

# HOW IS THE RATE OF CLIMATIC-NICHE EVOLUTION RELATED TO CLIMATIC-NICHE BREADTH?

M. Caitlin Fisher-Reid,<sup>1,2</sup> Kenneth H. Kozak,<sup>3</sup> and John J. Wiens<sup>1</sup>

<sup>1</sup>*Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York 11794–5245*

<sup>2</sup>*E-mail: mcaitlin@life.bio.sunysb.edu*

<sup>3</sup>*Bell Museum of Natural History and Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108*

Received August 5, 2011

Accepted June 18, 2012

The rate of climatic-niche evolution is important to many research areas in ecology, evolution, and conservation biology, including responses of species to global climate change, spread of invasive species, speciation, biogeography, and patterns of species richness. Previous studies have implied that clades with higher rates of climatic-niche evolution among species should have species with narrower niche breadths, but there is also evidence suggesting the opposite pattern. However, the relationships between rate and breadth have not been explicitly analyzed. Here, we examine the relationships between the rate of climatic-niche evolution and climatic-niche breadth using phylogenetic and climatic data for 250 species in the salamander family Plethodontidae, a group showing considerable variation in both rates of climatic-niche evolution and climatic-niche breadths. Contrary to some expectations, we find no general relationship between climatic-niche breadth and the rate of climatic-niche evolution. Climatic-niche breadths for some ecologically important climatic variables considered separately (temperature seasonality and annual precipitation) do show significant relationships with the rate of climatic-niche evolution, but rates are faster in clades in which species have broader (not narrower) niche breadths. In summary, our results show that narrower niche breadths are not necessarily associated with faster rates of niche evolution.

**KEY WORDS:** Amphibians, climate, niche conservatism, niche evolution, phylogeny, Plethodontidae.

The climatic niche is a central concept in ecology and evolutionary biology. It describes the set of temperature and precipitation conditions in which a species can persist (Hutchinson 1957). In general, the climatic niche is important because species are generally limited in the total range of climates they can occupy. For example, few species have physiological tolerances that allow them to occur from arctic regions to the tropics and live year-round in these extreme climates. That is, most species have a limited climatic-niche breadth, which represents the size of the range of climatic values over which a species can persist, on one or more axes of the multivariate climatic niche.

The rate of climatic-niche evolution may also have an important role in many ecological and evolutionary patterns and

processes, especially when species have limited climatic niche breadths (reviews in Wiens and Graham 2005; Wiens et al. 2010; Peterson 2011). For instance, climatic-niche conservatism (i.e., a relatively slow rate of change in niche position for populations or species over time), when combined with narrow niche breadths, can be important in limiting geographic range expansion (e.g., Wiens and Graham 2005), which in turn may be important for allopatric speciation (e.g., Kozak and Wiens 2006), patterns of large-scale biogeography and species richness (e.g., Wiens et al. 2006; Rangel et al. 2007; Kozak and Wiens 2010a), determining where invasive species can invade and spread to (e.g., Peterson and Vieglais 2001; Peterson 2003; Thuiller et al. 2005; Mandle et al. 2010), and understanding range shifts and local extinctions



of species in response to global climate change (e.g., Tingley et al. 2009). Conversely, rapid niche evolution may allow range expansion and lead to very different patterns.

Previous empirical studies have suggested that the rate of climatic-niche evolution in a clade and the climatic-niche breadths of species in that clade may be related, but implied very different relationships between these variables. Smith and Beaulieu (2009) found that woody plants have slower rates of climatic-niche evolution than herbaceous plants and that woody species occupy smaller areas of climate space (suggesting narrower climatic-niche breadths). They suggested that these narrower climatic-niche breadths are linked to slower rates of climatic-niche evolution, but did not explicitly test the relationship between niche breadth and rate. Kozak and Wiens (2010b) examined the relationship between rate of climatic-niche evolution and diversification rate and found that both rates are faster in the tropics (see also Baselga et al. 2011). In contrast to Smith and Beaulieu (2009), Kozak and Wiens (2010b) suggested that rates of niche evolution are faster in the tropics because climatic niches are narrower in tropical species (e.g., Ghalambor et al. 2006; Kozak and Wiens 2007). However, they did not explicitly test the relationship between niche breadth and rate either.

