; 2 = South Asia (including India, Pakistan,

Sri Lanka, Nepal, Bangladesh); 3 = Australasia (including Australia and New Guinea); 4 = Europe, including North Africa, the Middle East, and Central Asia; 5 = sub-Saharan Africa; 6 = Madagascar; 7 = North America (continental U.S. and Canada); 8 = Middle America (Mexico to Panama); 9 = South America; A = regions 0 + 1; B = 0 + 2; C = 7 + 8; D = 8 + 9; E = 0 + 3; F = 5 + 6; G = 0 + 1 + 2; H = 0 + 1 + 2 + 4. Maps depicting the geographic distribution of each species were obtained from the website of the Global Amphibian Assessment (GAA hereafter; IUCN et al. 2006).

There are many ambiguities in ancestral area reconstruction (Ronquist 1994), and some alternate methods have been proposed. However, current implementation of the likelihood method of Ree et al. (2005) and Ree and Smith (2008) only allow for a limited number of states (regions), and DIVA (Ronquist 1996, 1997) ignores branch lengths and allows only a limited number of taxa. Thus, neither approach was practical for this study. Importantly, our goal was not to estimate the history of dispersal and vicariance within the group, but rather to estimate the ages of endemic clades (although some clades give rise to clades inhabiting other regions). To be conservative, we considered only reconstructions that were supported as unambiguous based on a likelihood-ratio test (implemented in Mesquite).

Wiens et al. (2006) focused only on the age of the first (oldest) colonization of each region in hylids, regardless of how many times the region was colonized. We did the same for ranids in our first set of analyses. However, we also accounted (partially) for the possibility that some regions were colonized repeatedly by ranids, that each colonization event could potentially increase the species richness of the region, and that older colonization events can potentially contribute more species to a region than younger events (i.e., more time for in situ speciation). Therefore, we developed a score for each region based on adding together the ages of each colonization of that region, again using the age of the oldest inferred split within that region for each colonization event. For this analysis, we only included colonization events in which the colonizing lineage gave rise to two or more endemic species (among the species sampled in our tree), given that it is very difficult to determine when a single species invaded a region when sampling only a single individual per species. For similar reasons, we generally did not include colonizations associated with a polymorphic state within a species (we also know that the contribution of such events to the overall index should be very small, given that they should be younger than most speciation events). However, we made an exception for a clade of several *Amolops* species that all occur in both North Asia and Southeast Asia, and presumably did so for a long period of time.

Both of our approaches to quantifying the timing of colonization of different regions have their problems. Using the oldest colonization potentially ignores other relevant dispersal events into the region, each of which may strongly influence species richness. Using the summed ages of colonizations assumes that our taxon sampling was adequate to capture all of the relevant events, and ignores single-species colonizations. Despite these problems, it should be noted that our primary goal is to estimate the relative age of colonization for each region, and so having a comparable index across regions is more important than including every potential colonization event. Furthermore, both methods gave similar results after log-transformation (see Results).

The species richness of each of the 10 regions defined above was obtained using the website of the GAA (IUCN et al. 2006). This website allows one to submit a family and list of countries and then obtain a nonredundant list of all species in that family occurring in that set of countries. The relationship between colonization time and current diversity was estimated using linear regression in Statview (following Stephens and Wiens 2003). Given that species richness is thought to increase logarithmically over time (e.g., Magallón and Sanderson 2001), the species diversity of each region was log-transformed. Although the species richness of regions and clades is not perfectly known (i.e., new ranid species continue to be described), our primary goal was to have a comparable index of diversity to use to compare regions. Some of the regions used differ in area, but we found no relationship between area and ranid species richness, using either the raw ($r^2 = 0.111$; $P = 0.3480$) or log-transformed values ($r^2 = 0.120$; $P = 0.3271$). The area of each region was estimated by summing the areas of the relevant countries (but using provinces for China), obtained using internet resources.

RATES OF DIVERSIFICATION AND LATITUDINAL POSITION

We analyzed the relationship between the diversification rates of ranid clades and their latitudinal positions. To simplify somewhat, the diversification rate of a clade can be estimated by dividing the log of its present diversity by its age (see below). Here, ranids were divided into 22 clades for which we were relatively confident in the species composition and monophyly (i.e., likelihood bootstrap values $\geq$ 70%). Most clades correspond to subfamilies recognized by Bossuyt et al. (2006) with some additional clades within Raninae that correspond to genera or subgenera. However, some species within Raninae could not be assigned to clades because the taxonomy of genera and exact species composition of some clades is highly uncertain (e.g., compare Frost et al. 2006 and Stuart 2008) and because only about 33% of described ranid species were included in our phylogeny. Although it would be preferable to assign all ranid species to clades, we prefer to have fewer clades with more confident species composition (and species numbers) than have some clades with unknown species richness. The assignment of species to clades would also have

been an issue if we subdivided some of our clades (e.g., subfamilies) into smaller clades. Finally, the number of clades used in this study is twice the number of hylid clades considered by Wiens et al. (2006).

