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RESEARCH PAPER

# Is diversification rate related to climatic niche width?

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## ABSTRACT

**Aim** Diversification rates are critically important for understanding patterns of species richness, both among clades and among regions. However, the ecological correlates of variation in diversification rates remain poorly explored. Here, we test several hypotheses relating diversification rate and niche width across amphibian families (frogs and salamanders).

**Location** Global.

**Methods** We characterized climatic niches for 5784 amphibian species using databases for species distributions and climate. We estimated the niche width of each family using the range of values for climatic variables across all sampled species, and using the mean of species niche widths. We estimated diversification rates for families given their total number of described species and a time-calibrated phylogeny. We estimated relationships between variables using phylogenetic comparative methods.

**Results** We found a significant positive relationship between family niche width and diversification rate, but a weak relationship between mean species niche width and diversification rate, despite both niche width variables being correlated. In fact, the deviation from this relationship (i.e. residuals of family niche width versus mean species niche width) was the best predictor of diversification rate. The observed relationship between niche width and diversification was independent of clade range size and niche position (e.g. whether clades occurred in tropical or temperate climates) and significantly different from null patterns derived from random sampling effects.

**Main conclusions** Our results identify climatic niche width, and especially the relationship between family and species-level niche widths, as a major correlate of diversification rates among amphibian families. These results suggest that climatic niche divergence among species within clades can be important in explaining large-scale diversity patterns, possibly even more so than a clade's geographic area or whether it is primarily temperate or tropical.

**Keywords**
**Amphibians, diversification, niche conservatism, niche divergence, niche width, species richness.**

## INTRODUCTION

A major goal of ecology and evolutionary biology is to understand why certain clades (e.g. insects) and locations (e.g. the tropics) have more species than others. The diversification rates of clades are crucial for understanding both patterns (e.g. Ricklefs, 2007). The net diversification rate reflects the balance of speciation and extinction over time, and allows comparison among clades of different ages and assessment of ecological correlates of diversification. For example, several studies have shown faster diversification rates in tropical clades, which may help explain high tropical richness (e.g. Cardillo *et al.*, 2005;



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Ricklefs, 2006; Wiens, 2007; Condamine *et al.*, 2012; Pyron & Wiens, 2013).

Climatic niche width is a potentially important correlate of the variation in diversification rate among clades because niche width may be intimately related to speciation and extinction (e.g. Kozak & Wiens, 2010). However, the relationship between diversification rate and niche width has remained poorly explored. Note that we define the climatic niche as the large-scale conditions of temperature and precipitation where a species occurs (e.g. Soberón, 2007). Given this, the climatic niche width for a species can be estimated from the range of values for relevant climatic variables across its geographic range. A clade can also have a climatic niche width (Hadly *et al.*, 2009), defined here as the range across all localities for all species in that clade (for a given climatic variable).

No previous studies have statistically tested for a relationship between climatic niche width and diversification rate. However, some studies have provided important tests of related questions, which imply that such a relationship might be present. For example, Baselga *et al.* (2011) found that narrower climatic niches were associated with higher diversification rates in zopherine beetles, potentially associated with allopatric speciation via niche conservatism. Kozak & Wiens (2010) found a significant association between diversification rates and rates of climatic niche evolution in plethodontid salamanders, whereas Pyron & Wiens (2013) found no relationship between diversification rates and rates of climatic niche evolution across amphibian families. However, the rate of climatic niche evolution is not directly equivalent to climatic niche width, although they may be related (i.e. niche evolution reduces overlap between species niches, potentially increasing clade niche width). Fisher-Reid *et al.* (2012) found no relationship between the climatic niche widths of species and the rates of climatic niche evolution (although such a relationship was implied in previous studies; Smith & Beaulieu, 2009; Kozak & Wiens, 2010).

There could be a positive or negative relationship between climatic niche width and diversification rate, and these relationships could have several different causes (Table 1, Fig. 1). For example, a positive relationship could arise if clades with wide climatic niches were buffered from extinction caused by large-scale climatic fluctuations (e.g. glaciation). There might also be a strong positive relationship between clade-level niche width and diversification if speciation is driven primarily by climatic niche divergence (e.g. such that one species cannot tolerate the climatic conditions in which its sister species lives; e.g. Moritz *et al.*, 2000; Kozak & Wiens, 2007; Hua & Wiens, 2013). In this case, niche divergence would lead to parallel increases in both diversification rate and clade niche width. On the other hand, a negative relationship might arise if speciation is driven by climatic niche conservatism instead of divergence (i.e. species are geographically isolated by a climatically unsuitable habitat; e.g. Wiens, 2004; Kozak & Wiens, 2006; Hua & Wiens, 2013). If speciation via niche conservatism is common, then clades with narrower climatic niche widths may have higher rates of diversification, with the clade-level niche width reflecting the climatic similarity among species expected under niche conservatism (Baselga *et al.*, 2011).

There might also be more indirect relationships between climatic niche width and the diversification rates of clades (Table 1). For example, wider clade-level niches might be associated with larger geographic ranges, and greater area itself might increase diversification (e.g. buffering from extinction, promoting range fragmentation and allopatric speciation; Rosenzweig, 1995). Alternatively, diversification rate and climatic niche width might be negatively related because of higher diversification rates in tropical regions with species with narrow niches. However, even though the niche width for temperature-related climatic variables may be narrower in the tropics (e.g. Janzen, 1967; Ghalambor *et al.*, 2006), niche width for precipitation variables can be wider in tropical species (e.g. Vázquez & Stevens, 2004; Quintero & Wiens, 2013). Finally, a positive relationship between diversification rate and climatic niche width might appear artefactually because of sampling alone. Specifically, species-rich clades with higher diversification rates might have wider climatic niche widths merely because they include more species and collectively span more climatic regimes, with no causal relationship between diversification and niche width.

In this study we evaluate the relationship between niche width and diversification rate among the families of frogs and salamanders (i.e. all amphibians excluding the poorly known and species-poor caecilians). We explore both the family niche width and the mean value of niche width for all the species within each family, and how these two measures are related. We also test species richness, geographic extent and niche position as potential correlates of diversification that may covary with niche width. In addition we test competing hypotheses for why a relationship between niche width and diversification rate might be present (Table 1, Fig. 1). Amphibians are a good model system because range maps are available for most species (e.g. IUCN *et al.*, 2012), facilitating the estimation of their climatic niches. Moreover, the species composition, relationships and ages of families are relatively well studied and stable among recent studies (e.g. Roelants *et al.*, 2007; Wiens, 2007; Zhang & Wake, 2009; Pyron & Wiens, 2011; Wiens, 2011a; Zheng *et al.*, 2011; Gomez-Mestre *et al.*, 2012; Pyron & Wiens, 2013).

