Microhabitat and Climatic Niche Change Explain Patterns of Diversification among Frog Families

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ABSTRACT: A major goal of ecology and evolutionary biology is to explain patterns of species richness among clades. Differences in rates of net diversification (speciation minus extinction over time) may often explain these patterns, but the factors that drive variation in diversification rates remain uncertain. Three important candidates are climatic niche position (e.g., whether clades are primarily temperate or tropical), rates of climatic niche change among species within clades, and microhabitat (e.g., aquatic, terrestrial, arboreal). The first two factors have been tested separately in several studies, but the relative importance of all three is largely unknown. Here we explore the correlates of diversification among families of frogs, which collectively represent ~88% of amphibian species. We assemble and analyze data on phylogeny, climate, and microhabitat for thousands of species. We find that the best-fitting phylogenetic multiple regression model includes all three types of variables: microhabitat, rates of climatic niche change, and climatic niche position. This model explains 67% of the variation in diversification rates among frog families, with arboreal microhabitat explaining ~31%, niche rates ~25%, and climatic niche position ~11%. Surprisingly, we show that microhabitat can have a much stronger influence on diversification than climatic niche position or rates of climatic niche change.

Keywords: Anura, amphibians, climatic niche, diversification, ecology, evolution, phylogeny.

Introduction

Clades often differ dramatically in their species richness. Understanding the causes of this variation is a major challenge for both ecology and evolutionary biology. Two general hypotheses can explain differences in richness of clades. First, clades with more species may be older and thus have had more time to accumulate richness through speciation. Second, clades with more species may have faster rates of net diversification, where net diversification is the balance of spe-

ciation and extinction over time (e.g., Nee 2006; Ricklefs 2007; Wiens 2011). Thus, younger clades with more species will have faster rates of net diversification, and older clades with fewer species will have slower rates. Recent analyses suggest that most variation in richness among clades of the same taxonomic rank (e.g., families or phyla) is explained by variation in diversification rates and not clade ages (e.g., Scholl and Wiens 2016). What remains unclear is what causes this variation in diversification rates.

Numerous ecological and evolutionary factors have been proposed (and tested) as correlates of diversification rates. These factors include climatic niche position (e.g., occurrence in tropical vs. temperate climates; Pyron and Wiens 2013; Rolland et al. 2014), body size and sexual-size dimorphism (De Lisle and Rowe 2015), diet (Price et al. 2012; Wiens et al. 2015), habitat (e.g., marine vs. nonmarine; Wiens 2015b), defense mutualisms (Weber and Agrawal 2014), parasitism (e.g., Jezkova and Wiens 2017), and rates of change in climatic niches (e.g., Kozak and Wiens 2010; Schnitzler et al. 2012) and body sizes (e.g., Adams et al. 2009; Rabosky et al. 2013). However, most studies have each focused on only a single predictor variable. Therefore, it is difficult to make strong conclusions about which general types of variables may be the most important in driving patterns of diversification and richness among clades. For example, are traits related to local-scale resources and species interactions (e.g., diet, microhabitat, defense) as important as factors related to the large-scale distribution of species or clades (e.g., climatic niches)? Are variables describing changes in trait values (dynamic traits, sensu Wiens 2017) as important as those describing particular trait values (static traits)?

Here we use anuran amphibians (frogs and toads; hereafter, frogs) as a model system to test the relative importance of microhabitat, climatic niche position, and climatic niche change in driving large-scale patterns of clade diversification. Anurans include ~54 currently recognized families and 6,732 species, encompassing ~88% of described amphibian species (AmphibiaWeb 2016). Frogs offer an excellent model system for two main reasons. First, large-scale

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databases have been generated for amphibians, including time-calibrated phylogenies (Pyron and Wiens 2013; Pyron 2014), species richness of families (AmphibiaWeb 2016), climatic distributions of species (Gómez-Rodríguez et al. 2015), and natural history (IUCN 2014; AmphibiaWeb 2016). Second, there is reason to think that all three types of traits might be important in frogs. Some evidence suggests that occurrence in tropical climates increases diversification in amphibian clades (e.g., Pyron and Wiens 2013), especially since amphibians have higher richness in tropical regions (Duellman 1999; Buckley and Jetz 2007). However, climatic niche divergence within anuran families might be more important for explaining variation in diversification rates among families than their climatic niche position (Gómez-Rodríguez et al. 2015). Furthermore, recent studies have shown that microhabitat (i.e., whether species are primarily arboreal, aquatic, fossorial, or terrestrial) exerts a strong influence on morphological evolution in frogs (e.g., Moen et al. 2013, 2016). However, it remains unclear whether microhabitat also influences diversification rates in frogs and whether it does so more or less than climatic niche position or change. A recent study (Wiens 2015a) found that microhabitat use (specifically, aquatic vs. terrestrial) explained most variation in diversification rates among major vertebrate clades and speculated (but did not directly test) that there was little impact of climate on diversification at this level. Therefore, the relative importance of macroscale climate and microscale habitat for explaining patterns of diversification remains highly unclear—in frogs, in vertebrates, and across organisms in general.

In this study, we test whether patterns of diversification among frog families are explained primarily by microhabitat, climatic niche change, or climatic niche position. We use a time-calibrated phylogeny of anuran families and species (Pyron 2014) to estimate clade ages, estimate rates of climatic niche change within families, and conduct phylogenetic comparative analyses. We generate a new, large-scale data set on microhabitat use among anuran species using data from the literature, focusing on five general microhabitat categories (arboreal, aquatic, burrowing, terrestrial, torrential) and three states based on combinations of these categories (e.g., semiaquatic). We use existing climatic data (Gómez-Rodríguez et al. 2015) to estimate the climatic niche position of families (e.g., whether most species are tropical vs. temperate based on mean values of climatic variables among species) and rates of climatic niche change within them. We estimate net diversification rates of families given their species richness and clade ages (Magallón and Sanderson 2001). We use phylogenetic generalized least squares regression (PGLS; Martins and Hansen 1997) to test relationships between variables and diversification rates. Using phylogenetic multiple regression, we show that all three types of variables significantly influence amphibian diversification and

together explain most variation in diversification rates among anuran families. Moreover, we show for the first time that microhabitat (especially arboreal habitat use) has a demonstrably stronger influence on diversification than climatic niche position or climatic niche change. This is important given that microhabitat is only rarely tested as a driver of diversification rates.

Material and Methods

Overview

We first describe how we obtained microhabitat data from the literature for all included species and how we converted these data to proportions of microhabitat states present among species in each family for use in comparative analyses (e.g., 50% aquatic, 50% terrestrial). We then describe how we estimated the climatic niche position for each family (based on species' mean values of climatic variables) and rates of climatic niche change within each family based on both univariate and multivariate analyses (i.e., principal component analysis [PCA]). We then describe how we estimated a net diversification rate for each family based on its age and species richness. Finally, we describe our phylogenetic regression analyses that tested the impacts of microhabitat, climatic niche position, and climatic niche rate (independent predictor variables) on family-level net diversification rate (the dependent response variable). We tested the effects of each variable (and type of variable) separately and then in combination using phylogenetic multiple regression.