The clades that were used included some that are primarily tropical and some that are primarily temperate, and spanned the entire geographic range and phylogenetic breadth of the family. The unassigned species are confined to one clade (Raninae) and occur mainly in eastern Asia. We were able to assign 1002 of 1284 ranid species to clades.

To address the robustness of the results to alternate clade divisions, we also performed a limited set of analyses using 17 clades rather than 22. We combined groups of clades that together form monophyletic groups and that occur in the same general geographic region. Specifically, we combined the African subfamilies Conrauinae, Petropedetinae, and Pyxicephalinae into one clade (but note that support for the monophyly of this group is weak), the Neotropical *palmipes* and *tarahumarae* groups of *Rana* into a clade, and three North American subgenera of *Rana* (*Nenirana, Scurillirana, Stertirana*) into a clade. Results were similar to those using 22 clades.

The number of species in most clades was estimated from species lists in Frost (2007; accessed July 31, 2007). There is general correspondence between Bossuyt et al. (2006), Frost et al. (2006), and Frost (2007) regarding which species are assigned to each clade (especially for subfamilies), regardless of differences in the details of the generic taxonomy. For New World *Rana*, assignment of species to clades and species numbers were based on the detailed study by Hillis and Wilcox (2005). The monophyly and species composition of the *Rana everetti* species group was based on unpublished data from RMB. Again, new species continue to be described and added to these clades, but our goal was to compare estimated diversification rates across clades, which does not require perfect knowledge of the species richness of each clade.

Diversification rates were estimated using the method-of-moments estimators presented by Magallón and Sanderson (2001), for both stem groups (their eq 6) and crown groups (eq 7). The age of the stem group corresponds to the point in time when the clade first splits from its sister group, whereas the age of the crown group corresponds to the age of the oldest split between extant lineages within the clade. In general, we were confident that most clades were sufficiently well sampled to include the crown group (e.g., when a subfamily contained two genera, and both were represented).

Unlike the maximum-likelihood estimators, the method-of-moments estimators do not require assuming that the extinction rate is negligible, which avoids some potential biases in estimating diversification rate (Magallón and Sanderson 2001). Given that the relative extinction rate (ε, where ε = speciation rate/extinction rate) is unknown, we attempted to bracket the most likely rates by using two extreme values of the relative extinction rate. Following Magallón and Sanderson (2001), we used a value of 0.90 as an upper limit, and 0 (no extinction) as a lower limit. Note that when the extinction rate is 0, the diversification rate becomes equivalent to the rate of speciation. We also performed a limited set of analyses using an intermediate value for ε (0.45). We acknowledge that this approach requires assuming that relative extinction rates are similar across all clades in each analysis. However, violations of this assumption should not invalidate attempts to estimate and compare overall diversification rates, but make it difficult to disentangle the relative contributions of speciation and extinction rates to the overall diversification rate, which we do not attempt to do (Ricklefs 2006). Overall, our results were robust to different methods of estimating diversification rates.

The latitudinal position of each clade was estimated by determining its latitudinal midpoint, the midpoint between the northernmost and southernmost latitudinal extent of the clade (e.g., the northernmost extent of the range of the most northerly occurring species). Species range maps were obtained from the GAA (IUCN et al. 2006). The specific latitude of the range limits was estimated using the GAA range maps and ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, CA, 1992). After estimating the latitudinal midpoint of each clade, the absolute value was used in all subsequent analyses. The latitudinal midpoints seemed to capture the general latitudinal position of these clades, but to further test this, we repeated the basic analyses using the maximum latitude (maximum poleward extent of the clade) and minimum latitude (0 for clades that spanned the equator). All three analyses gave similar results.

We examined the relationship between diversification rate and latitude using standard linear regression as implemented in Statview. However, related clades may share their latitudinal position (and the associated effects on diversification rates) because of common ancestry. To account for this, we also repeated these analyses using independent contrasts (Felsenstein 1985b). The phylogeny used was taken from the maximum-likelihood analysis of all the taxa. Two sets of branch lengths were used, the branch lengths from the chronogram and equal branch lengths. For the analyses of independent contrasts we used the diversification rates based only on the crown groups (terminal branch lengths are potentially problematic for stem groups, given that they are effectively zero). Contrasts were calculated using COMPARE version 4.6 (Martins 2004), and the regressions were forced through the origin (e.g., Garland et al. 1992).