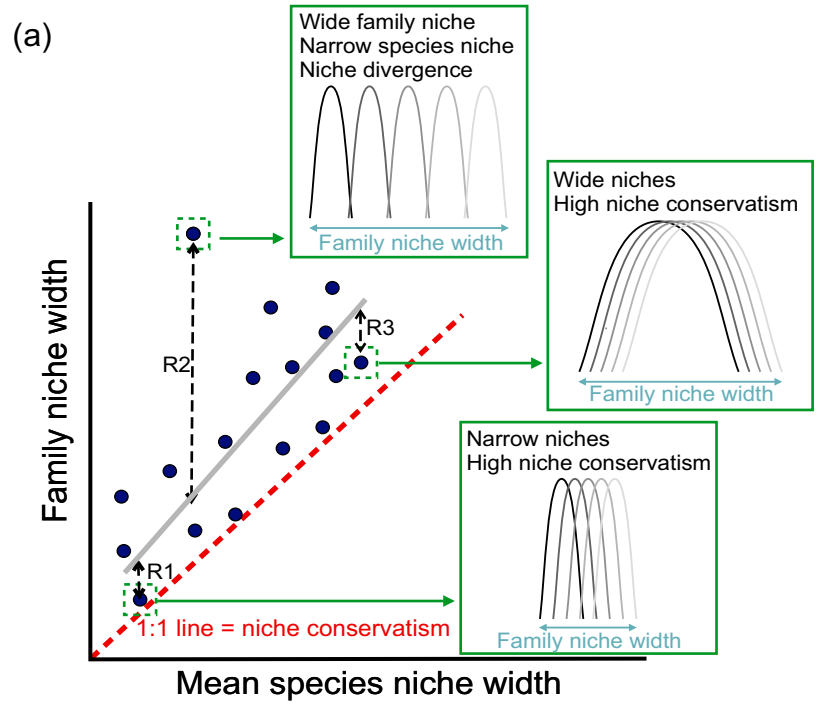
## MATERIAL AND METHODS

### Climatic niche widths

Distribution maps for 6037 amphibian species were downloaded from the Global Amphibian Assessment database (IUCN *et al.*, 2012) in October 2012, including almost all described frog and salamander species. These maps are based on documented records and expert knowledge. Climatic data, originally at 2.5-arc minute resolution, were downloaded from the WorldClim database (Hijmans *et al.*, 2005) and rescaled to a 1° resolution grid (*c.* 70 km) to make data handling computationally feasible. We acknowledge that this relatively coarse scale may create errors when estimating climatic niches for narrowly distributed

Table 1 Potential hypotheses accounting for a relationship between diversification rate and niche width among clades, including their rationales and predictions. See also Fig. 1 for hypotheses H1–H3.

| Hypothesis | Rationale | Predictions |
|---|---|---|
| H1: Narrower niches increase diversification via speciation through niche conservatism | If speciation via niche conservatism (e.g. Wiens, 2004; Hua & Wiens, 2013) is common, the probability of speciation should increase with narrower niches (Baselga *et al.*, 2011), increasing diversification rates | (1) Positive and strong relationship between clade-level niche width and mean species level niche width (reflecting high overlap among species niches within clade)<br>(2) Negative relationship between diversification rate and mean species niche width<br>(3) Negative relationship between diversification rate and clade-level niche width<br>(4) No relationship between diversification rate and the residuals from clade-level versus mean species niche widths regression |
| H2: Wider niches increase diversification via increased speciation through niche divergence | If speciation via climatic niche divergence is common (e.g. Moritz *et al.*, 2000; Hua & Wiens, 2013), clades with high niche divergence among species may have higher speciation and diversification rates | (1) Imperfect positive relationship between clade-level and mean species niche widths (imperfect because niche divergence increases the residuals)<br>(2) No relationship between diversification rate and mean species niche width<br>(3) Positive relationship between diversification rate and clade-level niche width<br>(4) Positive relationship between diversification rate and the residuals of clade-level versus mean species niche width regression |
| H3: Wider niches increase diversification via reduced extinction | Clades with wide climatic niches may be buffered from extinction caused by large-scale climatic fluctuations, leading to a positive relationship between niche width and diversification rate | (1) Positive relationship between clade-level and mean species niche widths<br>(2) Positive relationship between diversification rate and mean species niche width<br>(3) Positive relationship between diversification rate and clade-level niche width<br>(4) No relationship between diversification rate and the residuals of clade-level versus mean species niche width regression |
| H4: Wider niches indirectly related to diversification via geographic extent | Wider climatic niches of species may be associated with larger species ranges (and/or larger clade-level niche width may be associated with larger clade-level geographic area), and greater area itself could increase diversification rate, reducing extinction and promoting allopatric speciation (Rosenzweig, 1995) | (1) Positive relationship between diversification rate and geographic area of clade, potentially higher than that between diversification rate and clade-level niche width |
| H5: Niche width of clades indirectly associated with diversification rate via separate geographic effects on niche widths and diversification rates (e.g. narrower niches and faster diversification rates in tropics) | Niche widths for temperature tend to be narrower in the tropics (e.g. Janzen, 1967; Ghalambor *et al.*, 2006), but niche widths for precipitation tend to be wider in the tropics (e.g. Vázquez & Stevens, 2004; Quintero & Wiens, 2013). Many studies show faster diversification rates in the tropics (e.g. Condamine *et al.*, 2012; Pyron & Wiens, 2013), but not all (e.g. Wiens *et al.*, 2006, 2009) | (1) Positive relationship between diversification rate and the position (i.e. central tendency) of clade niche, instead of with niche width |
| H0: Artefactual relationship between diversification and clade-level niche width via sampling more species | Diversification rate would control species richness, whereas richness of clades alone would drive clade-level niche width (i.e. reversed causality) by increasing the probability of sampling a wider set of environmental conditions by chance alone | (1) Strong positive relationship between diversification rate and species richness of clades<br>(2) Positive relationship between clade-level and mean species niche widths<br>(3) Positive relationship between diversification rate and mean species niche width<br>(4) Positive relationship between diversification rate and clade-level niche width<br>(5) No or weak relationship between diversification rate and the residuals of clade-level versus mean species niche width regression, since speciation would not be related to niche conservatism or divergence |