Microhabitat Data

We obtained microhabitat data primarily from the IUCN (2014) and AmphibiaWeb (2016) databases, supplemented with more detailed sources in some cases (for data on individual species and references, see the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3p46b [Moen and Wiens 2017]). We obtained data from 3,394 species, representing 53 of 54 anuran families. Microhabitat data were sampled in proportion to the species richness of each family: among families, the correlation between the total richness of each family and number of species sampled here is $r = 0.976$ ($P < .001$; total richness based on AmphibiaWeb 2016).

We assigned species to microhabitats following Moen et al. (2016), focusing on adult behavior outside the breeding season given that many anurans breed in water but are not necessarily adapted (morphologically or behaviorally) to live in water all year (Duellman and Trueb 1986; Wells 2007; Moen et al. 2013, 2016). We first assigned most species to one of five general microhabitat categories: (i) aquatic (almost always in water), (ii) arboreal (typically on above-

ground vegetation), (iii) burrowing (nonbreeding season spent underground in burrows they have dug), (iv) terrestrial (found on the ground, under rocks, or in leaf litter), and (v) torrential (found in high-gradient, fast-flowing streams, usually on rocks in the stream or under waterfalls).

Most species (82.7%; 2,809 of 3,394) could be readily classified into these five categories. Other species (550 of 3,394) were classified as either semiaquatic, semiarboreal, or semiburrowing given that they were partially terrestrial and then either partly aquatic, arboreal, or burrowing. Very few species (20 of 3,394) combined nonterrestrial states (e.g., arboreal and burrowing), and even fewer species (15 of 3,394) had three states. We classified these latter two sets of multistate species in two ways. First, in analyses that included all eight states (five single states and three partial states: semiarboreal, semiaquatic, and semiburrowing), we gave these multistate species a partial state that reflected where they spent most of their time. For example, a species spending most of its adult life in trees but that digs burrows only for egg deposition was considered semiarboreal, not semiburrowing. Second, in analyses in which we lumped states (see below), we treated each state of these multistate taxa as contributing equally to the family total. For example, a species that is both arboreal and burrowing contributed 0.5 to the number of arboreal species and 0.5 to the number of burrowing species in the family. Note that these multistate species represented a small percentage of the species considered here (1.03%) and so should have little impact on the results. Indeed, conducting our analyses without these species resulted in qualitatively identical results (see Results).

We used these microhabitat data to estimate the proportion of species in each category in each family (table A1; tables A1–A9, B1 are available online). We estimated proportions in two ways to see whether intermediate states (e.g., semiarboreal) contributed independent information relative to the base state (e.g., arboreal or terrestrial). First, we calculated the proportion of sampled species in each family in each of the eight categories. Second, given that the four complex states (semiaquatic, semiarboreal, semiburrowing, torrential; see below) were combinations of the four basic states (aquatic, arboreal, burrowing, terrestrial), we split those complex states among the four basic states, as described above (e.g., a semiarboreal species contributed 0.5 to the number of arboreal species and 0.5 to the terrestrial total). In the case of torrential species, we split them among arboreal and aquatic given that many climb vegetation and rocks in the stream and also swim (e.g., Kam et al. 1998; Liao and Lu 2010). This lumping approach also accounts for the fact that some species could not be neatly fitted into the eight-state classification (see above).

We tested the relationship between diversification rates and proportions of species in each microhabitat category in each family (see below). However, analyzing proportions can be statistically problematic (Sokal and Rohlf 1995). Therefore, we calculated logits, a transformation based on the equation $\ln[x/(1 - x)]$, where x is the original proportion. Because some families had 0% or 100% of species in some microhabitat categories, we added a small value (ε) to this transformation equation (following Warton and Hui 2011), resulting in the equation $\ln[(\varepsilon + x)/(\varepsilon + 1 - x)]$. Choosing the value of ε is best done by considering many possible values and choosing the one that best balances obtaining reasonable regression residuals and distancing the (untransformed) zero values from the lowest actual nonzero proportions (Warton and Hui 2011). The latter is more difficult the larger ε becomes, whereas residuals are poorly distributed at very low values of ε (Warton and Hui 2011). We tested many possible values (powers of 10 from 10^{-4} to 10^{-1}, plus the minimum observed nonzero proportions) by examining plots of logits versus diversification rates and also residual values of model fits. Based on these plots, we followed Warton and Hui (2011) and used the minimum nonzero observed proportion for ε ($\varepsilon = 0.0018$ for eight microhabitats; $\varepsilon = 0.0038$ for the four lumped microhabitats).

Finally, we acknowledge that comprehensive multiresearcher databases such as AmphibiaWeb or IUCN can result in heterogeneity in data availability, format, and quality across species. Thus, determining microhabitat use from such sources can result in considerable uncertainty in the states for some species. We addressed this uncertainty in two ways. First, we included only species that we could confidently classify. For example, we included microhabitat data for only 3,394 species even though there are over 5,500 anuran accounts in the IUCN database. Second, we tested the robustness of our results to possible misclassification of species into microhabitat states. We randomly reassigned microhabitat states to a subset of species and redid our multiple regressions comparing the effects of microhabitat, niche position, and rate of niche change on net diversification rates (see below). We considered two possible error rates (10% and 20% of species misclassified) and implemented three ways of randomly reclassifying species. Regardless of the error rate or method of reassigning microhabitat states to species, we found that our multiple regression results were almost entirely unaffected (see app. B for full details of procedures and results; apps. A, B are available online). In other words, even with up to 20% of the species being assigned incorrectly (i.e., different than how we classified them based on published data), we found qualitatively identical results in terms of model rankings and how much variation in diversification rates each predictor variable explained.

Climatic Niche Position and Rates of Niche Change

We used climatic data from Gómez-Rodríguez et al. (2015) to estimate mean climatic niche position and rates of cli-

matic niche change for anuran families. Gómez-Rodríguez et al. (2015) used range maps from the IUCN (2014) for nearly all amphibian species and extracted data from the WorldClim database (Hijmans et al. 2005) for six key variables. These six variables were selected based on their use in previous analyses in amphibians (e.g., Quintero and Wiens 2013; Bonetti and Wiens 2014). The first three variables indicate annual mean temperature (BIO1) and yearly maxima (hottest month; BIO5) and minima (coldest month; BIO6). The last three are annual precipitation (BIO12) and precipitation of the wettest (BIO16) and driest (BIO17) quarters. The species-level climatic data are provided in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3p46b (Moen and Wiens 2017).