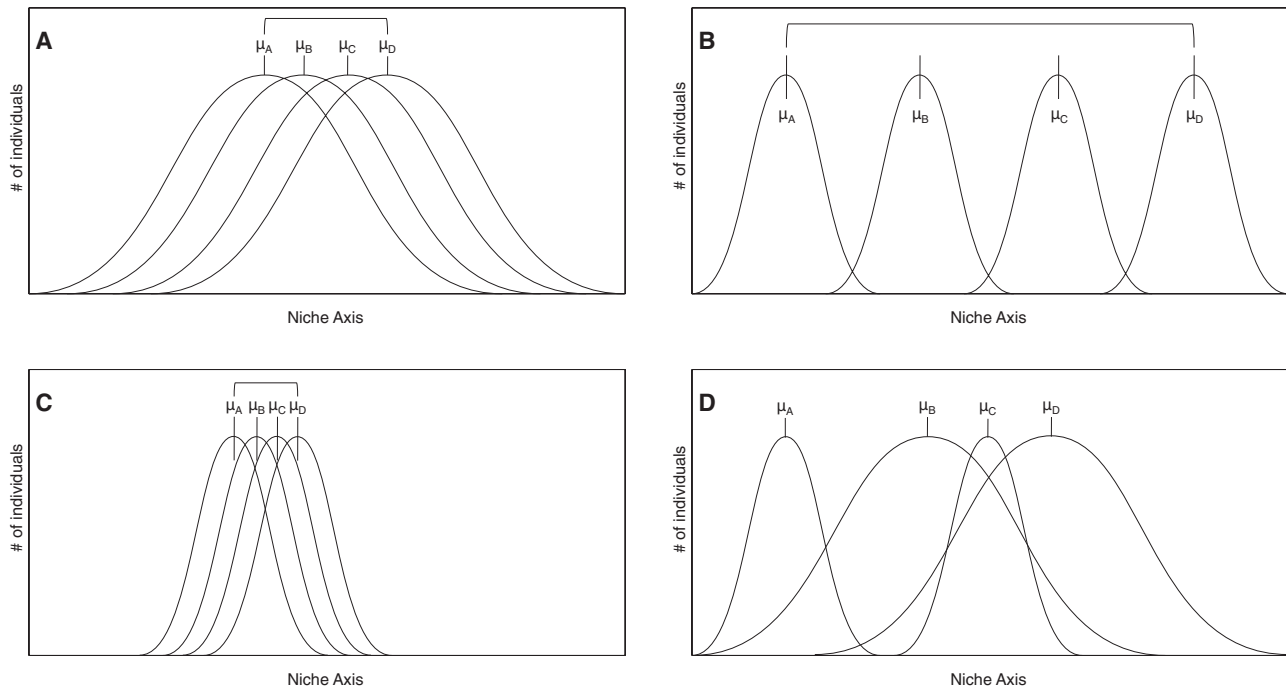
Why and how should niche breadth and the rate of niche evolution be related? There are many possible relationships between niche breadth and rate. For example, if every species in a region occupies all available climatic zones (i.e., broad climatic niches; Fig. 1A), then the potential for divergence between the mean climatic niches of species may be low. Alternatively, if each species occupies a small subset of the climatic zones in the region (i.e., narrow climatic niches; Fig. 1B), then the potential for divergence between species' climatic niches should be higher, allowing for a faster rate of niche evolution. Thus, we might expect a relationship between narrow niche breadths and faster rates of climatic-niche evolution (e.g., Kozak and Wiens 2010b). We might also expect a negative relationship between the rate of climatic-niche evolution of a clade and the amount of climatic-niche space that species within the clade occupy relative to the total climatic-niche space occupied by the clade (i.e., the proportional climatic-niche breadth). Nevertheless, there may also be positive relationships between niche breadth and rate (e.g., Smith and Beaulieu 2009). For instance, species with narrow niches might be constrained in their ability to evolve (i.e., a slow rate) due to phenotypic trade-offs during specialization (review in Futuyma and Moreno 1988).

The relationships between niche breadth and rate have not been explicitly tested in either empirical or theoretical studies, but some theoretical studies have addressed related issues. Huey and Kingsolver (1993) addressed the response of species' thermal performance to gradual, constant climate warming. Populations with large performance breadths were predicted to show a greater lag time for their population mean phenotype to catch up to the en-

vironmental optimum than populations with narrow performance breadths (eq. 1 in Huey and Kingsolver 1993), implying a negative relationship between niche breadth and rate of niche evolution. Whitlock (1996) demonstrated that specialized species (i.e., narrow niche breadth) may be able to evolve faster than generalized species (i.e., broad niche breadth) because purifying selection acting on performance in one environment (eliminating genotypes that maximize genotype–environment interactions) is expected to be more effective than selection acting on performance across many environments, allowing specialists to increase mean fitness faster than generalists. This implies that species with narrow niches generally evolve faster than broad-niched species in the same environment, but does not directly address if there is a faster rate of changes between different niches.

Variance in climatic-niche breadth among species in a clade and rates of climatic-niche evolution may also be related (Fig. 1A, C–D). Species in a clade may have low variance in their climatic-niche breadths if they (1) have very broad climatic niches (Fig. 1A); or (2) have narrow niches near the same position on the niche axis (Fig. 1C). Both cases may have low rates of climatic-niche evolution. However, in a clade in which niches are evolving rapidly (Fig. 1D), there may be a broad range of niche breadths, especially if niche evolution involves niche expansion of narrow-niched species or niche subdivision of broad-niched species, and if species are at various stages in these processes. Thus, groups with a high rate of niche evolution may have high variance in climatic-niche breadth.