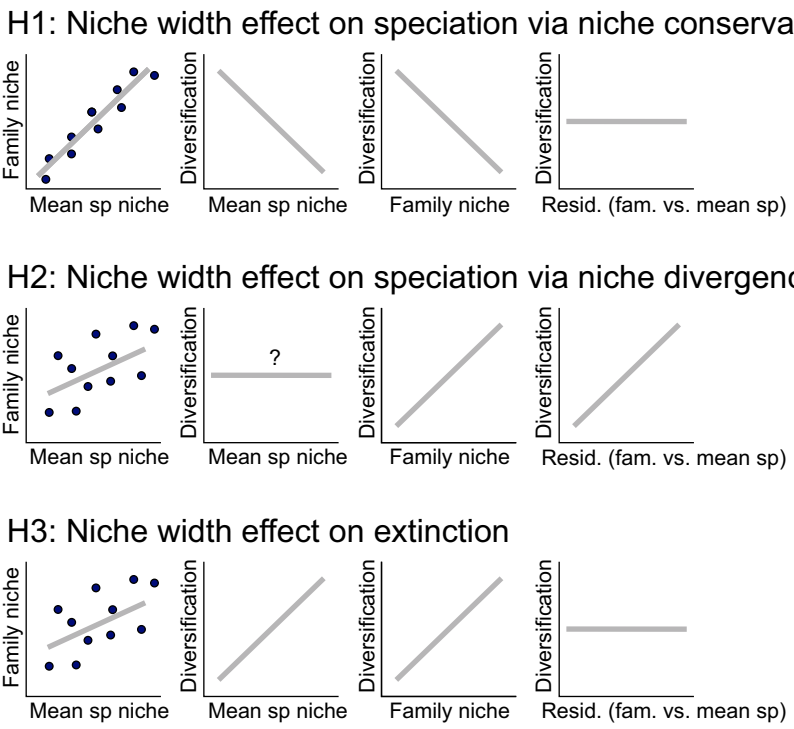




**Figure 1** Schematic representation of (a) the predicted relationships between clade-level (i.e. family) niche width and within-family mean species niche width and of (b) relationships with diversification rate under three major hypotheses considering the effects of niche width on speciation (either via niche conservatism in H1 or via niche divergence in H2) or extinction (H3). Note that the residuals of the relationship between family and mean species niche widths account for niche divergence (i.e. deviations from perfect niche conservatism). See hypotheses H1–H3 in Table 1 for further development of these predictions.

montane species; however, this issue does not prevent us from finding significant patterns (see Discussion).

The selection of climatic variables followed previous studies of niche width in amphibians (e.g. Quintero & Wiens, 2013; Bonetti & Wiens, 2014): annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the wettest quarter (BIO16) and precipitation of the driest quarter (BIO17). These represent standard measures of yearly average and extremes. For precipitation, we considered quarterly values to be more relevant than monthly extremes (i.e. a 3-month drought is more

challenging for population survival than a 1-month drought). Spearman correlations among mean values of these variables are provided in Appendix S1 in Supporting Information. Range maps were converted to 1° resolution to fit the climatic data. Two hundred and fifty-three species with very small ranges could not be converted to this resolution due to software limitations and were eliminated, giving a total of 5784 species for the evolutionary analyses. The GIS analyses were done in Idrisi 14.02 (Clark Labs, Worcester, MA, USA) except estimates of range area, which were computed in gvsig 1.10 (free/open source software; http://www.gvsig.org).

For each family, climatic niche width was estimated based on the range of environmental conditions across all species in the family (family niche width) and on the mean species niche width across all species (mean species niche width). For family niche width, all species in the family were merged to form a single distributional area. Then the range, i.e. Rg = max(var) – min(var), for each climatic variable was computed across this area, and standardized by subtracting the minimum range value across all families and then dividing it by the difference between the maximum and minimum values of ranges across families. That is, for a given family $i$ in a dataset with $j$ families: $StRg_i = [Rg_i - \min(Rg_1{:}Rg_j)]/[\max(Rg_1{:}Rg_j) - \min(Rg_1{:}Rg_j)]$. This yields a value between 0 and 1. Standardization was required to remove the effect of different units (temperature versus precipitation). The overall niche width for a family was computed by multiplying the standardized ranges of all six climatic variables to obtain the niche hypervolume. Temperature niche width was based on multiplying standardized ranges for BIO1, BIO5 and BIO6. Precipitation niche width was based on multiplying standardized ranges for BIO12, BIO16 and BIO17. Species niche width was computed following the same protocol but applied to the range of climatic values across the grid cells for each species for a given climatic variable. The mean species niche width was then the average niche width of all species within the family. For each climatic variable and taxon, niche position was computed as the average of all observed values in its distribution range. Again, in the case of the family niche, all species in the family were merged to form a single distributional range.

### Diversification rates

Diversification rates for each family were initially estimated given the number of species in the family and the family's stem age (Fig. 2). The number of species belonging to each family was estimated from the Global Amphibian Assessment database (IUCN *et al.*, 2012; downloaded October 2012). In some cases the IUCN taxonomy (i.e. assignment of a genus to a family) was updated to follow a more recent, phylogeny-based classification (i.e. Pyron & Wiens, 2011). Family ages (divergence dates) were extracted from two time-calibrated phylogenies: Gomez-Mestre *et al.* (2012) for Anura ('fixed ages' tree) and Wiens (2007) for Caudata (using the intermediate crown-group age of 210 Myr). The tree of Gomez-Mestre *et al.* (2012) is based on multiple nuclear and mitochondrial genes and is largely concordant with previous studies in topology and clade ages (Roelants *et al.*, 2007; Pyron & Wiens, 2011; Wiens 2011a). The tree of Wiens (2007) is based on extensive taxon sampling in salamanders with a slowly evolving nuclear gene (*RAG-1*) and multiple fossil calibration points. Other time-calibrated trees are available for salamanders, but give similar results and are based on more limited taxon sampling. For example, the tree preferred by Zheng *et al.* (2011; their Fig. 3) from multiple nuclear genes gives a similar topology and dates but lacks two salamander families. The estimated trees preferred by Roelants *et al.* (2007; their Fig. 1) and Zhang & Wake (2009) for salamanders also have similar topologies and dates, although they estimate several clades as somewhat older and younger (respectively) than Wiens (2007) or Zheng *et al.* (2011).