Our estimation of rates of niche change required a phylogeny within each family. The within-family sampling in the phylogeny used (Pyron 2014; see below) is proportional to richness (the correlation among families between total species richness per family and species sampled per family is 0.962). Therefore, we do not expect differential phylogenetic sampling across families to influence our results. The species-level phylogeny used for these analyses is provided in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3p46b (Moen and Wiens 2017).

Five families could not be included in these analyses because at least two species per clade are needed to estimate rates of niche change among species within families. The families Nasikabatrachidae and Rhinophrynidae are monotypic, and the combined climatic and phylogenetic data sets had either incomplete data or data on only one species for the families Allophrynidae, Ceuthomantidae, and Hemisotidae. We eliminated these five families from all analyses based on climatic niches (to maintain the same sampling of clades between niche rate and niche position analyses), including those with both microhabitat and climatic niches, leaving 48 families in these analyses. Note that these families were maintained in our initial microhabitat analyses that did not have climatic data (53 total families included). There are also many species-poor families for which we had data for few species (e.g., five or fewer), but in almost all cases our proportional sampling of these families was high. Thus, even though low sample sizes may introduce small errors in rate estimation (O'Meara et al. 2006), we could not simply eliminate those families because it would bias our study to only compare diversification rates among more species-rich clades.

Many climatic variables can be autocorrelated, and we wanted to characterize an overall climatic position and rate of climatic niche change (i.e., not simply temperature or precipitation alone). Therefore, we conducted a phylogenetic principal component analysis (PCA; Revell 2009) on all six climatic variables using the phytools package (Revell 2012) in R (R Core Development Team 2012). We conducted the PCA on correlation matrices (rather than covariance matrices) given that the scales of variation differ between temperature and precipitation variables.

We used overall temperature (BIO1), overall precipitation (BIO12), climatic PC1, and climatic PC2 means to test the effects of climatic niche position on net diversification rates. We used mean values of BIO1 and BIO12 to characterize the niche position of families as well as more complex variables (PC1 and PC2) that characterized overall temperature and precipitation (see Results). We did not consider PC3 and PC4 here because they represented climatic variability and explained much less variation in climate than PC1 and PC2 (see Results).

To estimate climatic niche position, we calculated the phylogenetic mean (i.e., ancestral-state estimate; O'Meara et al. 2006) of each family for each variable. We calculated the maximum-likelihood estimates of these means (Schluter et al. 1997) in R with equation (A16) from Blomberg et al. (2003), assuming a Brownian motion model of evolution. We preferred phylogenetic means to arithmetic means since diversification may be more influenced by a clade's climatic niche position when it began to diversify rather than the mean position of its resulting species. Moreover, our results should not be affected by this choice given the strong correlations between the arithmetic and phylogenetic means among families (r between 0.949 and 0.976 for all variables).

We next estimated rates of climatic niche change using the likelihood approach of O'Meara et al. (2006). We refer to these as rates of change rather than evolution because we recognize that changes in realized climatic niches among species could result from both evolutionary and nonevolutionary factors. Regardless, the primary question here is whether these changes are related to diversification or not. We calculated rates directly in R using equations from O'Meara et al. (2006). Because our goal was to estimate rates and not model niche evolution per se, we did not consider more complex models (e.g., Ornstein-Uhlenbeck; Hansen and Martins 1996). Such models, with their additional parameters, would have been difficult to use in subsequent analyses of diversification rates. Finally, we ln-transformed rates of niche change in our regression analyses to produce reasonable regression residuals (i.e., those with homogeneous variances and equal distribution about the regression line).

Note that using climatic niche rates should reduce spurious relationships between climatic divergence and diversification. For example, using divergence (e.g., the range of climatic values among species within families) might suggest a strong relationship between niche change and diversification but only because families with more species occur under a greater variety of climatic conditions, without a causal relationship between diversification and climatic niche divergence (but see Gómez-Rodríguez et al. 2015). Here we use rates of climatic niche change in families, which

will show higher values only if there is faster niche change among species, regardless of how many species the family contains. Therefore, using rates of niche change should better reflect a causal relationship between diversification and niche change among species (if present).

Estimating Diversification Rates

We placed species (for which we had data) into families based on the March 2016 classification of AmphibiaWeb (2016), which had 54 total families that were all consistent with the phylogeny used here (Pyron 2014). However, this phylogeny lacked the recently described family Odontobatrachidae, and so we considered only 53 families. We used the species diversity of families from the March 2016 version of AmphibiaWeb (2016) for estimating diversification rates. We acknowledge that many new species of frogs are described every year, which means that species diversity of families (and thus their estimated diversification rates) will change in the future. However, new species seem to be added to families based on their present described richness. For example, using the 123 species described in 2015 (from Frost 2016), we found a significant positive relationship between the number of new species added to each family and each family's total described richness (Spearman rank correlation = 0.763, $P < .001$). This means that our main conclusions should not change as more species are described in the future.

We also note that ranks (e.g., families) are arbitrary, but use of ranked clades allowed us to assign species to clades without having a complete phylogeny for all species, and estimation of diversification rates accounts for these ranked clades potentially having different ages. Comparison of higher taxa of the same rank is standard in many studies of diversification. Higher taxa of the same rank may be biased to be of more similar age than a random sample of clades (e.g., Wiens 2011; Scholl and Wiens 2016), but this should not be problematic for comparing diversification rates among clades.

We used the chronogram of Pyron (2014) to calculate stem ages of clades (table A1; fig. A1; figs. A1, B1 are available online). This multilocus phylogeny is the most comprehensively sampled to date (2,785 species) and is based on multiple genes (mean ∼4 genes/species). Note that only a single phylogeny was estimated by Pyron (2014), making it difficult to address the sensitivity of our results to phylogenetic uncertainty. Nevertheless, this tree has very similar topology and branch lengths to a previous large-scale estimate (Pyron and Wiens 2013), suggesting that different analyses converge on trees similar to the one used here.

We calculated net diversification rates using the stem group method-of-moments estimator of Magallón and Sanderson (2001). This estimator uses clade ages, species richness, and a correction (ε, the relative extinction rate of Ma-

gallón and Sanderson 2001) to account for the failure to sample extinct clades across the entire tree. Note that ε is not used here as an estimate of extinction rates within extant clades, so we use the term "relative extinction fraction" to avoid ambiguity. Following standard practice, we used three ε values: 0.0, 0.5, and 0.9. However, in the main text, we present results only from the intermediate value (0.5) given that all three gave similar results (see Results). Net diversification rates for clades are presented in table A1.

A recent study (Stadler et al. 2014) suggested that the way higher taxa are defined can affect studies of their diversification. Stadler et al. (2014) advised using crown ages over stem ages to avoid potential problems. However, we did not use crown ages for estimating diversification rates because many families have relatively few species, and estimated crown ages are sensitive to undersampling species within clades (Sanderson 1996). Furthermore, the conclusions of Stadler et al. (2014) were sensitive to how they defined higher taxa in their models, and it is unclear which scenario best applies to anurans (though results for stem and crown ages were qualitatively similar for most scenarios). Finally, simulations show that estimates of net diversification rates become more accurate as clade ages increase (e.g., since older clades are more likely to have the richness expected given their diversification rate than younger clades; Kozak and Wiens 2016). For any given clade, the crown group age is always younger than the stem group age.