Finally, latitudinal variation in climate may also play an important role in the relationship between climatic-niche breadth and rate of climatic-niche evolution. Previous work suggests that tropical species, in addition to having faster rates of climatic-niche evolution (Kozak and Wiens 2010b), have narrower temperature niches than temperate species (i.e., Janzen's (1967) hypothesis; MacArthur 1972; Vázquez and Stevens 2004; Ghalambor et al. 2006; Kozak and Wiens 2007; McCain 2009; Hua and Wiens 2010). The relationship between lower latitudes and narrower climatic-niche breadths is attributed to greater climatic stability at a given location in the tropics compared to the temperate zone (lower annual variation in temperature; Janzen 1967). Climatic stability is thought to lead to narrower and more distinct climatic zones along elevational gradients, stronger climatic barriers to dispersal, and the evolution of species that occur in relatively narrow climatic zones (e.g., Janzen 1967; Kozak and Wiens 2007; Hua and Wiens 2010). These predictions are partially supported in empirical studies. Kozak and Wiens (2007) found narrower temperature niche breadths for tropical species in a comparison of 30 sister-species pairs of plethodontid salamanders from a wide range of latitudes, whereas Hua and Wiens (2010) found a similar pattern across 79 sister-species pairs of frogs. McCain (2009) found that vertebrates have narrower elevational ranges



**Figure 1.** Hypothetical examples illustrating different possible distributions of niche breadth and niche divergence among four species in a clade. The x-axis represents a given climatic niche axis (e.g., annual mean temperature, annual precipitation), and the y-axis represents the number of individuals of a given species that occur at that position on the niche axis (e.g., based on the mean distribution of an individual along that axis). (A) A scenario in which all species have relatively wide niche breadths on this niche axis, and limited divergence in their mean values among species (leading to low rates of niche evolution among species). (B) A scenario in which all species have narrow niche breadths and extensive divergence in their mean values among species (leading to high rates of niche evolution among species). (C) A scenario in which all species have relatively narrow niche breadths on this niche axis but are clustered around one position along the niche axis, thus showing limited divergence in their mean values among species (leading to low rates of niche evolution among species). (D) A scenario in which species have both wide and narrow niche breadths (leading to high variance in niche breadths among species) and intermediate levels of divergence in their mean values among species.

in the tropics (which partially supports the hypothesis of Janzen 1967), but did not examine climatic-niche breadths. Vázquez and Stevens (2004) examined global mean monthly temperature and precipitation ranges and found that temperature does become more temporally stable with decreasing latitude (i.e., narrower range of values as latitude decreases). However, they also found that mean monthly precipitation ranges are larger in the tropics. Thus, Janzen's (1967) hypothesis may only hold for temperature.

Here, we explore the relationships between the rate of climatic-niche evolution and climatic-niche breadth in the salamander family Plethodontidae. Plethodontidae contains 419 of 615 recognized salamander species (AmphibiaWeb 2011). Plethodontids occupy a wide range of microhabitats from aquatic to terrestrial, and even arboreal (e.g., Wake and Lynch 1976; Petranka 1998; Blankers et al. 2012). Plethodontidae also contains the only salamander clade that has radiated substantially in the tropics (tropical bolitoglossines; Wake and Lynch 1976; Wiens 2007).

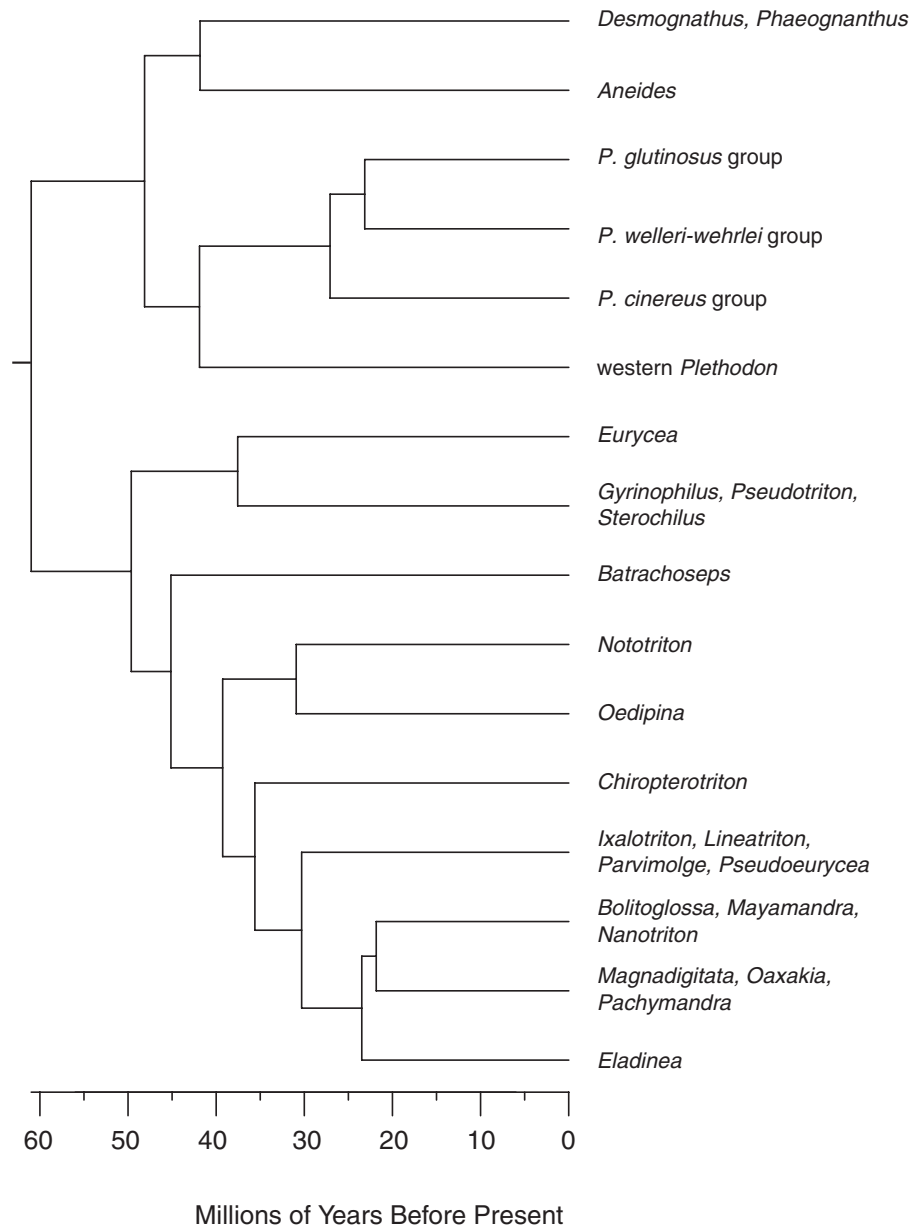
Plethodontids are an excellent study system in which to address the relationship between niche breadth and rate. First, there