These anuran and salamander trees were combined for comparative analyses assuming that the most recent common ancestor of anurans and caudates had a crown-group age of 332.2 Myr (from Wiens, 2011a), although this date does not influence estimates of diversification rates or niche widths and should have negligible impact on other comparative analyses. Representatives of Micrixalidae (11 species; AmphibiaWeb, 2013), Nyctibatrachidae (29 species) and Telmatobiidae (61 species) were not included by Gomez-Mestre *et al.* (2012) and are not included here. Batrachylidae (15 species) was also excluded because it was not monophyletic in their tree. Overall, few species were excluded relative to the overall amphibian diversity sampled (5784 species) and many families remained for analysis ($n = 57$).

Diversification rates for each family were estimated from species richness and family age using the method-of-moments estimator for stem groups from Magallón & Sanderson (2001). These estimators incorporate extinction rates into the estimation of diversification rate (rather than simply using log-richness over age). Stem-group ages were used since crown-group ages would require more complete sampling of species (or at least genera) in each family and cannot incorporate monotypic families, whereas stem-group ages require only a single species be sampled per family and can include monotypic families. Given that relative extinction rates ($\varepsilon$, where $\varepsilon$ is the speciation rate/extinction rate) were unknown, three different values were considered (no extinction, $\varepsilon = 0.0$; intermediate extinction, $\varepsilon = 0.45$; high extinction, $\varepsilon = 0.9$), following standard practice (e.g. Magallón & Sanderson, 2001; Wiens, 2007; Kozak & Wiens, 2010). However, these different values generally gave concordant results in our comparative analyses and only those for $\varepsilon = 0.45$ are presented (see Appendix S4 for additional results). Estimated diversification rates and niches widths are provided in Appendix S2.

An alternative time-calibrated tree containing 2871 species (Pyron & Wiens, 2013) has recently become available and was used to address the robustness of the results to somewhat different clades ages, tree topology and diversification rate estimates. Pyron & Wiens (2013) provided stem- and crown-group ages for almost all amphibian families. We calculated diversification rates for both ages, using the method-of-moments

estimators and $\varepsilon = 0.45$. Despite the potential underestimation of crown ages given incomplete sampling, the extensive genus-level sampling in this tree (86% complete) suggests that the crown-group age estimates should be reasonable (see Pyron & Wiens, 2013). We also included their diversification rate estimates based on the method of Nee *et al.* (1994), which incorporates all species in these families, both sampled and unsampled (Pyron & Wiens, 2013).

### Comparative phylogenetic analyses

Analyses were conducted using comparative phylogenetic methods given that families may share diversification rates, niche widths and other traits due to a shared phylogenetic history. We evaluated the phylogenetic signal and best-fitting evolutionary model for each response variable with the fitContinuous function (in *geiger*; Harmon *et al.*, 2008). Four

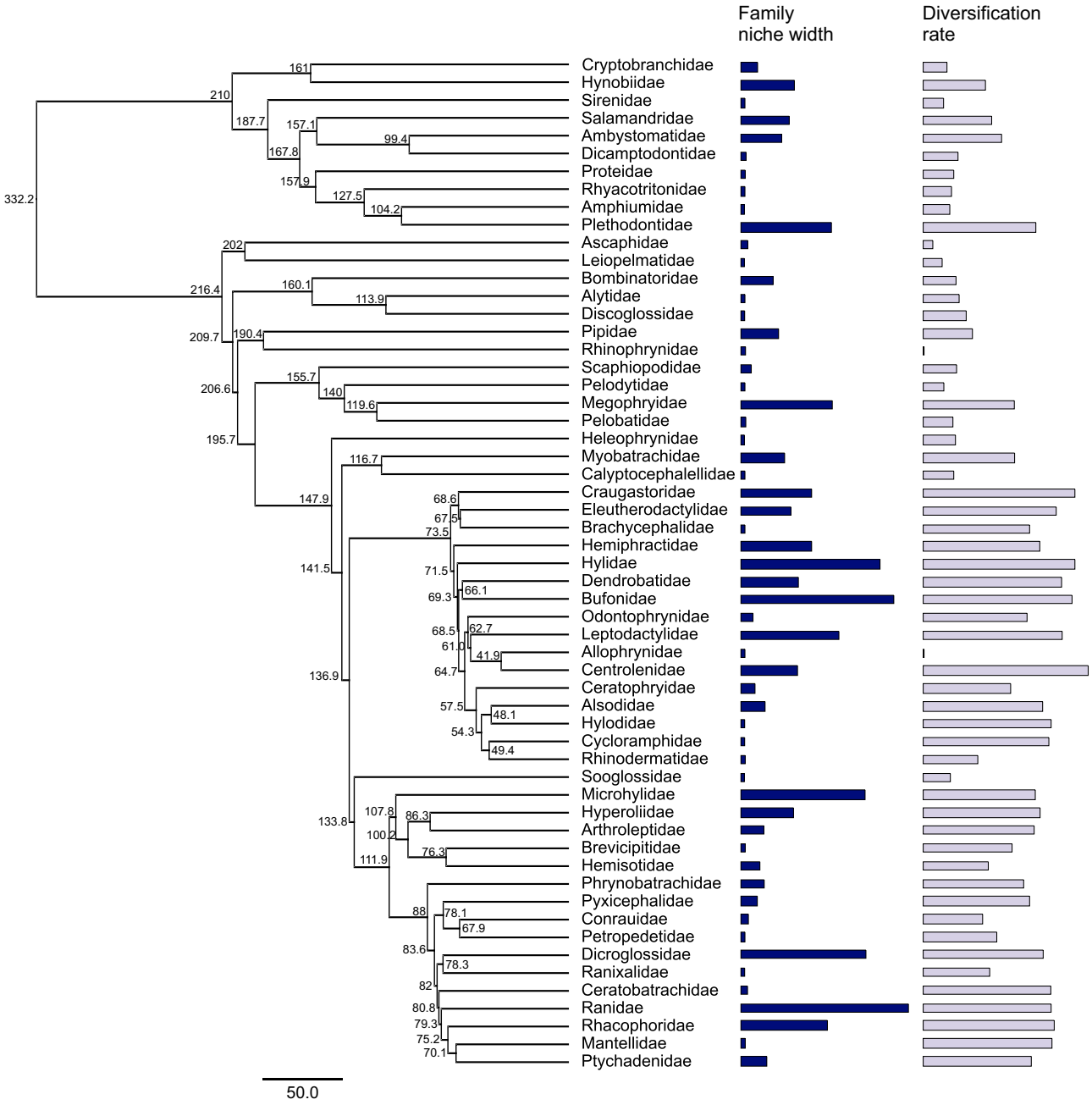



Figure 2 Time-calibrated phylogeny of the amphibian families used in this study. Node values are stem ages. Bars represent family niche width and diversification rate. Niche width and diversification rate were log-transformed (natural logarithm). Original data are available in Appendix S2.