Various statistical methods are now available to analyze patterns of diversification over time on a phylogeny (e.g., Nee et al. 1994; Rambaut et al. 1997; Rabosky 2006). We did not use these methods for two reasons. First, such analyses would be potentially compromised by the fact that less than 33% of ranid species

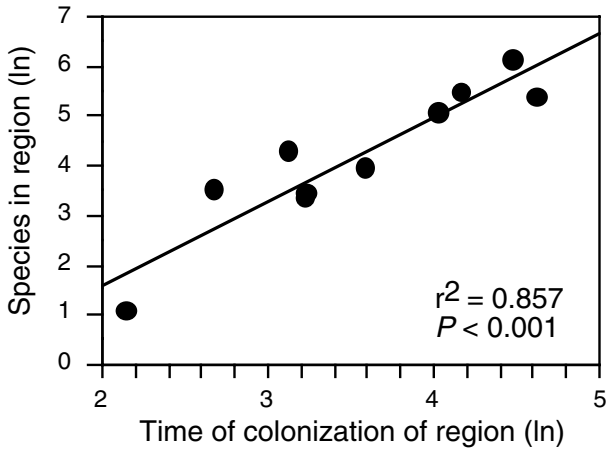

Figure 3. Strong relationship between the timing of colonization of a region and the current species richness of the region, based on log-transformed data from Table 1. The timing of colonization is based on the oldest endemic lineage within a region.

are included in our phylogeny, and we cannot guarantee that our sampling of taxa is unbiased. Thus, we used an approach that includes every species in each group in the estimation of diversification rates, but does not require having every species actually included in the phylogeny. Second and more importantly, our primary interest is not in how diversification rates change over time, but if and how they change over space (i.e., by comparing rates in clades inhabiting different regions).

Results

Our phylogenetic hypothesis is summarized in Figures 1 and 2. This phylogeny supports many clades that were also found in previous studies (e.g., Bossuyt et al. 2006; Frost et al. 2006). Most importantly, we support all of the same subfamilies that were recognized by Bossuyt et al. (2006), despite our more extensive taxon sampling. This lends support to our use of these clades in our analyses of biogeography and diversification rates. There are some differences in the reconstructed relationships among subfamilies between the three studies, but these are weakly supported in our analysis. Major findings that are also seen in previous studies include the following: (1) placement of the African Ptychadeninae as sister group to other ranids (Bossuyt et al. 2006; Frost et al. 2006); (2) a basal African clade consisting of Pyxicephalinae, Conrauinae, and Petropedetinae (van der Meijden et al. 2005), with the latter two clades as sister taxa (Bossuyt et al. 2006); and (3) a clade consisting of Mantellinae + Rhacophorinae (van der Meijden et al. 2005; Bossuyt et al. 2006; Frost et al. 2006). Many clades within Raninae are also consistent with these two previous studies, such as the placement of *Staurois* as the sister taxon to other Raninae, and a group that includes all New World ranids (exclusive of the *Rana boylii* group). Our phylogeny suggests that many of the currently recognized ranine genera (as per Amphibiaweb 2008) are not monophyletic (e.g., *Amolops, Huia, Rana*). Many of the genera recognized by Frost et al. (2006) appear nonmonophyletic as well (e.g., *Amolops, Glandirana, Huia, Hydrophylax, Pulchrana, Sylvirana*), but some are tentatively supported (e.g., *Babina, Hylarana, Lithobates, Meristogenys, Pelophylax, Rana*), at least based on our sampling.

Overall, historical biogeographic patterns in ranid frogs (Figs. 1 and 2) suggest that Ranidae originated in the tropics of Africa and Asia and then spread to other areas (i.e., N Asia, Europe, Madagascar, Australia, the New World) more recently. Current ranid diversity in each region is summarized in Table 1, along with the estimated ages of the first colonization of each region and the summed ages of colonization events. There is a strong relationship ($r^2 = 0.701$; $P = 0.0025$) between the timing of the first colonization of each region and the number of species there today, which becomes even stronger if time is log-transformed to account for nonlinearity ($r^2 = 0.857$; $P = 0.0001$; Fig. 3). The relationship remains strong when the New World regions are deleted ($r^2 = 0.779$; $P = 0.0085$), indicating that the timing of biogeographical dispersal is important in explaining species richness patterns in the Old World. The relationship is also strong when the summed and log-transformed ages of colonization events are considered ($r^2 = 0.769$; $P = 0.0009$), suggesting that colonization events after the first colonization of a region do not necessarily disrupt this general relationship between time and regional diversity. However, in the raw data, South Asia forms an outlier that weakens this general relationship when summed ages of colonization events are considered ($r^2 = 0.355$; $P = 0.0693$; with South Asia removed: $r^2 = 0.772$; $P = 0.0018$).

We acknowledge that uncertainty in the phylogeny could affect these biogeographic inferences. However, even though relationships among many ranid subfamilies are only weakly supported, all of the basal clades occur in tropical regions with high diversity (i.e., Africa, South Asia, Southeast Asia). Thus, different rearrangements of these clades should have little impact on the results of the analyses of regional diversity. In contrast, the placement of each of the clades occurring in lower diversity areas is relatively well-supported based on bootstrapping (e.g., Australasia, North Asia, Europe, Madagascar, the New World). The most relevant result for the origin of the latitudinal diversity gradient is the nesting of young temperate lineages within old tropical clades, and this is well corroborated given the many clades with high bootstrap values that support this pattern (Figs. 1 and 2).