is a well-resolved, time-calibrated phylogeny for 250 plethodontid species, along with extensive climatic data for each species (Kozak and Wiens 2010b). These climatic data can be used to estimate the niche breadth of each species, and the phylogeny allows estimation of rates of niche evolution within clades. Second, previous work (Kozak and Wiens 2010b) showed extensive variation between clades in their rates of climatic-niche evolution (where rates were estimated based on changes in mean multivariate niche position among species). Third, there is substantial variation in niche breadths among species (Kozak and Wiens 2007). However, the relationship between breadth and rate has only been implied (Kozak and Wiens 2010b), and has not been explicitly tested in plethodontids (or other groups).

## Materials and Methods

### PHYLOGENY

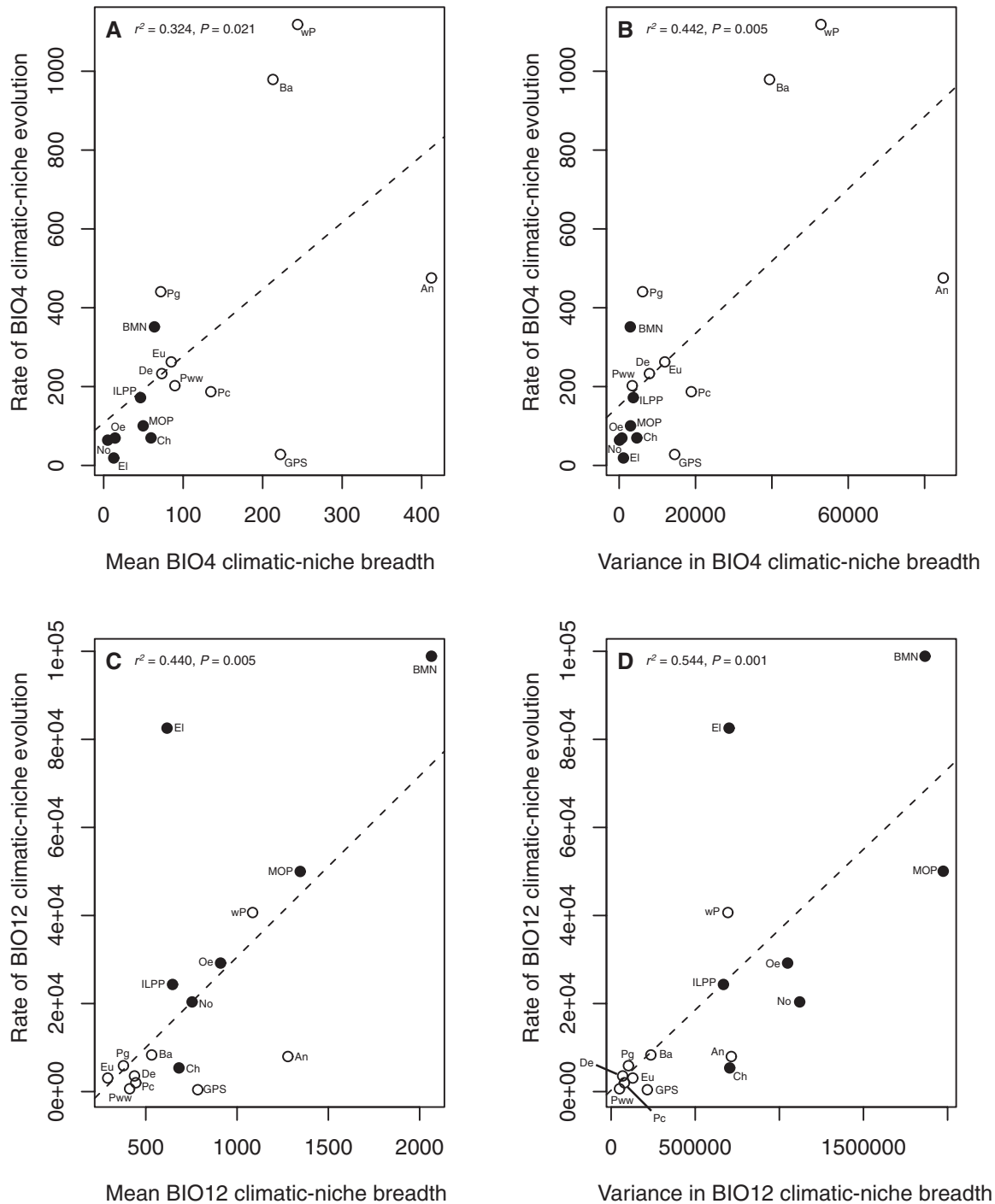
We used the same time-calibrated phylogeny used by Kozak and Wiens (2010b). This phylogeny (from Adams et al. 2009) contains 250 putative plethodontid species, and was constructed by