evolutionary models [Brownian motion, BM; Ornstein–Uhlenbeck, OU; lambda; and no phylogenetic signal (white noise, WN)] were compared based on their size-corrected Akaike information criterion score (AICc) (Burnham & Anderson, 2002). The best-fitting evolutionary model for both family-level and species-level niche widths was the WN model (Appendix S3). Therefore, a simple linear regression was conducted in this case. In contrast, the best-fitting evolutionary model for diversification rate was lambda (Appendix S3), with lambda = 0.608. Thus, for analyses involving diversification rates, a phylogenetic generalized least-squares regression (PGLS) (Martins & Hansen, 1997) was conducted with the R package *caper*, version 0.5 (Orme *et al.*, 2012), after transforming branch lengths based on estimated lambda. Prior to PGLS analyses, the tree was reduced to one arbitrarily selected species per family (Fig. 2). Note that all species in a family share the same stem age. All variables were natural-log transformed to improve the normality of model residuals, including diversification rates, niche widths, area and climatic variables.

Linear regression was conducted to assess the relationship between family and species niche widths since the best-fitting model for these variables was WN. This relationship provides an index of niche overlap and divergence within families (Fig. 1): with perfect niche conservatism, species and family niches are equivalent (i.e. no residuals), whereas residuals reflect non-overlap of species niches (niche divergence) within families.

Relationships between diversification rate (response variable) and niche width (family and mean species) were assessed using PGLS. To assess the relationship between diversification rate and niche divergence (among species in a family) we performed a PGLS analysis using diversification rate as the response variable and the residuals from the regression between family and mean species niche widths as the predictor variable. These relationships were also assessed with diversification rates estimated from the alternative tree and the results are provided in Appendix S5.

The independent effects of temperature and precipitation on diversification rates were also assessed (PGLS analysis with

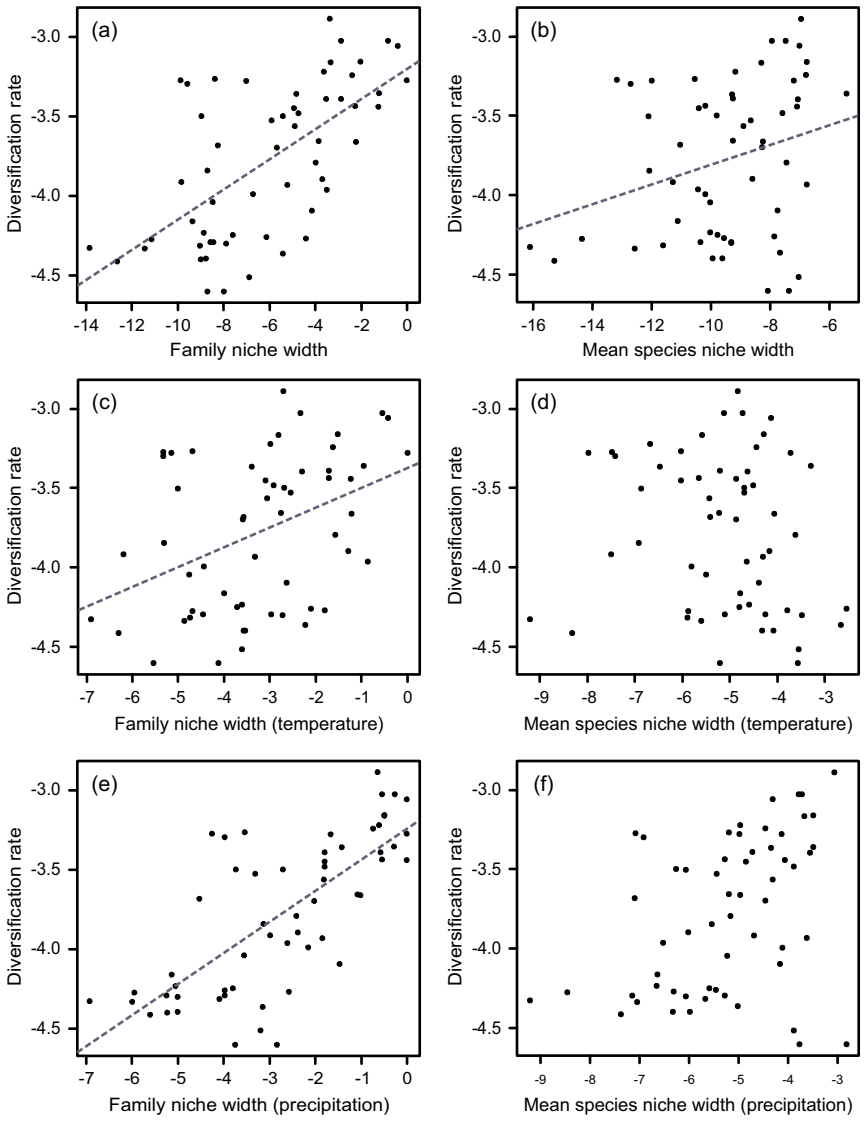



Figure 3 Scatterplots of the relationship between diversification rate ($\varepsilon = 0.45$) and niche width variables. Results are shown both for the family niche width (a, c, e) and the mean species niche width (b, d, f) as well as for the overall niche width (a, b), the temperature niche width (c, d) and the precipitation niche width (e, f). Variables are log-transformed (natural logarithm). For significant relationships, Ordinary Least Squares regression lines are provided for visual clarity only.

diversification rate as the response variable and temperature and precipitation niche width as potential predictors). The relevance of each variable was evaluated using a forward stepwise procedure based on their significant contribution to the model. Thus, univariate models were compared with the intercept-only model (command 'anova' in R) and the best univariate model was compared with the full model (i.e. including both variables). Analyses were conducted independently for family and mean species niche widths.