We recognize that there has been some controversy about use of these net rate estimators. Specifically, some authors have claimed that using these net rate estimators requires constant diversification rates within clades and is valid only if there is a positive relationship between clade ages and richness among clades (e.g., Rabosky et al. 2012). However, previous critiques have not actually tested the accuracy of these net rate estimators, and recent simulations (Kozak and Wiens 2016) show that the accuracy of this approach can be high (true and estimated rates are highly correlated). Moreover, its accuracy is effectively the same whether there is a positive relationship between clade ages and richness or a negative one (Kozak and Wiens 2016). Additionally, net rates estimated from this approach depend only on clade ages and richness. Therefore, a young clade with many species should be correctly inferred as having a high net rate, and an older clade with few species should be correctly inferred as having a lower net rate, even if there were variation in instantaneous rates within each clade over time or among its subclades (e.g., genera).

Nevertheless, these recent simulations also show that fast diversification rates in young, species-poor clades can decouple diversification rates and richness patterns (Kozak and Wiens 2016). We therefore tested the relationship between diversification rates and (ln) richness of clades. These were consistently and strongly related (phylogenetic $r =$

0.930, 0.939, and 0.948 for ε of 0.0, 0.5, and 0.9, respectively; see below).

Finally, we note that there are many other approaches for analyzing diversification (reviewed in Morlon 2014). However, most methods would not be relevant here (e.g., those focused on detecting rate shifts or heterogeneity over time) since our primary interest is in estimating net diversification rates of clades and then testing which factors explain the most variation in these rates (e.g., climatic niche, microhabitat). Many other methods do not estimate rates for individual clades.

Regression Analyses

We used PGLS regression in the R package caper (Orme et al. 2013) to account for phylogenetic relatedness among anuran families. For all models, we estimated and used the maximum-likelihood value of λ (Pagel 1999; Freckleton et al. 2002), a parameter that scales the phylogeny's role in the fit between predictor and response variables. The value λ balances similarity among clades due to common ancestry and similarity due to a shared fit between the predictor and response variables (i.e., phylogenetic inertia vs. shared adaptation; Hansen and Orzack 2005). The values κ and δ were each set at 1, following standard practice. All r^2 values were adjusted for multiple variables.

We first tested the effect of microhabitat on net diversification rates. We began with bivariate analyses that individually regressed net diversification rate on the proportion of species in each family with each microhabitat state, estimating separate models for each of the eight microhabitat types. We then estimated two types of multiple regression models: (1) a model that simultaneously considered all microhabitat categories as predictors and (2) a model that considered only the three microhabitats (arboreal, semiarboreal, and torrential) that were each significant predictors in bivariate analyses (see Results). We compared these models using the small sample size–adjusted Akaike information criterion (AICc) and the models' associated AICc weights, w_i (Burnham and Anderson 2002).

We next estimated similar regression models with the intermediate microhabitat types (e.g., semiarboreal) lumped into four major categories (e.g., arboreal and terrestrial). We found results that were similar to those using all eight microhabitats individually (but yielding weaker relationships with diversification), so we did not use the lumped categories in further analyses.

We also estimated the importance of climatic niche position for diversification rates. We estimated bivariate regression models of diversification rate versus climatic niche position by separately testing relationships between diversification and BIO1, BIO12, PC1, and PC2 (see above). We then analyzed multiple regression models that combined BIO1 and BIO12, PC1 and PC2, and BIO1 and PC1. These analyses allowed us to compare the combined versus individual effects of these variables on diversification (e.g., BIO1 and BIO12 to examine the combined effect of temperature and precipitation). The final model was estimated because BIO1 and PC1 each explained similar amounts of variation in net diversification rates when tested separately, and BIO12 and PC2 made model fits worse when combined with BIO1 and PC1, respectively (see Results). We thus wanted to test whether BIO1 and PC1, as the best single-variable predictors, were redundant or additive in their effects on net diversification rates.

We next estimated the effects of rates of climatic niche change on diversification. We first estimated the individual effect of rates of the first four climatic PC axes by bivariate regression. We also summed rates across axes to estimate the effect of an overall rate of climatic niche change. We then conducted multiple regression analyses that incorporated multiple axes, starting with PC1 and PC2 and then sequentially adding higher axes.

Finally, we estimated multiple regression models that included all three types of variables: microhabitat, climatic niche position, and rates of climatic niche change. We started with the most strongly supported model for each type of variable (e.g., BIO1 for climatic niche position; see Results). We then compared all four possible combinations of the three types of variables. The best-fitting model was selected based on AICc values, as described above for microhabitat. For this best-fitting model, we also calculated standardized partial regression coefficients. These coefficients allow one to compare the relative importance of different factors in multiple regression, because they reflect the influence of variables when others are held constant (Sokal and Rohlf 1995). We calculated these coefficients by simply reestimating our optimal model after centering and scaling our variables (Sokal and Rohlf 1995), which produced a fitted model with identical statistical results (e.g., P values, r^2, AICc) but with a set of regression coefficients that could be directly compared (e.g., if one unit of variable A changes the response variable by two units, whereas one unit of variable B changes it by four units, then variable B has twice the influence on the response variable). To compare the relative influence of the different predictor variables, we summed these coefficients, divided each regression coefficient by the sum, and compared the percent of the sum that each variable contributed. For the three arboreal categories, we summed their independent coefficients to obtain an overall influence of microhabitat. Finally, we tested the effect of excluding multistate species (i.e., those with three states or two non-terrestrial states) on the importance of microhabitat in these model comparisons. We also tested the impact of not including torrential species as one of the three arboreal types (given that torrential species are partially aquatic; see above).

For these comparative analyses, we used a reduced version of the tree (Pyron 2014) in which each family is represented by one species. The choice of species was inconsequential since all species in a family have the same branch length to the family's crown or stem. This reduced tree is provided in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3p46b (Moen and Wiens 2017).

Results

Overview

In the sections that follow, we describe the relationships between net diversification rates of families (response variable) and three general types of predictor variables: microhabitat, climatic niche position, and niche rate. We first analyzed how each type of variable impacts diversification rates separately. Because each category includes multiple variables, we used multiple regression to identify the model that best fits that general type of data (comparing model fit primarily based on the AICc). We then performed multiple regression analyses that combined the best-fitting model for each type of variable into an overall model that best explained diversification rates among anuran families. The phylogeny, net diversification rates, and microhabitats among families are summarized in figure 1. Data for each family are shown in table A1. Results are presented here for net diversification rates estimated with an ε value (relative extinction fraction) of 0.5, with corresponding results (which were very similar) for values of 0.0 and 0.9 presented in online tables.