**Figure 2.** Chronogram of 16 major clades of Plethodontidae used in this study (using a root age of 61 Myr).

combining the trees from Kozak et al. (2009; for higher level relationships and North American species; from multiple nuclear and mitochondrial genes) and Wiens et al. (2007; for tropical bolitoglossines; from mitochondrial genes). Although not every species has data for every gene in these datasets, focused analyses suggest that missing data are not generally problematic for either one, a hypothesis also supported by extensive results from simulations and empirical data (for results and review see Wiens and Morrill 2011). This phylogeny is generally strongly supported and similar to other recent estimates with more limited taxon sampling (e.g., Vieites et al. 2011). The phylogeny is time calibrated using three potential root ages for the family (48, 61, and 69 Million years ago, Myr; from Wiens 2007). These three potential root ages

influence both the absolute and relative ages of clades, although we find that they generally have little impact on our results. These root ages are somewhat younger than other estimates (e.g., those based on mitochondrial and nuclear data; Roelants et al. 2007; Vieites et al. 2007, 2011), but the important issue for our study is whether the ages of more nested clades (e.g., genera) are likely to be accurate. Recent analyses by Zheng et al. (2011) using multiple nuclear genes across all salamanders (using Bayesian estimation in BEAST; Drummond et al. 2006; Drummond and Rambaut 2007) show that their preferred results are very similar to those of Kozak et al. (2009; their Fig. 4) for the median root age (61 Myr) for more nested clades. Specifically, Zheng et al. (2011) estimate the crown-group age of Spelerpinae at approximately 40 Myr,



**Figure 3.** The relationships between the rate of climatic-niche evolution for temperature seasonality (BIO4) and annual precipitation (BIO12), and (A and C, respectively) the mean climatic-niche breadth for BIO4 and BIO12 among species in each clade and (B and D, respectively) the variance in climatic-niche breadth for BIO4 and BIO12. The dashed lines represent PGLS results for the 61 Myr root, and the  $r^2$  and  $P$ -values are listed in each panel. Filled circles are tropical clades (BMN, subgenera *Bolitoglossa*, *Mayamandra*, *Nanotriton* (genus *Bolitoglossa*); Ch, *Chiropterotriton*; EI, subgenus *Eladinea* (genus *Bolitoglossa*); ILPP, *Ixalotriton*, *Lineatriton*, *Parvimolge*, *Pseudoeurycea*; MOP, subgenera *Magnadigitata*, *Oaxakia*, *Pachymandra* (genus *Bolitoglossa*); No, *Nototriton*; Oe, *Oedipina*); open circles are temperate clades (An, *Aneides*; Ba, *Batrachoseps*; De, *Desmognathus*; Eu, *Eurycea*; GPS, *Gyrinophilus*, *Pseudotriton*, *Stereochilus*; Pc, *Plethodon cinereus* group; Pg, *Plethodon glutinosus* group; Pww, *Plethodon welleri-wehrlei* group; wP, western *Plethodon*). See Table S2 for rate, mean, variance, and proportional niche values for each clade, and Table S3 for summary statistics from PGLS.

**Table 1.** Factor loadings, eigenvalues, and percent variation explained for the first four axes of the principal components analysis on the 19 climatic variables. PC1–PC4 account for 89.22% of the variation among species, and account for significantly more variation than expected by chance according to a broken-stick distribution.