To evaluate whether the effects of niche width on diversification rate were due to an indirect effect of geographic extent or niche position, a PGLS model was built for each hypothesis (i.e. diversification rate versus niche width; diversification rate versus niche position; diversification rate versus geographic extent). Since niche position was described by the six climatic variables, a forward step-wise procedure based on significant contribution was used to select the most parsimonious model explaining diversification rate with niche position information. The basic models for each hypothesis allowed the identification of significant variables for inclusion in the full model. The unique and shared contribution of each variable was assessed by means of variance partitioning on the full model.

Finally, null models were used to test if the observed relationship between diversification rate and niche width might be an artefact of high diversification rates driving high clade species richness, with higher richness then driving wider family niches (rather than wider niches driving diversification). First, a PGLS analysis was conducted to test the relationship between diversification rate and species richness. Second, three null models were used (each sampling with replacement) testing whether observed relationships between diversification rate and niche width differ from relationships between diversification rate and null niche width estimated from randomly sampled species pools of richness equivalent to real families (without any causal relationship between niche width and clade diversification).

**1.** Unconstrained: the number of species in each family is randomly sampled from the world-wide pool of 5784 species.

**2.** Spatially constrained: sampling only species within the latitudinal and longitudinal range of each family. With this model, we correct for the fact that randomly chosen species could come from distant regions with very different climates, unrealistically increasing null-family niche widths.

**3.** Climatically constrained: sampling only species within the ranges of BIO1, BIO5, BIO6, BIO12, BIO16 and BIO17 observed for each family.

Niches were calculated as for the empirical data. The relationship between null-family and null-mean species niche widths was assessed using linear regression. Three univariate PGLS analyses were conducted using observed diversification rate as the dependent variable and null-family niche width, null-mean species niche width and null-model residuals (from linear regression between null-family niche width and null-mean species niche width) as predictors. The distributions of $R^2$ parameters in these regressions were computed across 1000 replicates and compared with observed $R^2$ values.

All phylogenetic analyses were done in R 3.0 (R Development Core Team, 2011).

## RESULTS

Diversification rate showed a significant, positive relationship with niche width, and more variance in diversification rate was explained by family niche width (43%) than by mean species niche width (8%) (Table 2, Fig. 3). This result was surprising given the significant positive relationship between family and mean species niche widths ($R^2 = 0.63$, $F_{1,55} = 94.38$, $P < 0.001$; Fig. 4). The latter result suggests that it is the variation in family niche width that is independent of mean species niche width that explains the variation in diversification rates. This hypothesis was confirmed by regressing diversification rate against the residuals of the family versus mean species niche width relationship: the variance explained by the residuals was larger than the variance explained by family niche width (PGLS, $R^2 = 0.53$, $F_{2,55} = 61.37$, $P < 0.001$). Thus, diversification rates seem to be related to niche divergence. Results were similar using the alternative tree and alternative measures of diversification rate (see Appendices S4 & S5).

When the effects of temperature and precipitation were assessed independently, a relationship with diversification rates was significant for family niche width but not for mean species niche width (Table 2, Fig. 3). Despite both variables being significant in univariate models of family niche width (Table 2), a stepwise procedure showed that temperature niche width did

Table 2 Results from univariate phylogenetic generalized least-squares (PGLS) regression models assessing the relationship between diversification rate ($\varepsilon = 0.45$) and niche width variables, niche position variables and geographic extent. Niche is computed considering the family-level niche (i.e. the range of environmental conditions across all species in the family) and (separately) the mean value of all species niche widths within the family.

| | Family niche | | | Mean species niche | | |
|---|---|---|---|---|---|---|
| | $R^2$ | $F$ | $P$-value | $R^2$ | $F$ | $P$-value |
| Niche width | 0.43 | 41.4 | **< 0.001** | 0.08 | 4.73 | **0.013** |
| T niche width | 0.34 | 28.1 | **< 0.001** | 0.01 | 0.287 | 0.752 |
| P niche width | 0.43 | 40.8 | **< 0.001** | 0.05 | 3.08 | 0.054 |
| Geographic extent | 0.27 | 19.9 | **< 0.001** | 0.00 | 0.000 | 1.000 |
| Niche position: | | | | | | |
| BIO1 (mean T) | 0.00 | 0.205 | 0.815 | 0.06 | 3.52 | **0.037** |
| BIO5 (max. T) | 0.04 | 2.13 | 0.128 | 0.00 | 0.037 | 0.964 |
| BIO6 (min. T) | 0.00 | 0.012 | 0.989 | 0.07 | 3.91 | **0.026** |
| BIO12 (annual P) | 0.00 | 0.154 | 0.858 | 0.05 | 2.96 | 0.060 |
| BIO16 (max. P) | 0.00 | 0.112 | 0.894 | 0.04 | 2.04 | 0.140 |
| BIO17 (min. P) | 0.00 | 0.107 | 0.898 | 0.07 | 4.14 | **0.021** |

The explained variance ($R^2$), $F$-value and $P$-value are provided. Degrees of freedom are 2,55 in all models. Significant $P$-values are highlighted in bold.

P, precipitation; T, temperature.

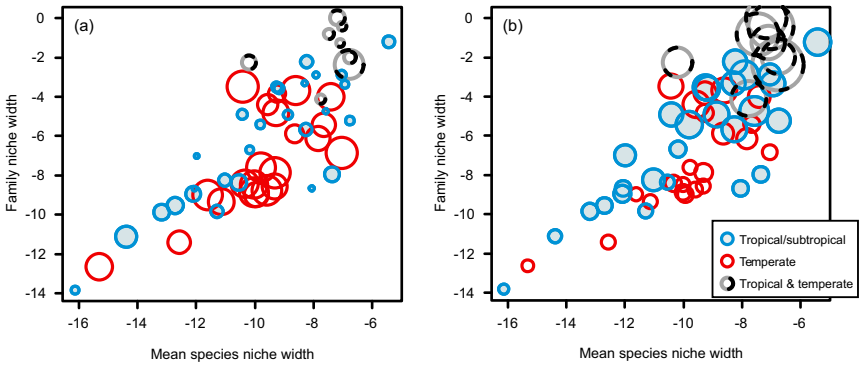



Figure 4 Scatterplot of the relationship between family niche width and mean species niche width. Variables are log-transformed (natural logarithm). The size of the circles corresponds to mean absolute latitude (a) or latitudinal range (b). Note: tropical/subtropical families are those with maximum absolute latitude < 36°, except Dicroglossidae and Ceratophryidae (40°); temperate families have maximum absolute latitude > 38°; tropical and temperate families have latitudinal range > 70°.

not make a significant contribution to explaining diversification rate once precipitation niche width was included in the model ($F_{1,54} = 1.47$, $P = 0.230$; see Appendix S6). In fact, the variance explained by precipitation niche width was almost identical to the variance explained by the overall niche width including both temperature and precipitation (Table 2). Thus, these analyses identify precipitation niche width specifically as a major driver of variation in diversification rates in amphibians.