Microhabitat Analyses

We first performed bivariate regressions of net diversification rates on the eight microhabitat categories. The proportions of arboreal, semiarboreal, and torrential species in each family all had a significant positive effect on net diversification rates, but other microhabitat types did not (tables 1, A2; fig. 2). These three states each explained from 10.7% to 16.8% of the variation in diversification rates. When we lumped the eight categories into four base categories (arboreal, aquatic, fossorial, terrestrial), the proportion of arboreal species remained a significant predictor of diversification (tables 2, A3), explaining 11.6% of the variation. Other microhabitats remained nonsignificant.

Multiple regression analyses that included only the three arboreal types as separate variables (arboreal, semiarboreal, and torrential) had much higher statistical support and predictive power for explaining diversification rates than any microhabitat alone ($r^2 = 0.270$; AICc weight $= 0.464$; minimum AICc improvement of 4.19 over the single arboreal-type predictors; tables 3, A4). Including all the remaining microhabitat categories that were nonsignificant in bivariate regressions explained more variation ($r^2 = 0.361$). However, this model had slightly weaker AICc support than the arboreal-only model (AICc weight $= 0.446$; tables 3, A4).

Climatic Niche Position and Rates of Climatic Niche Change

We initially summarized the six climatic variables using phylogenetic PCA. PC1 represented differences between warm and wet versus cool and dry environments (table A5) and explained 54.0% of the variation in climate among species. PC2 explained 30.7% of climatic variation and represented wet, cool climates (high values) and warm, dry climates (low values). PC3 (10.0%) and PC4 (4.7%) represented seasonality of precipitation and temperature, respectively. PC5 and PC6 together explained less than 1% of the climatic niche variation.

Estimated rates of niche change within families were very similar for all PC axes. Thus, families with high rates on one axis tended to have high rates on other axes. To test the correlation among rates on different PC axes, we used R to calculate PGLS correlations, using equations from Rohlf (2006; see the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3p46b [Moen and Wiens 2017]) and the family-level frog phylogeny. The correlations among rates on all four PC axes ranged from 0.609 to 0.838.

Rates of climatic niche change were strongly and positively related to diversification rates. Rates of niche change on PC1 explained 23.5% of the variation in diversification rates ($P < .001$; table 4; fig. 2). Rates of niche change for other PC axes showed similar but weaker relationships with diversification rates (table A6). Furthermore, multiple regression models that considered multiple PC axes were not statistically supported over models using single PC axes, nor were models that used the sum of rates (as an overall rate of climatic change) instead of single PC axes (table A6). This lack of independent information from different PC axes may be explained by the high correlations among PC axes. Thus, we considered only PC1 for all further tests of the effect of rates of climatic niche change on net diversification rates, given that this axis had higher statistical support for explaining variation in net diversification rates than PC2–PC4 (table A6).

In contrast to climatic niche rates, climatic niche position was only weakly related to diversification rates. In bivariate regressions of BIO1, BIO12, PC1, and PC2, we found that BIO1 (annual mean temperature) explained the most variation ($r^2 = 0.111$) in diversification rates (table A7) and showed a positive relationship ($P = .012$; fig. 2). PC1 explained slightly less variation ($r^2 = 0.095$), while BIO12 and PC2 explained very little. Models that combined BIO1 and BIO12, PC1 and PC2, and BIO1 and PC1 did not
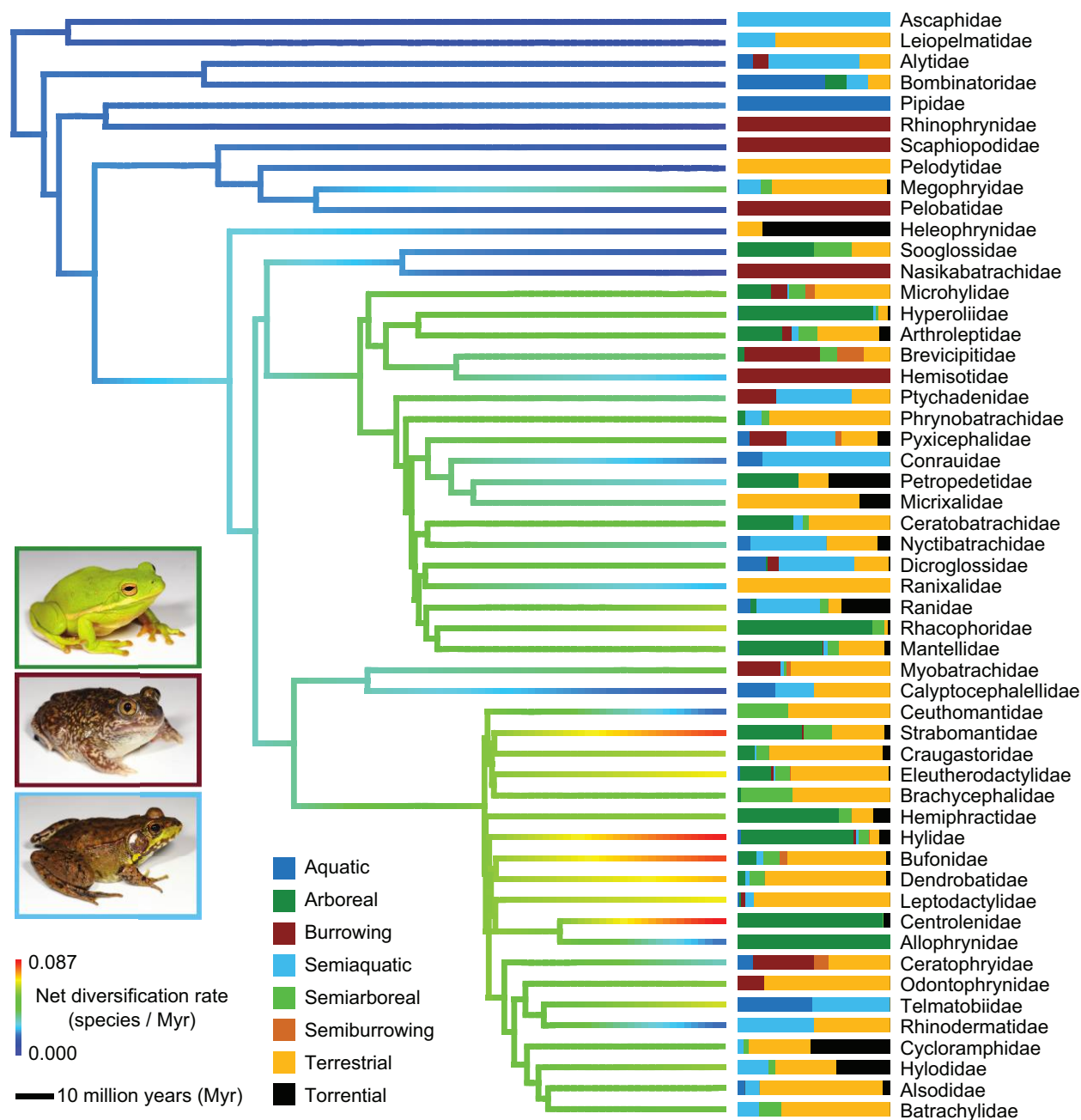
Figure 1: Summary of phylogeny, net diversification rates, and microhabitats among anuran families. Phylogeny is from Pyron (2014). Diversification rates shown here were calculated with an ε value (relative extinction fraction) of 0.5 and mapped on the phylogeny using the contMap function in phytools in R (Revell 2012, 2013), which infers the maximum likelihood ancestral states and then interpolates gradual change along branches. Note that we use this tool to simply visualize net diversification rates among families, not to model their evolution. The small black bar on the lower left represents the scale for the phylogeny's branch lengths. Colored bars to the right of the phylogeny represent the proportion of species in each family that use each microhabitat, with multistate species split evenly between the microhabitats they use (see the main text). Photographs show three examples of frog microhabitat ecomorphs (from *top* to *bottom*): arboreal (*Hyla cinerea*), burrowing (*Spea bombifrons*), and semiaquatic (*Lithobates clamitans*). All photos by D. S. Moen.