The age, diversity, and latitudinal distribution of the selected clades are shown in Table 2 and their estimated diversification rates are shown in Table 3. Analyses of the raw data show that the relationship between the diversification rate of clades and their latitudinal position is either absent or weakly significant (Fig. 4), depending on whether crown group or stem group ages

Table 3. Estimated diversification rates for 22 ranid clades. Clades are ordered phylogenetically.

Clade	Diversification rates			
	Crown-group		Stem-group	
	ε=0	ε= 0.90	ε=0	ε= 0.90
Ptychadeninae	0.054	0.029	0.039	0.018
Phrynobatrachinae	0.050	0.028	0.046	0.022
Conrauinae	0.035	0.011	0.024	0.005
Pyxicephalinae	0.051	0.028	0.050	0.024
Nyctibatrachinae	0.029	0.011	0.031	0.010
Ranixalinae	0.031	0.011	0.029	0.008
Petropedetinae	0.040	0.015	0.031	0.009
Micrixalinae	0.075	0.028	0.029	0.008
Ceratobatrachinae	0.058	0.033	0.054	0.026
Rhacophorinae	0.074	0.049	0.076	0.045
Mantellinae	0.079	0.050	0.069	0.039
Dicroglossinae	0.059	0.037	0.061	0.034
Staurois	0.027	0.008	0.023	0.004
Pelophylax	0.090	0.041	0.068	0.026
Rana boylii group	0.080	0.026	0.084	0.020
Rana catesbiana group	0.102	0.034	0.077	0.019
Rana tarahumarae group	0.046	0.014	0.064	0.013
Rana palmipes group	0.061	0.021	0.082	0.021
Rana (subgenus *Stertirana*)	0.113	0.036	0.112	0.025
Rana (subgenus *Nenirana*)	0.085	0.025	0.105	0.020
Rana (subgenus *Scurillirana*)	0.266	0.117	0.226	0.080
Rana everetti group	0.064	0.019	0.057	0.012

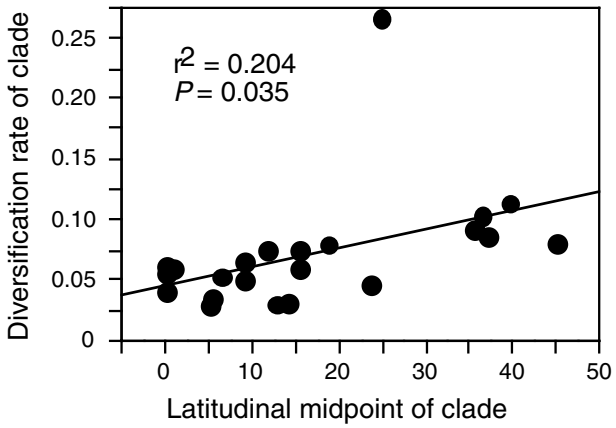

Figure 4. Relationship between the diversification rate and latitudinal midpoint of 22 ranid clades, showing a tendency toward higher diversification rates in temperate clades. In this analysis, diversification rates were estimated using the method-of-moments estimator assuming no extinction and using the crown-group ages of clades. The raw data are provided in Table 3. Results from alternate methods (including stem group ages, higher relative extinction rates, and independent contrasts) are similar, and are provided in Table 4.

are considered and on the assumed extinction rate (Table 4). This relationship becomes stronger when a single outlier with a very high diversification rate (the New World clade *Scurillirana*) is removed (i.e., for analyses assuming $\varepsilon = 0$, $r^2 = \sim 0.500$, $P = \sim 0.0003$, for both stem and crown groups). However, the relationship found between diversification rate and latitude is exactly the opposite of that which is predicted; the results show that temperate clades tend to have higher diversification rates than tropical clades. Thus, differences in the rates of speciation and extinction are unlikely to explain the higher species richness of ranid frogs in the tropics. When these relationships are analyzed using independent contrasts, there is no significant relationship between the latitude and diversification rates of clades (Table 4). These relationships are also similar using the maximum latitude (poleward extent) and minimum latitude of clades, either showing no significant relationship between diversification and latitude, or else a trend towards higher diversification rates in more temperate clades (J. J. Wiens, unpubl. data). They remain similar using intermediate values for relative extinction rates ($\varepsilon = 0.45$) and when using 17 clades rather than 22, again either showing higher diversification rates in the temperate regions or no significant relationship (J. J. Wiens, unpubl. data).

Given that tropical clades are older, temperate clades might have higher diversification rates merely because they are younger (Table 2), as expected from previous studies (e.g., Ricklefs 2006; Phillimore and Price 2008). Indeed, we find that there is a significant negative relationship between the latitudinal midpoint of clades and their crown-group ages ($r^2 = 0.281$; $P = 0.0112$).