Variable	PC1	PC2	PC3	PC4
BIO1—Annual mean temperature	0.62	−0.24	0.72	−0.08
BIO2—Mean diurnal range (mean of monthly [maximum temperature — minimum temperature])	0.12	−0.62	0.08	0.41
BIO3—Isothermality (BIO2/BIO7 × 100)	0.92	0.14	0.01	−0.19
BIO4—Temperature seasonality (SD × 100)	−0.93	−0.20	0.09	0.22
BIO5—Maximum temperature of warmest month	−0.08	−0.69	0.62	0.33
BIO6—Minimum temperature of coldest month	0.94	−0.04	0.28	−0.12
BIO7—Temperature annual range (BIO5 — BIO6)	−0.86	−0.36	0.11	0.29
BIO8—Mean temperature of the wettest quarter	−0.24	0.01	0.55	−0.64
BIO9—Mean temperature of the driest quarter	0.74	−0.24	0.10	0.44
BIO10—Mean temperature of the warmest quarter	−0.21	−0.48	0.81	0.15
BIO11—Mean temperature of the coldest quarter	0.91	−0.07	0.34	−0.13
BIO12—Annual precipitation	0.14	0.87	0.32	0.32
BIO13—Precipitation of wettest month	0.65	0.62	0.18	0.24
BIO14—Precipitation of driest month	−0.72	0.52	0.29	0.13
BIO15—Precipitation seasonality (coefficient of variation)	0.88	−0.34	−0.26	−0.01
BIO16—Precipitation of wettest quarter	0.63	0.63	0.15	0.26
BIO17—Precipitation of driest quarter	−0.69	0.55	0.29	0.17
BIO18—Precipitation of warmest quarter	−0.30	0.74	0.45	−0.16
BIO19—Precipitation of coldest quarter	0.33	0.23	−0.22	0.74
Eigenvalue	8.04	4.22	2.73	1.96
% Variation	42.33	22.21	14.39	10.29

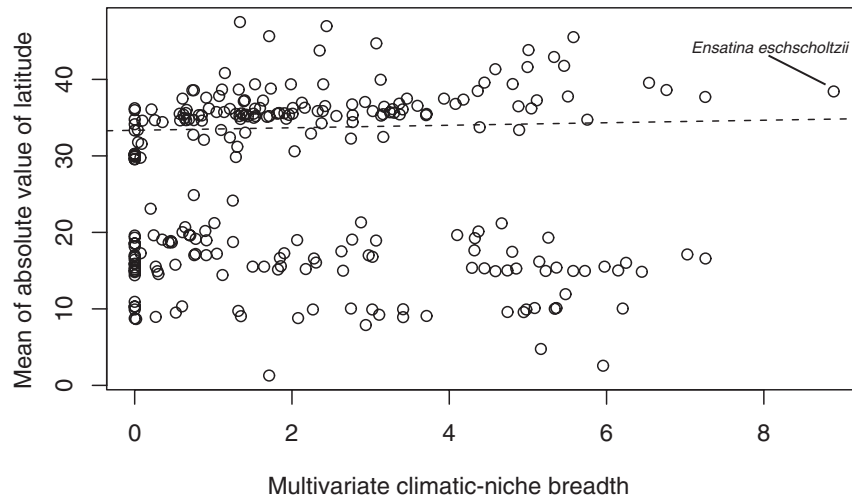
*Desmognathus-Phaeognathus* at approximately 40 Myr, *Aneides* at approximately 30 Myr, and *Plethodon* at approximately 45 Myr, whereas Kozak et al. (2009) estimate Spelerpinae at approximately 36 Myr, *Desmognathus-Phaeognathus* at approximately 36 Myr, *Aneides* at approximately 30 Myr, and *Plethodon* at approximately 42 Myr (i.e., estimates are within approximately 5 Myr).

We used the same 16 clades as Kozak and Wiens (2010b) for comparative analyses (Fig. 2; see below). These 16 clades were chosen for several reasons. First, because they correspond to previously recognized groups (e.g., genera), it is possible to assign many species to these clades which are included in these genera but are not in our tree. Second, they are phylogenetically nonoverlapping (i.e., no clade is a subset of another), and they together encompass most plethodontid species. Third, each clade contains at least four species that are included in the phylogeny, which facilitates estimation of rates of climatic-niche evolution. Previous analyses (Kozak and Wiens 2010b) suggest that use of alternate clade divisions (given these same constraints) has little impact on the overall patterns of climatic-niche evolution and their rates.

#### CLIMATIC DATA AND RATES OF CLIMATIC-NICHE EVOLUTION

We used climate data from 16,914 geo-referenced localities from 354 species (mean = 48 locations/species, range = 1–2287 loca-

tions/species) for which 19 climatic variables (see Table 1) from the WorldClim dataset (Hijmans et al. 2005) had previously been extracted (Kozak and Wiens 2010b). Geo-referenced localities for each species were carefully vetted to ensure that they correspond to known geographic ranges, and that the broad-scale geographic distribution of wide-ranging species was represented. Not all 354 species belong to the 16 focal clades (e.g., the genus *Thorius*), and these were dropped from subsequent clade-level analyses of climatic-niche breadth for a total of 299 species (see below). We performed a principal components analysis (PCA) on the correlation matrix of these 19 climatic variables. PC1–PC5 account for >90% of climatic variation among species. We used PC1–PC4 (explaining a total of 89.22% of the variation) in all subsequent analyses, because these axes each explain more variation than expected by chance (broken-stick distribution; Jackson 1993). Loadings of each climatic variable on each of the first four PC axes are shown in Table 1. Of the 12 variables that load strongly onto PC1 (absolute value >0.5), the four with the largest magnitudes are temperature variables. Of the eight variables that load strongly onto PC2, six are precipitation variables, including the two with the largest magnitudes. The PCA results from Kozak and Wiens (2010b) are similar in magnitude, but often have the opposite sign, presumably due to their use of an additional non-climatic variable (elevation). We obtained a PC score for each locality on each PC axis, and then estimated a mean PC score



**Figure 4.** Relationships between mean absolute values of latitude and multivariate climatic-niche breadth among 250 species of plethodontid salamanders. Temperate species are represented by the points above 25°, and tropical species are represented by the points below 25°. The dashed line represents PGLS results for the 61 Myr root:  $r^2 = 0.018$ ,  $P = 0.032$ . See Table S3 for summary statistics from PGLS.

for each species on each PC axis, by averaging PC scores across localities.