Table 1: Relationships between net diversification rate (response variable) and microhabitat (predictor variable) for each of the eight original microhabitat categories analyzed separately

Microhabitat	Slope	P	r^2	AICc	λ	λ 95% CI
Aquatic	.0007	.594	−.014	−254.07	.600	(.239, .945)
Arboreal	.0026	.004	.134	−262.21	.495	(.154, .854)
Burrowing	−.0009	.277	.004	−254.97	.546	(.183, .911)
Semiaquatic	.0004	.695	−.017	−253.94	.591	(.233, .937)
Semiarboreal	.0045	.001	.168	−264.17	.466	(.109, .844)
Semiburrowing	.0022	.358	−.003	−254.66	.575	(.217, .925)
Terrestrial	.0005	.635	−.015	−254.00	.569	(.207, .926)
Torrential	.0034	.010	.107	−260.78	.600	(.218, .960)

Note: Net diversification rates were estimated assuming an ε value (relative extinction fraction) of 0.5. See table A2, available online, for results with ε values of 0.0 and 0.9, which gave qualitatively identical results. AICc = corrected Akaike information criterion; CI = confidence interval; λ = the estimated phylogenetic signal of the model residuals.

perform as well as BIO1 alone (table A7). Therefore, we considered only BIO1 in analyses that compared climatic niche position to microhabitat in explaining diversification rates.

Comparing Effects of Microhabitat and Macroclimate on Diversification

We finally compared the fit of different models incorporating the best-fitting variables from the preceding analyses of microhabitat (all three arboreal types), climatic niche rate (PC1 rate), and climatic niche position (mean BIO1). Specifically, we compared the ability of each model to predict

diversification rates. We included each type separately (microhabitat, niche rate, niche position) and then all possible combinations, including (*a*) microhabitat + niche position, (*b*) niche rate + niche position, (*c*) niche rate + microhabitat, and (*d*) niche rate + niche position + microhabitat. The most highly supported model (table 4) was one that combined all three variables: rates of climatic niche change (in PC1), niche position (BIO1), and microhabitat. This model explained the most variation in net diversification rates ($r^2 = 0.668$) and had the lowest AICc (3.40 units below any other model; AIC weight = 0.846). Standardized partial regression coefficients showed that microhabitat had the
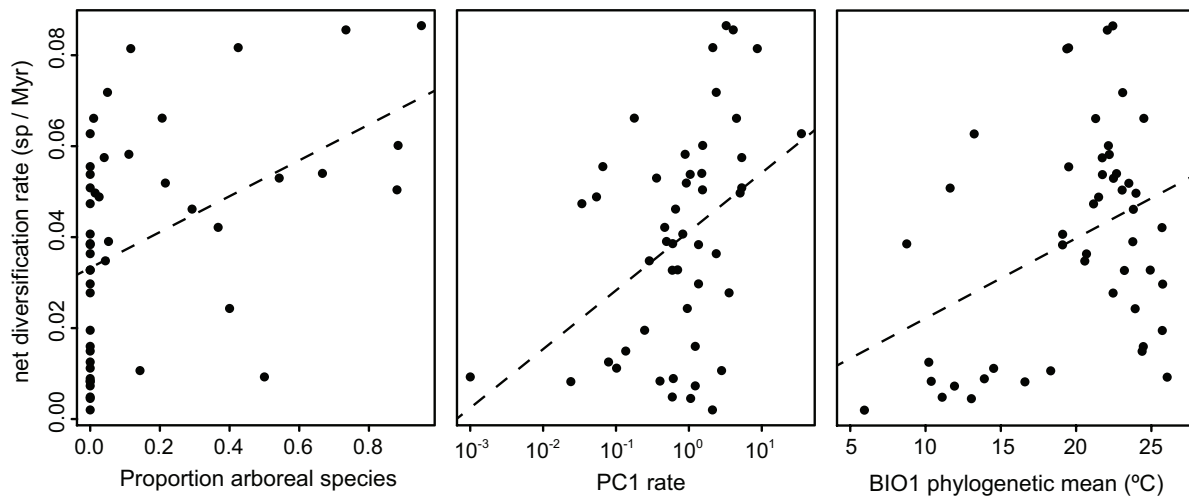

Figure 2: Relationships between net diversification rates and three variables (arboreality, *left*; rates of climatic niche change, *middle*; and climatic niche position, *right*) among 48 frog families. In all cases, relationships were statistically significant (arboreality: $r^2 = 0.134$, $P = .004$; climatic rates: $r^2 = 0.235$, $P < .001$; climatic niche position: $r^2 = 0.111$, $P = .012$). Net diversification rates were estimated with an ε value (relative extinction fraction) of 0.5. Note that arboreality is based on the proportion of arboreal species in each family (using raw values for ease of visualization), but statistical tests were done with a logit transformation of these raw proportions. Proportions of semiarboreal and torrential species showed similar relationships. Rates of niche change are shown for PC1 of six climatic variables, whereas niche position is represented by annual mean temperature (BIO1). Note that PC1 rate is plotted on a logged scale. Dotted lines are least squares best-fit lines from nonphylogenetic bivariate regressions, used to show general trends.