To evaluate whether the effect of niche width on diversification rate was due to an indirect effect of niche position, the niche position model had to be defined first. Univariate PGLS models of the relationship between diversification rate and niche position showed that none of the six climatic variables were significant in the analyses of family niche (Table 2). Thus, the niche position hypothesis was not supported. In the case of mean species niche, the variables annual mean temperature (BIO1), minimum temperature of the coolest month (BIO6) and precipitation of the driest quarter (BIO17) all showed a significant relationship with diversification rate (Table 2). However, a stepwise procedure showed that once BIO17 was introduced into the model the other climatic variables did not significantly contribute to explaining diversification rate (addition of BIO1, $F_{1,54} = 2.74$, $P = 0.103$; addition of BIO6, $F_{1,54} = 2.78$, $P = 0.101$). Therefore, the final niche position model for mean species niche was the one that included only precipitation of the driest quarter (BIO17).

In analyses using family niche variables, both niche width and geographic extent had a significant relationship with diversification rate in univariate PGLS models (Table 2). However, variance partitioning showed that the unique contribution of geographic extent was negligible (explained variance = 0.15%), with its effect completely nested within the effect of niche width (Table 3). In contrast, the unique contribution of niche width was 16.5%, representing more than 38% of the total variance explained. Thus, family niche width explains substantial variation in diversification rate that cannot be attributed to geographic extent or niche position. In univariate PGLS models for mean species niche variables both niche width and niche position had a significant relationship with diversification rate while geographic extent did not (Table 2). Both variables had a similar unique contribution and the shared variance was very low (0.2%). Thus, the inclusion of niche position improved the PGLS model explaining diversification rate, but the total variance explained by niche position was low (6.8%).

Table 3 Variance partitioning showing the contribution of unique and shared predictors to the full phylogenetic generalized least-squares (PGLS) regression models of diversification rate. The total explained variance of the full model is shown. Niche width is computed considering the family-level niche (i.e. the range of environmental conditions across all species in the family) and (separately) the mean value of all species niche widths within the family).

| | Diversification rate | |
|---|---|---|
| | Family niche | Mean species niche |
| Niche width (unique contribution) | 16.51% | 7.75% |
| Geographic extent (unique contribution) | 0.15% | n.s. |
| Niche position (unique contribution) | n.s. | 6.83% |
| Shared contribution | 26.41% | 0.17% |
| Total explained variance | 43.07% | 14.75% |

n.s., non-significant variables (see Table 2 for details) that were not included in the full model.

Diversification rate showed a strong, positive relationship with family species richness (PGLS, $R^2 = 0.86$, $F_{2,55} = 336.5$, $P < 0.001$). However, the observed $R^2$ between diversification rates and species and family niche widths are significantly lower than expected from the null-model $R^2$ ($P < 0.025$ in all models; see Appendix S7 for details), suggesting that the observed patterns differ from those expected from species richness alone. Similarly, the observed $R^2$ between diversification rate and model residuals (from family versus species niche widths) is significantly higher ($P < 0.001$) than expected from the null-model $R^2$ for both the spatially and climatically constrained

null models, but not the unconstrained model ($P = 0.176$). Null models also showed that the observed $R^2$ between family and mean species niche widths is significantly lower than expected from the null-model $R^2$ ($P < 0.001$), except for the unconstrained model ($P = 0.491$). Thus, the null models suggest that niche divergence among species within families is higher than expected by chance under the constrained models, and equivalent to randomly sampling species across the globe (see Appendix S7 for more details).

## DISCUSSION

In this paper, we provide the first large-scale test of whether clades with wider climatic niche widths have faster rates of species diversification. Our results strongly support the idea that families with wider niches tend to have faster diversification rates. Remarkably, we find that family niche width shows a stronger relationship with diversification rate than either geographic area or niche position (e.g. whether clades are temperate or tropical). Moreover, the relationships between diversification rate and species niche width, family niche width and niche divergence are significantly different from null expectations derived from a random, constrained accumulation of species, suggesting a mechanistic process linking higher diversification rates with family niche width through greater niche divergence. Finally, we specifically identify precipitation as the most important aspect of niche width related to diversification rates in amphibians.

Our results raise the obvious question: why do we see this relationship between family climatic niche width and diversification rate? In Table 1 we described three possible mechanistic explanations: speciation through climatic niche conservatism, leading to a negative relationship between diversification rate and niche width (H1); speciation through climatic niche divergence, leading to a positive relationship between diversification rate and niche width (H2); and wider climatic niches buffering species and clades from extinction, leading to a positive relationship between diversification rate and niche width (H3). Alternatively, non-causal links might also explain a positive relationship between diversification rate and niche width, including: wider climatic niches allowing for larger geographic ranges, and range size itself influences diversification more directly (H4); differences in diversification rate are associated with the distribution of narrow-niched clades in tropical regions (H5); and species richness is related to niche width due to random sampling of species niches in more species-rich clades (H0).

Our results are clearly inconsistent with these three latter non-causal hypotheses (H4, H5, H0). First, we find that wider climatic niches do not facilitate faster diversification by allowing greater range expansion. In fact, we find that the geographic extent of clades (H4) explains less variation in diversification rate than niche width and makes no unique contribution to the variation already explained by niche width (Table 3). Likewise, niche position (H5) is not a strong predictor of diversification rate (Tables 2 & 3). Finally, significant differences between observed parameters and those predicted by null models suggest that the relationships between diversification rate and species and family niche width and niche divergence are not the outcome of sampling effects (H0).