The mean PC score for each species was used as a continuous character to calculate the rate of climatic-niche evolution for each of the 16 clades for each PC axis. Rates of climatic-niche evolution ( $\sigma^2$ ) for each PC axis for each clade were estimated using a censored test in the application Brownie version 2.1.2 (O’Meara et al. 2006). Brownie yields a maximum-likelihood estimate of the rate of phenotypic evolution based on the observed values of the terminal taxa for a character and the estimated value at the root of the tree, given a tree with branch lengths and a Brownian motion (BM) model of evolution. Kozak and Wiens (2010b) assessed the relative fit of a BM model versus an Ornstein–Uhlenbeck (OU) model of evolution for these 16 clades, and found that BM has the best fit for most clades. Additionally, excluding the four clades, which do not consistently fit a BM model (Kozak and Wiens 2010b), does not change the phylogenetic generalized least-squares (PGLS; Martins and Hansen 1997) results for the multivariate analysis of climatic niche breadth in this study (see below; results not shown). A multivariate estimate of rate for each clade was calculated using an unweighted average of the rate estimates for the individual PC axes. Calculating a multivariate rate using a weighted average of the PC axes (each PC axis is weighted by the relative amount of variation it accounts for) does not change the overall results (see Table S3 for PGLS results). Hereafter, we use the term “multivariate” to refer to the unweighted average of rates on the PC axes (or niche breadths, see below), because they encompass multiple PC axes simultaneously and to distinguish this metric of rate from those for individual PC axes and climatic variables. We note, however, that this is not a multivariate metric in a strict, statistical sense.

These average estimates of climatic niche across localities for each species might be biased if some parts of the species range were sampled more extensively than others. Estimating rates from the midpoint of the range of each climatic variable may be less sensitive to this bias than use of the mean (although this approach may instead be more sensitive to outliers). Spearman rank correlation of the midpoint PC scores and mean PC scores for each species on each axis are highly correlated ( $r_s = 0.93$ – $0.98$ ,  $P < 0.0001$ ; for PC1–PC4), strongly suggesting that they should give very similar estimates of rate. Additionally, we expect species to be more common (and thus more likely to be sampled) in parts of their range where climatic conditions are most suitable for them. Thus, if sampling is biased, it should be toward climatic conditions that are optimal for the species.

The estimated rates of climatic-niche evolution do not include all plethodontid species because not all species are included in the phylogeny. However, Kozak and Wiens (2010b) found no significant relationship between the estimated rate for a given clade and the proportion of species sampled within that clade, suggesting that the estimated rates are not strongly biased by incomplete sampling. In addition, they found the highest rates in the most poorly sampled clade, even though poorly sampled clades are more likely to have their rates be underestimated (O’Meara et al. 2006).

To calculate climatic-niche breadth for each species on a given PC axis, we subtracted the minimum PC score from the maximum PC score from all localities for that species. A species represented by only one locality has a climatic-niche breadth of zero on all axes. These species are included in our analyses, given that these species presumably do indeed have very narrow climatic-niche breadths (e.g., additional localities close

to the one recorded would likely have nearly identical climate). Niche breadth was calculated separately for PC1–PC4, generating four orthogonal estimates of climatic-niche breadth for each species. As was done for rates, an unweighted average of climatic-niche breadths across PC1–PC4 was calculated for each species, and was used as the multivariate climatic-niche breadth for a given species. Again, using a weighted average of climatic-niche breadths yielded very similar results (see Table S3). For each of the 16 clades, the mean and variance in climatic-niche breadth of all species within the clade were calculated for each PC and for the multivariate climatic-niche breadth. These estimates of climatic-niche breadth included all species in a clade for which we had climatic data (total among 16 clades: 299 species), even if that species was not represented in the phylogeny. Because the 16 clades represent well-supported, well-established taxonomic groups (e.g., genera), we were able to unambiguously assign species not present in the phylogeny to a clade when calculating mean climatic-niche breadths for species within the clade, rather than restricting these estimates to only the species in the tree. Further, our estimates of climatic-niche breadth (both mean and variance) for each clade are strongly correlated between these two sets of taxa (all species in phylogeny vs. all species with climatic data; for PC1–PC4:  $r_s = 0.79$ – $0.99$ , all  $P < 0.0005$ ).