Table 2: Relationships between net diversification rate (response variable) and microhabitat (predictor variable) based on the four lumped microhabitat categories (e.g., each semiaquatic species treated as 0.5 aquatic and 0.5 terrestrial)

Microhabitat	Slope	P	r^2	AICc	λ	λ 95% CI
Aquatic	.0007	.577	−.013	−254.10	.602	(.239,.950)
Arboreal	.0028	.007	.116	−260.98	.466	(.114,.844)
Burrowing	−.0010	.271	.005	−255.00	.546	(.183,.910)
Terrestrial	.0004	.701	−.017	−253.93	.575	(.212,.929)

Note: Net diversification rates were estimated assuming an ε value (relative extinction fraction) of 0.5. See table A3, available online, for results with ε values of 0.0 and 0.9, which gave qualitatively identical results. AICc = corrected Akaike information criterion; CI = confidence interval; λ = the estimated phylogenetic signal of the model residuals.

strongest influence (sum $b = 0.0141$), then rates of niche change ($b = 0.0112$), and niche position had the least influence ($b = 0.0048$). Given the near independence of our predictor variables (e.g., PGLS $r = 0.040$ between climate PC1 rate and proportion of arboreal species), these partial regression coefficients mean that the microhabitat, niche rates, and niche position explain roughly 31%, 25%, and 11%, respectively, of the total variation in diversification rates. The second-best model was similar but excluded niche position, reflecting the stronger influence of rates of niche change and microhabitat on diversification. The model with all three factors accounted for nearly as much variation as the sum of the three separate models' r^2, further reflecting the low correlations among variables. Results were similar for the other two ε values (relative extinction fractions; table A8). Moreover, all of our results were qualitatively identical when excluding multistate species and when including only arboreal and semiarboreal proportions for microhabitat (i.e., excluding torrential; see table A9).

Discussion

In this study, we tested the relative contributions of microhabitat, climatic niche position, and rates of climatic niche change to patterns of diversification in a major clade of vertebrates. Our results support a model that includes all three types of variables and explains most (67%) variation in net diversification rates among families. The results show that microhabitat (specifically, arboreality) best explains patterns of diversification (explaining ~31% of the variation), whereas rates of climatic niche change explain somewhat less variation (~25%), and climatic niche position explains the least of all (~11%). The role of microhabitat in driving large-scale patterns of diversification among clades has been largely neglected in macroevolutionary studies. Thus, it is surprising that microhabitat explained net diversification rates better than the more widely studied macroclimatic variables. Numerous studies have focused on diversification and climatic niche position (i.e., tropical vs. temperate climate), especially given the observation that there are more species in the tropics (in most clades; Hil-

lebrand 2004) and the idea that this pattern may be explained by higher diversification rates in tropical clades (e.g., Mittelbach et al. 2007). Our results highlight the need to consider multiple variables when trying to explain patterns of diversification and richness among clades and the value of considering microhabitat as one of those variables. Our results also raise the intriguing possibility that local-scale ecological factors might be more important than landscape-scale factors (i.e., climate) in driving patterns of diversification. They also support the idea (Wiens 2017) that dynamic traits (e.g., rates of niche change) may be more important drivers of diversification than static traits (e.g., niche position). Below we compare our results to those of previous studies and discuss areas for future research.

Comparison to Other Studies

Our findings show interesting similarities and contrasts with previous studies. First, most previous studies of diversifica-

Table 3: Relationships between net diversification rate (response variable) and microhabitat (predictor variable), comparing optimal single-variable models and multiple regression models of microhabitat

Model	r^2	AICc	ΔAICc	w_i
Intercept	na	−255.94	12.42	.001
Arboreal only	.134	−262.21	6.15	.021
Semiarboreal only	.168	−264.17	4.19	.057
Torrential only	.107	−260.78	7.58	.010
All three arboreal types	.270	−268.36	.00	.464
All microhabitats	.361	−268.28	.08	.446

Note: The results include the null model (intercept), three simple regression models including each of three arboreal types separately (arboreal only, semiarboreal only, torrential only; as in table 1), a multiple regression model with all three arboreal types included but treated as separate variables (all three arboreal types), and a multiple regression model including all eight microhabitat types (all microhabitats). Net diversification rates were estimated assuming an ε value (relative extinction fraction) of 0.5. See table A4, available online, for results using ε values of 0.0 and 0.9. AICc = corrected Akaike information criterion; ΔAICc = change in AICc; na = not applicable; w_i = AICc weight of each model.

Table 4: Relationships between net diversification rate (response variable) and different predictor variables, comparing models that include rate of climatic niche change (in PC1), niche position (phylogenetic mean of BIO1 for families), microhabitat (all three arboreal types included but treated as separate variables), and different combinations of these variables

Model	r^2	AICc	ΔAICc	w_i
Intercept	na	−241.60	46.29	.000
BIO1 mean	.111	−245.94	41.95	.000
Climate PC1 rate	.235	−253.27	34.62	.000
All three arboreal types	.322	−256.38	31.51	.000
Arboreal types + BIO1 mean	.326	−255.24	32.65	.000
Climate PC1 rate + BIO1 mean	.393	−263.16	24.73	.000
Climate PC1 rate + arboreal types	.633	−284.49	3.40	.154
Climate PC1 rate + BIO1 mean + arboreal types	.668	−287.89	.00	.846

Note: Results are for net diversification rates estimated using an ε value of 0.5 (see table A8, available online, for results using other values). Results for the model including all three arboreal types are somewhat different from those in table 3, since here only the 48 families for which we could estimate the rate of climatic niche change are included (table 3 includes 53 families). AICc = corrected Akaike information criterion; ΔAICc = change in AICc; na = not applicable; w_i = AICc weight of each model.

tion have not considered microhabitat, but of those that have, some also found strong effects. For example, among animal phyla, microhabitat (marine vs. terrestrial and freshwater) explained ~33% of the variation in diversification rates (Wiens 2015*b*). Moreover, among major vertebrate clades, microhabitat (terrestrial vs. aquatic) explained most variation in diversification rates (~67%), with aquatic clades showing lower rates than largely terrestrial clades (Wiens 2015*a*). Here we found no evidence that aquatic microhabitats lowered diversification rates. However, many frogs remain tied to aquatic microhabitats for reproduction, even if they predominantly occur in nonaquatic habitats (Duellman and Trueb 1986; Gomez-Mestre et al. 2012).

Second, previous studies have given mixed results about the importance of niche position and rates of climatic niche change for amphibian diversification. Within amphibians, Kozak and Wiens (2010) strongly supported the role of climatic niche rates for plethodontid salamander clades, whereas Pyron and Wiens (2013) did not among amphibian families, using similar methods to those used here. Pyron and Wiens (2013) supported the effect of niche position on diversification rates of amphibian families, but not strongly, consistent with our results. Gómez-Ródriguez et al. (2015) supported the importance of climatic niche change to diversification rates among anuran and salamander families and showed little impact of niche position. However, they analyzed the total amount of divergence within families, not rates of climatic niche change.