Our results are also inconsistent with the niche conservatism and extinction hypotheses. We reject the idea that speciation driven by niche conservatism drives higher rates of diversification across amphibian families (H1), given that we find wider family-level climatic niches in more rapidly diversifying families (supporting niche divergence rather than conservatism). Support for the buffered extinction hypothesis (H3) is also limited. Based on our results, the extinction hypothesis does not seem to operate at the species level by wider niches reducing the probability of extinction (buffering individual species from extinction), because the relationship between species-level niche width and diversification rate is relatively weak. However, families with wider niches, in combination with low species niche overlap, might suffer less extinction than families with high species niche overlap, given the potentially increased risk of extinction when all species occupy a similar climatic niche (i.e. families with narrow climatic niches have effectively put all their eggs in one climatic basket). Moreover, the extinction hypothesis does not predict a strong correlation between diversification rate and niche divergence (see also below).

In contrast, our results are mostly compatible with the speciation through niche divergence hypothesis (H2). This hypothesis assumes that family-level climatic niches are wider because of lack of overlap between species climatic niches. This interpretation is confirmed by finding that the residuals of the relationship between family- and species-level niche widths explain even more variation in diversification rate than family niche width. Moreover, the observed relationship between diversification rate and niche divergence is higher than expected from the null models, even though the relationships with niche widths are lower than expected. Thus, despite wider family-level niches being associated with wider species niches, it is the reduction in overlap of climatic niches among species (i.e. residuals between family- and species-level niche widths) that is associated with higher diversification rates. Under perfect niche conservatism we would expect complete overlap of species niches within families and a perfect relationship between mean species and overall family-level niche widths. Thus, the scatter of points (i.e. dispersion on the *y*-axis) reflects relative differences in the degree of overlap of species niches within families and can be interpreted as a surrogate of niche divergence among species within a family. However, the niche divergence hypothesis also predicts that there is no relationship between diversification rate and mean species niche width, as there is no evidence that narrow niches facilitate niche divergence (Fisher-Reid *et al.*, 2012). We observe a positive, albeit weak, relationship, suggesting that additional processes may be involved. Of course, results that support a hypothesis do not necessarily rule out all other possible hypotheses, as other mechanisms (not directly assessed) might instead explain the observed patterns. We emphasize that our main goal was to test the relationship between diversification rate and niche width, and not necessarily resolve the causes of this relationship.

All these hypotheses will need to be tested more thoroughly with further analyses. For example, future studies could attempt to parse out the contributions of speciation and extinction to the relationship between diversification rate and niche width, using more detailed phylogenies and additional methods (e.g. FitzJohn *et al.*, 2009). We note that Pyron & Wiens (2013) provided estimates of extinction rates for many amphibian families. Our initial analyses (Appendix S8) show that these estimated extinction rates are not significantly related to family niche widths or to the residuals of the relationship between family and species niche widths. Thus, these results further support the idea that wider niches increase diversification by promoting speciation, not reducing extinction. Future studies could also test for greater climatic niche divergence between sister species (e.g. Kozak & Wiens, 2007; Hua & Wiens, 2010; Cadena *et al.*, 2012) in more rapidly diversifying families to address the role of niche divergence in speciation.

We do acknowledge several potential issues in our analyses. First, our climatic data are at a relatively coarse spatial scale, and this may obscure important climatic variation at fine spatial scales in montane regions. However, it seems that the coarseness of our climatic data should increase the noise in our data instead of leading to statistically significant relationships with diversification rate, as we have found. We note that some analyses with more fine-scale climatic data (i.e. Kozak & Wiens, 2010) show a strong relationship between rate of climatic niche divergence and rate of diversification (consistent with our results), whereas others do not (i.e. Pyron & Wiens, 2013). However, the climatic data analysed by Pyron & Wiens (2013) to estimate rates of niche evolution emphasized temperature differences between tropical and temperate regions (i.e. using principal component 1 from a multivariate analysis) and may not reflect the precipitation variables that seem to drive diversification patterns here. Also, our analyses may not incorporate all relevant aspects of the climatic niche. But again this might explain a non-significant result, rather than a significant relationship. Second, some authors have questioned the value of estimating net diversification rates because of the potential for rates to vary over time (e.g. Rabosky, 2009b). However, regardless of changes over time, the net diversification rate of a clade (the outcome of speciation and extinction over time) is still of considerable intrinsic interest. The most problematic situation is if diversification rates of clades are decoupled from their species richness (Wiens, 2011b), but we found that diversification rate and species richness have a tight relationship among amphibian families. We also acknowledge that our analyses are based on utilizing amphibian families as units. Although the families used are demonstrably monophyletic they are somewhat arbitrary, since there are many other possible ways to partition species into clades. However, the use of families as units allowed us to incorporate information from 5784 species even though the largest amphibian phylogenies to date include fewer than half of these (e.g. Pyron & Wiens, 2011). Furthermore, we reiterate that fine-scale analyses (i.e. within Plethodontidae) are broadly consistent with our findings (Kozak & Wiens, 2010).

In conclusion, we find strong support for the hypothesis that clades with faster diversification rates tend to have wider climatic niches and greater climatic divergence among their species. The causes of this pattern are not yet clear. Nevertheless, we show that the observed relationships are not the outcome of sampling effects and that climatic niche width and divergence explain substantially more variance in diversification rate than either geographic extent or climatic niche position. These results contrast with previous studies showing the general importance of geographic range area to clade diversity and diversification (e.g. Losos & Schluter, 2000; Rabosky, 2009a) and the importance of niche position for amphibian diversity and diversification (e.g. Buckley & Jetz, 2007; Pyron & Wiens, 2013). Overall, our results show a potentially important new pattern in macroevolution and macroecology, and suggest the need for additional, finer-scale studies in amphibians and similar broad-scale studies in other groups.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** Spearman rank correlations among bioclimatic variables.

**Appendix S2** Species richness, stem age, diversification rates and niche widths of amphibian families.

**Appendix S3** Size-corrected Akaike information criterion (AICc) values for the evolutionary models for diversification rate and niche width variables.

**Appendix S4** Supplementary results considering alternative values of relative extinction rate.

**Appendix S5** Supplementary results using an alternative time-calibrated tree (Pyron & Wiens, 2013).

**Appendix S6** Comparison of phylogenetic generalized least-squares regression models for the relationship of diversification rate with temperature niche width and precipitation niche width.

**Appendix S7** Supplementary results from the null models of the relationship between diversification rate and niche width.

**Appendix S8** Supplementary analyses of the relationship between estimated extinction rate and niche width.

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