Table 4. Results from analyses of the relationship between the diversification rate and latitudinal midpoint of clades.

Clade age	Extinction rate	r^2	P
Raw data			
Crown	ε=0	0.204	0.0349
	ε=0.90	0.079	0.2063
Stem	ε=0	0.256	0.0163
	ε=0.90	0.060	0.2718
Independent contrasts (estimated branch lengths)			
Crown	ε=0	0.011	0.6428
	ε=0.90	0.019	0.5405
Independent contrasts (equal branch lengths)			
Crown	ε=0	0.000	0.9295
	ε=0.90	0.002	0.8516

However, if we exclude the 10 clades that are older than the mean crown-clade age (38 MY), the relationship between latitude and diversification rate remains nonsignificant and tends toward higher diversification rates in more temperate clades (crown-group, $\varepsilon = 0$: $r^2 = 0.124$; $P = 0.2623$; $\varepsilon = 0.90$: $r^2 = 0.077$; $P = 0.3826$). Finally, if we exclude the youngest clades (those less than 10 MY old using the root ages of 111.3 million years ago [mya]), the results are again similar, with diversification rates in more temperate clades either similar to or higher than those in tropical clades (J. J. Wiens, unpubl. data).

Discussion

A plethora of hypotheses have been proposed to explain why there are more species in the tropics than in temperate regions for so many groups (e.g., Pianka 1966; Rahbek and Graves 2001; Willig et al. 2003). However, any complete explanation of this pattern must consider the processes that directly change species numbers within a region: speciation, extinction, and biogeographic dispersal (e.g., Ricklefs 2004; Wiens and Donoghue 2004; Mittelbach et al. 2007). Many studies of species richness patterns do not consider any of these processes, and very few consider all three (but see Jablonski et al. 2006; Wiens et al. 2006; Diniz-Filho et al. 2007; Rangel et al. 2007).

Our results from ranid frogs show that diversification rates (i.e., rates of speciation−extinction) are generally similar between tropical and temperate regions, or else vary in the opposite direction needed to explain high tropical diversity. Instead, differences in regional species richness seem to arise from patterns of historical biogeography (i.e., the recent colonization of temperate regions from the tropics, leaving less time for speciation to build up temperate species richness). Because many proposed explanations for the latitudinal diversity gradient explicitly or implicitly assume differences in speciation or extinction rates, our study helps eliminate several potential hypotheses, at least for ranid frogs. For example, we find no evidence for the evolutionary rates hypothesis (Rhode 1992), which postulates higher speciation rates in the tropics. Nor do we find support for related hypotheses that ascribe high tropical diversity to higher tropical speciation rates caused by temperature-driven metabolic processes (e.g., Allen et al. 2002, 2006; Allen and Gillooly 2006) or more intense coevolutionary relationships (e.g., Schemske 2002).

In theory, our results could be dismissed as being unique to this particular group of organisms or this particular biogeographic region. However, Wiens et al. (2006) found very similar results in hylid frogs, a group of similar age and species diversity that occurs primarily in the New World tropics. Together, the hylids and ranids make up nearly a third of all amphibian species (Amphibiaweb 2008). These concordant results suggest that similar processes may be responsible for high tropical species richness in both the Old and New World. They also show that large-scale historical biogeography should be considered in studies that attempt to explain the latitudinal diversity gradient, and not just rates of diversification (e.g., Wiens and Donoghue 2004; Stevens 2006; Hawkins et al. 2007; Rangel et al. 2007). In the sections that follow, we address the possible causes of the biogeographic patterns, and whether these biogeographic patterns offer a general explanation for high tropical diversity.

ECOLOGICAL CAUSES OF BIOGEOGRAPHIC PATTERNS

If historical biogeography drives patterns of diversity in ranid and hylid frogs, then what causes the patterns of historical biogeography? According to the first two parts of the tropical conservatism hypothesis (Wiens and Donoghue 2004; see also Farrell et al. 1992; Ricklefs and Schluter 1993; Futuyma 1998), many clades have high tropical species richness because (1) they originated in the tropics and spread to the temperate zone more recently (time-for-speciation effect), and (2) tropical species have difficulty dispersing to temperate regions because they are unable to tolerate climatic conditions there, such as freezing winters (niche conservatism; review in Wiens and Graham 2005). In hylids, latitudinal variation in temperature seasonality (i.e., cooling in winter) seems to set the northern range limits of tropical clades in Mexico, and this variable shows significant phylogenetic conservatism across hylids (Wiens et al. 2006). It is possible that similar climatic factors might set the northern range limits of tropical ranids. However, we lacked the extensive georeferenced locality data for Asian ranids that would allow us to test this hypothesis rigorously with ecological niche modeling (as in Wiens et al. 2006).