Beyond amphibians, other studies have supported the importance of climatic niche change but found mixed support for the role of climatic niche position. Increased rates of climatic niche change within clades has been supported as a driver of diversification in diverse groups, including plants (Schnitzler et al. 2012) and birds (Title and Burns 2015; Cooney et al. 2016). The importance of climatic niche position may be more scale dependent. For example, large-

scale studies in mammals show that net diversification rates are higher in tropical than temperate climates (Rolland et al. 2014), but analyses of mammalian genera show no impact of latitude on diversification (Soria-Carrasco and Castresana 2012). Other smaller-scale analyses often fail to support higher tropical diversification rates (e.g., Jansson et al. 2013). The failure to find strong effects of climate on diversification at smaller phylogenetic scales may reflect a general property of diversity gradients (Pontarp and Wiens 2017).

Overall, our results are consistent with a limited number of previous studies showing a strong impact of microhabitat on diversification (but not arboreality per se) and with those showing a strong effect of climatic niche rates and a weaker effect of climatic niche position. However, ours may be the first to explicitly compare the impacts of microhabitat and climate on diversification.

Areas for Future Research

Our results reveal several novel areas for future research. Perhaps the most intriguing question raised is, what explains the strong relationship between arboreality and diversification rates found here? One potential explanation is that use of arboreal habitats (even partially, as in semiarboreal and torrential species) expands the available microhabitat space into the vertical dimension, potentially reducing competition. For example, frogs potentially compete for insect prey (e.g., Duellman and Trueb 1986; Moen and Wiens 2009), and there are numerous plant-feeding or plant-dwelling insects that may be far more accessible to arboreal frogs. Thus, arboreal habitats may offer a new adaptive zone that spurs rapid radiation, as expected under the ecological theory of adaptive radiation (Schluter 2000). This idea might also extend to torrential species, which are tied to fast-flowing streams (like semiaquatic and aquatic species in streams) but climb on surrounding vegetation and rocks (unlike semi-

aquatic and aquatic species). If this explanation is true, we might also expect to see accelerated rates of diversification in arboreal lineages in other major groups (e.g., squamates, mammals, birds, arthropods).

Arboreality may also expand the possibilities for reproduction, and amphibian biologists have emphasized the importance of reproductive diversity (e.g., different egg deposition sites) in anuran radiations (Duellman and Trueb 1986; Callery et al. 2001). Arboreal taxa can lay eggs in tree holes and bromeliads, on leaves, or in foam nests on branches in addition to water bodies on the ground (Duellman and Trueb 1986; Haddad and Prado 2005; Wells 2007; Blackburn et al. 2013). However, Gomez-Mestre et al. (2012) found that life-history modes do not appear to strongly influence anuran diversification.

Intriguingly, the use of arboreal habitats among extant frog lineages appears to be far younger than the origin of frogs. Specifically, based on the phylogeny used here, the crown group of living anurans is roughly 218.8 Myr old, whereas arboreal lineages are more recent (e.g., stem ages of the major tree frog clades Hylidae and Rhacophoridae are 72.1 and 88.1 Myr, respectively; fig. A1). Yet according to the theory of adaptive radiation (e.g., Schluter 2000), frogs might have been expected to rapidly expand into all potential microhabitats soon after their origin, including arboreality. One possible explanation for the young age of arboreal frogs is that their origins are tied to that of angiosperms (or insects that utilize them) at ~150 Myr (Magallón et al. 2015). Another possible explanation is that there were intrinsic constraints (e.g., functional, developmental) that limited the origin of the arboreal ecomorph in the basal frog lineages (i.e., failure to develop expanded toepads; Emerson and Diehl 1980; Barnes et al. 2006; Emerson 1991; Moen et al. 2013, 2016). Our results are also surprising in that no other microhabitats significantly affected diversification even though there are conspicuously species-poor families specialized for fossorial (e.g., Rhinophrynidae, Nasikabatrachidae) and aquatic (e.g., Ascaphidae, Pipidae) microhabitats.

Another major area for future research is to explain the remaining variation in diversification rates among frog families. While our best-fitting model explains most variation in diversification rates among frog families, 33% remained unexplained. Potential candidates to explain the remaining variation include body size, sexual-size dimorphism, reproductive modes, diet, areas of clade geographic ranges, and mating calls. Divergence in body size can be important for resource competition in frogs, and there may be extensive body-size evolution within a microhabitat category (e.g., tree frogs; Moen and Wiens 2009). However, analyses across genera in one of the largest frog families (Hylidae), which is dominated by the arboreal ecomorph, showed no relationship between rates of change in body size and rates of diversification (Wiens et al. 2011). This may be worth exploring across frog families,

but the results from hylids suggest it may be unimportant. Furthermore, a previous study across amphibians did not find a significant relationship between mean family body size and net diversification rates (De Lisle and Rowe 2015). That study did find a significant relationship between sexual-size dimorphism (SSD) and net diversification rates across amphibian families (De Lisle and Rowe 2015). However, it is unclear whether similar results would be found within anurans, how much variation in diversification is explained by SSD, and whether SSD is correlated with particular microhabitats (e.g., higher SSD in arboreal-type microhabitats). Frogs also show extensive variation in life-history modes, including many species with the primitive mode (aquatic eggs and tadpoles), others with terrestrial eggs and aquatic tadpoles, and many with terrestrial eggs and direct development from eggs to juveniles with no aquatic larval stage (e.g., Duellman and Trueb 1986; Haddad and Prado 2005). But again, explicit analyses suggest that reproductive modes have limited impact on anuran diversification (Gomez-Mestre et al. 2012). Diet seems unlikely to be a factor since most anurans are generalist insectivores, and divergence among species in diet seems primarily based on prey size, not prey type (e.g., Duellman and Trueb 1986; Moen and Wiens 2009). Similarly, areas of geographic ranges of families might be important, but they appear to have little contribution to diversification that is not already incorporated by climatic niche divergence (Gómez-Rodríguez et al. 2015). Sexual selection, specifically variation in frog mating calls (and associated neuroanatomy), might also be important in explaining large-scale diversification patterns, but there is also some evidence against this idea (Richards 2006). A final possible explanation is that various sources of error might underlie much of the unexplained variance in our model rather than variables that were not included.

A third area for future research is to understand the weak relationship between diversification rates and climatic niche position found in our study (and other anuran studies; e.g., Wiens et al. 2011). If climatic niche position has only weak impacts on diversification rates, this suggests that other factors might also play a significant role in explaining the strong latitudinal diversity gradient in anurans, such as extinction of entire clades in temperate regions, greater time for speciation in tropical regions, and asymmetric dispersal of lineages between tropical and temperate zones (e.g., Wiens et al. 2006; Smith et al. 2012; Pyron and Wiens 2013).

Conclusions

In summary, we analyzed patterns of net diversification rates across one of the major clades of vertebrates, comparing the relative effects of three types of factors (microhabitat, climatic niche position, and rates of climatic niche change). Our best-supported model shows that all three factors are important, but microhabitat was the most im-

portant and niche position the least. These results provide a baseline for understanding the relative impacts of local-scale microhabitat and broad-scale climate on patterns of diversification and support the idea that local-scale microhabitat is more important than macroclimate, even over hundreds of millions of years.

Acknowledgments

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