Nevertheless, hylids and ranids do show parallels in their patterns of diversity and biogeography, which are consistent with the idea that only a limited number of clades are capable of invading temperate regions from the tropics. In hylids, only one major clade of hylids is represented in temperate North America (tribe Hylini), and other tropical clades approach the temperate zone but fail to enter (Wiens et al. 2006). In ranids, clade diversity in temperate Eurasia is also very limited, with only one major clade of ranids (Raninae) present in Europe and northern Asia. In contrast, other ranid clades are present in tropical and subtropical regions farther south (e.g., in SE Asia, there are dicroglossines, rhacophorines, and many other clades within Raninae).

Given that species richness generally shows strong correlations with climate (e.g., Willig et al. 2003), latitudinal variation in climate is doubtless a critical factor in generating the latitudinal diversity gradient, especially in amphibians (e.g., Buckley and Jetz 2007). However, climate must act on the processes that change species numbers (i.e., speciation, extinction, dispersal) to

create this pattern. In groups in which historical biogeography seems to be important in explaining the latitudinal diversity gradient, climatic constraints on dispersal may offer a bridge between the biogeographic and ecological explanations for this pattern.

AN INTEGRATIVE EXPLANATION FOR THE LATITUDINAL DIVERSITY GRADIENT

Historical biogeography (i.e., ancient tropical origin and recent dispersal to the temperate zone) seems to explain why clades like hylids and ranids have more species in the tropics, but the question remains as to why many clades have originated in the tropics in the first place. In fact, historical biogeography is unlikely to explain this pattern across all frogs, because many basal clades of anurans (and the sister group to anurans, salamanders) are primarily temperate (Wiens 2007).

Analyses of diversification rates across all frogs and salamanders suggest that, contrary to results in ranids and hylids, diversification rates are higher in the tropics (Wiens 2007). Anurans and salamanders have many ancient, low-diversity clades confined primarily to temperate regions, and a small number of clades that have invaded the tropics and now have very high diversity (e.g., bolitoglossine salamanders, megophryid and neobatrachian frogs). Within salamanders (for which more thorough taxon sampling allows for more detailed analyses), the low diversity of temperate clades may be related to higher temperate extinction rates and the pruning of entire subclades during the long history of each family in the temperate zone, rather than higher speciation rates in the primarily tropical clade (Wiens 2007). If this hypothesis applies to anurans as well, it may explain an obvious paradox: if diversification rates are higher in the tropics across all frogs, why is there no evidence of this in hylids and ranids? We speculate that because hylids and ranids have only been present in the temperate zone for a relatively brief period, the temperate hylid and ranid clades have not had enough time for stochastic extinction events to lower their net diversification rates.

In a similar vein, Weir and Schluter (2007) have shown results suggesting that there are higher rates of speciation in the most northerly lineages of birds and mammals (note that a similar trend seems to occur in ranids; Fig. 4). They argued that there must be higher extinction rates in temperate areas to counteract these high speciation rates and keep temperate diversity low (although this pattern could also be explained by the more recent colonization of temperate regions, as in ranids). Thus, there may be higher extinction in the temperate zone over long periods of time, even though this is not apparent from diversification rates in clades that have only recently invaded temperate regions.

Why might there be higher extinction rates in the temperate zone? According to the third part of the tropical conservatism hypothesis, more clades arise in the tropics because the tropics were more extensive until recently (~30–40 mya), and thus had a much larger area (review in Wiens and Donoghue 2004). There is support for this idea from a study of trees (plants), where the area of major biomes in the past seems to explain the current diversity of each biome (e.g., high in tropical rainforests), but present-day area does not (Fine and Ree 2006). At the global scale, the area of a biome may influence diversification rates in the clades that inhabit it (Fine and Ree 2006); a biome with a larger area may offer more opportunities for speciation, whereas clades confined to smaller biomes may experience higher rates of extinction (e.g., Rosenzweig 1995). Of course, other factors besides area may contribute to higher extinction rates in temperate areas, such as climatic oscillations.

In summary, a comprehensive explanation for diversity patterns in anurans (and other groups) must consider the ancient history of the group as well as more recent patterns. At the deepest temporal and phylogenetic scales, more clades of anurans may have arisen in the tropics due to relatively higher diversification rates of (primarily) tropical clades. This latitudinal difference in diversification rates may be associated with higher extinction rates in ancient temperate clades rather than higher tropical speciation rates. In contrast, within more recent clades of tropical origin, such as the hylids and ranids, higher tropical diversity seems to be related to their biogeographic history rather than to latitudinal differences in diversification rates. In addition to studies of diverse tropical groups (like ranids and hylids), understanding patterns of species richness across all anurans may also benefit from detailed studies of the ancient temperate groups, including better phylogenetic sampling to help tease apart extinction and speciation and integrated paleontological and ecological analyses to address possible causes of extinction.

Conclusions

A fundamental problem in biology is to understand why there are more species in the tropics. Our results for ranid frogs suggest that historical biogeography plays an important role in creating this pattern. Ranids have been present in tropical areas longer and have dispersed into the temperate zone more recently, leaving less time for speciation to build up species richness in temperate regions. We found no evidence that different rates of speciation and extinction drive this pattern, given that diversification rates are similar between latitudes or else differ in the opposite direction needed to explain high tropical diversity. Intriguingly, similar patterns were found in a group of frogs (Hylidae) with similar age and diversity that occurs primarily in the New World. Future work in ranids is needed to understand the ecological processes that underlie the historical biogeography (i.e., what prevents most tropical clades from invading cool temperate areas?). Furthermore, more comprehensive analyses of frog phylogeny and diversity are needed to reconcile the contrasting patterns in ancient frogs with those in

more recent clades (e.g., hylid, ranids), given that frogs may be ancestrally temperate and show higher diversification rates in the tropics at the deepest phylogenetic scale. Nevertheless, ranids and hylids help illustrate a principle that may apply to many groups of organisms and many patterns of diversity: that the regions or habitats that have been inhabited for the longest amount of time by the group may often have the highest species richness (e.g., Stephens and Wiens 2003).

ACKNOWLEDGMENTS

We are grateful to the dozens of researchers who collected and sequenced the hundreds of ranid frog species that were analyzed in this study, and who made their data publicly available on GenBank. We thank S. Steppan and three anonymous reviewers for helpful comments on the manuscript. We thank the U.S. National Science Foundation for financial support during preparation of this manuscript (EF 0334923 to JJW and EF 0334952 to RMB).

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of maximum likelihood. Pp. 267–281 *in* B. N. Petrov and F. Csáki, eds. Proceedings of the 2nd international symposium on information theory. Akademia Kaido, Budapest.

Allen, A. P., and J. F. Gillooly. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecol. Lett. 9:947–954.

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics and the energetic-equivalence rule. Science 297:1545–1548.

Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. Proc. Natl. Acad. Sci. USA 103:9130–9135.

AmphibiaWeb. Information on amphibian biology and conservation. [web application]. 2008. AmphibiaWeb, Berkeley, California. Available at http://amphibiaweb.org/. (Accessed: February 29 April 2008).

Bossuyt, F., R. M. Brown, D. M. Hillis, D. C. Cannatella, and M. C. Milinkovitch. 2006. Phylogeny and biogeography of a cosmopolitan frog radiation: late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. Syst. Biol. 55:579–594.

Buckley, L. B., and W. Jetz. 2007. Environmental and historical constraints on global patterns of amphibian richness. Proc. R. Soc. Lond. B 274:1167–1173.

Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. Proc. R. Soc. Lond. B 266:1221–1225.

Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in diversification rates: an example using New World birds. Ecology 86:2278–2287.

Che, J., J. Pang, H. Zhao, G. F. Wu, E. M. Zhao, and Y. P. Zhang. 2007. Phylogeny of Raninae (Anura: Ranidae) inferred from mitochondrial and nuclear sequences. Mol. Phylogenet. Evol. 43:1–13.

Diniz-Filho, J. A. F., T. F. L. V. B. Rangel, L. M. Bini, and B. A. Hawkins. 2007. Macroevolutionary dynamics of species in environmental space and the latitudinal diversity gradient in New World birds. Proc. R. Soc. Lond. B. 274:43–52.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7:214.

Drummond A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4:e88.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32:1792–97.

Farrell, B. D., C. Mitter, and D. J. Futuyma. 1992. Diversification at the insect-plant interface. BioScience 42:34–42.

Felsenstein, J. 1985a. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

———. 1985b. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Fine, P. V. A., and R. Ree. 2006. Evidence for a time-integrated species- 804.

Francis, A. P., and D. J. Currie 2003. A globally consistent richness-climate relationship for angiosperms. Am. Nat. 161:523–536.

Frost, D. R. 2007. Amphibian species of the world: an online reference. American Museum of Natural History, New York. Electronic Database Available at http://research.amnh.org/herpetology/amphibia/index.html. (Accessed: July 31, 2007) .

Frost, D. R., T. Grant, J. Faivovich, R. Bain, A. Haas, C. F. B. Haddad, R. O. de Sá, S. C. Donnellan, C. J. Raxworthy, M. Wilkinson et al. 2006. The amphibian tree of life. Bull. Am. Mus. Nat. Hist. 297:1–370.

Futuyma, D. J. 1998. Evolutionary biology. 3rd ed. Sinauer Associates, Sunderland, MA.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

Gaston, K. J., and T. M. Blackburn. 1996. The tropics as a museum of biological diversity: an analysis of the New World avifauna. Proc. R. Soc. Lond. B 263:63–68.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170:S16–S27.

Hillis, D. M., and T. P. Wilcox. 2005. Phylogeny of the New World true frogs (*Rana*). Mol. Phylogenet. Evol. 34:299–314.

IUCN, Conservation International, and NatureServe. 2006. Global Amphibian Assessment. Available at www.globalamphibians.org.

Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314:102–106.

Maddison, D. R., and W. P. Maddison. 2000. MacClade 4.0. Sinauer Associates, Sunderland, MA.

Maddison, W. P., and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Version 1.05 http://mesquiteproject.org.

Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55:1762–1780.

Martins, E. P. 2004. COMPARE, version 4.6. Computer programs for the statistical analysis of comparative data. Department of Biology, Indiana Univ., Bloomington, IN. Distributed by the author at http://compare.bio.indiana.edu/.

Mittelbach, G. G., D. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. Bush, S. Harrison, A. Hurlbert, N. Knowlton, and H. A. Lessios. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecol. Lett. 10:315–331.

Nee, S., R. M. May, and P. H. Harvey. 1994. The reconstructed evolutionary process. Phil. Trans. R. Soc. Lond. B 344:305–311.

Phillimore, A. B., and T. Price. 2008. Density-dependent cladogenesis in birds. PLoS Biol. 6:e71.

Philippe, H., E. A. Snell, E. Bapteste, P. Lopez, P. W. H. Holland, and D. Casane. 2004. Phylogenomics of eukaryotes: impact of missing data on large alignments. Mol. Biol. Evol. 21:1740–1752.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100:33–46.

Rabosky, D. L. 2006. Likelihood methods for detecting temporal shifts in diversification rates. Evolution 60:1152–1164.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. Proc. Natl. Acad. Sci. USA 98:4534–4539.

Rambaut, A., P. H. Harvey, and S. Nee. 1997. End-Epi: an application for reconstructing phylogenetic and population processes from molecular sequences. Comput. Appl. Biosci. 13:303–306.

Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and R. K. Colwell. 2007. Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. Am. Nat. 274:165–174.

Ree, R. H., and S. A. Smith. 2008. Maximum-likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst. Biol. 57:4–14.

Ree, R. H., B. R. Moore, C. O. Webb, and M. J. Donoghue. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 59:2299–2311.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7:1–15.

———. 2006. Global variation in the diversification rate of passerine birds. Ecology 87:2468–2478.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity: regional and historical influences. Pp. 350–363 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. Univ. of Chicago Press, Chicago, IL.

Roelants, K., D. J. Gower, M. Wilkinson, S. P. Loader, S. D. Biju, K. Guillaume, and F. Bossuyt. 2007. Patterns of diversification in the history of modern amphibians. Proc. Natl. Acad. Sci. USA 104: 887–892.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.

Ronquist, F. 1994. Ancestral areas and parsimony. Syst. Biol. 43:267–274.

———. 1996. DIVA version 1.1. Computer program and manual available by anonymous FTP from Uppsala Univ. at ftp.uu.se or ftp.syst.bot.uu.se.

———. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst. Biol. 45:195–203.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, Cambridge, UK.

Schemske, D. 2002. Tropical diversity: patterns and processes. Pp. 163–173 *in* R. Chazdon and T. Whitmore, eds. Ecological and evolutionary perspectives on the origins of tropical diversity: key papers and commentaries. Univ. of Chicago Press, Chicago, IL.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. Am. Nat. 161:112–128.

Stevens, R. D. 2006. Historical processes enhance patterns of diversity along latitudinal gradients. Proc. R. Soc. Lond. B 273:2283–2289.

Stuart, B. L. 2008. The phylogenetic problem of *Huia* (Amphibia: Ranidae). Mol. Phylogenet. Evol. 46:49–60.

Svenning, J.-C., F. Borchsenius, S. W. Bjorholm, and H. Balslev. 2008. High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. J. Biogeogr. 35:394–406.

Swofford, D. L. 2002. PAUP*: phylogenetic analysis using parsimony*, version 4.0b10. Sinauer, Sunderland, MA.

Van Der Meijden, A., M. Vences, S. Hoegg, and A. Meyer. 2005. A previously unrecognized radiation of ranid frogs in Southern Africa revealed by nuclear and mitochondrial DNA sequences. Mol. Phylogenet. Evol. 37:674–685.

Wiens, J. J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. Syst. Biol. 52:528–538.

———. 2007. Global patterns of species richness and diversification in amphibians. Am. Nat. 170:S86–S106.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology, and species richness. Trends Ecol. Evol. 19:639–644.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Ann. Rev. Ecol. Evol. Syst. 36:519–539.

Wiens, J. J., and D. S. Moen. 2008. Missing data and the accuracy of Bayesian phylogenetics. J. Syst. Evol. 46:307–314.

Wiens, J. J., J. W. Fetzner, C. L. Parkinson, and T. W. Reeder. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. Syst. Biol. 54:719–748.

Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat. 168:579–596.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Ann. Rev. Ecol. Evol. Syst. 34:273–309.

Associate Editor: S. Steppan

Supporting Information

The following supporting information is available for this article:

Appendix S1. GenBank Numbers for DNA sequences used in the phylogenetic analyses.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).