Finally, the mean proportional climatic-niche breadth for each clade was calculated. This value represents the extent to which species in a clade occupy the full range of climatic conditions that the clade occupies (on a given climatic-niche axis). First, a climatic-niche breadth for each clade was determined by subtracting the minimum value for each PC score from the maximum value for all localities for all species contained in the clade. Next, the estimates of climatic-niche breadth for individual species (see above) were divided by this clade-level niche breadth to get a proportional niche breadth for each species (i.e., the proportion of the clade's niche breadth that a given species occupies). Proportional niche breadths were then averaged across all species within a clade to estimate a mean proportional climatic-niche breadth for each clade.

The estimates described above were calculated for each root age, for each PC axis, and for several individual climatic variables: BIO1 (annual mean temperature), BIO4 (temperature seasonality), BIO5 (maximum temperature of the warmest month), BIO6 (minimum temperature of the coldest month), BIO7 (temperature annual range), BIO12 (annual precipitation), and BIO15 (precipitation seasonality). Plethodontid salamanders are thought to be sensitive to temperature (BIO1), particularly to extremes of temperature (BIO5, BIO6), and to be dependent on mesic environments that require higher precipitation (BIO12; e.g., Petranka 1998; Kozak and Wiens 2010a). BIO4, BIO7, and BIO15 reflect climate seasonality, and allow us to more directly address predictions made from Janzen's hypothesis which is based on

latitudinal differences in annual temperature variability (see also Vázquez and Stevens (2004) for precipitation). These last three variables could be considered measures of climatic-niche breadth on their own. However, by calculating our metric of climatic-niche breadth with these variables, we are looking at how large or small the range of temperature and precipitation seasonality is across the range of each species within a clade. We found that results were generally similar across the different root ages. The results presented below are those for the 61 Myr root age (i.e., the intermediate value between 48 and 69 Myr).

## COMPARATIVE PHYLOGENETIC ANALYSES

To explore the relationship between the rate of climatic-niche evolution and climatic-niche breadth among clades, we performed analyses using PGLS (Martins and Hansen 1997), implemented in the R-package CAIC (Orme 2007) with R version 2.11.1 (R Development Core Team 2010). The 250-species tree was pruned so that each clade was represented by a single species (given the time-calibrated tree, all species in a clade have the same time-span to the root of the clade, making the choice of species irrelevant). This 16-clade tree was then used for PGLS (Fig. 2). Based on the predictions described in the introduction, we tested if a clade's multivariate rate of climatic-niche evolution was (1) negatively related to the mean multivariate climatic-niche breadth among the species in the clade, (2) positively related to the variance in multivariate climatic-niche breadth among species in the clade, or (3) negatively related to the mean proportional multivariate climatic-niche breadth of a clade. We then tested the same three relationships for each of PCs 1–4 separately, and for each of the individual climatic variables (BIO1, BIO4–7, BIO12, and BIO15).

To test the hypothesis that climatic-niche breadths are narrower in the tropics, we used PGLS with the 250-species phylogeny to test if the multivariate climatic-niche breadth for a given species is positively related to the mean absolute value of latitude of the localities where that species occurs. We expected narrower climatic-niches as the absolute value of latitude approached zero. We also tested for a relationship between latitude and niche breadth for individual climatic variables (BIO1, BIO4–7, BIO12, and BIO15). Alternatively, we treated species as being either temperate or tropical, and tested for a difference between the mean values for each group using nonphylogenetic methods (i.e., assuming that latitudinal differences within tropical and temperate regions are unimportant and might obscure this relationship). A Wilcoxon rank-sum two-sample test (nonparametric *t*-test) was used to test for differences between mean niche breadths of tropical versus temperate species (given that climatic-niche breadths are not normally distributed). There is a distinct separation in latitudinal distributions between tropical species (below 25°N; only two otherwise tropical species are found just north of the Tropic of Cancer) and temperate species (above 25°N). This break was



used to categorize species, and agrees with previous classifications of clades as temperate or tropical (e.g., Kozak and Wiens 2010b).

Janzen's (1967) hypothesis suggests that tropical niche breadths should be narrower primarily due to limited temperature seasonality in the tropics. Subsequent research has found that tropical species also have faster rates of niche evolution (Kozak and Wiens 2010b), which suggests the following scenario: limited seasonality leads to narrower niche breadths that lead to faster rates of niche evolution. Each of the analyses above focuses on the second part of this scenario: the relationship between niche breadth and rate. Because there are many possible relationships between niche breadth and rate, we also tested for a relationship between seasonality and rate of niche evolution. Based on the scenario described above, we might expect to find temperature seasonality negatively related to rates of temperature niche evolution. We may also expect this relationship for precipitation seasonality and rate, although the latitudinal pattern will be reversed (precipitation has greater seasonality in the tropics; Vázquez and Stevens 2004). For each species, we calculated a mean BIO4 (temperature seasonality) and mean BIO15 (precipitation seasonality) value. These values were then used to calculate mean temperature and precipitation seasonality values for each clade (mean of species means). We then used PGLS to test for relationships between (1) mean temperature seasonality versus rate of climatic-niche evolution for BIO1, BIO5, and BIO6 (the basic temperature variables; Table 1) and (2) mean precipitation seasonality versus rate of climatic-niche evolution for BIO12 (annual mean precipitation).

Finally, the analyses described above involve many tests and  $P$ -values. Although a Bonferroni correction is often appropriate (e.g., Rice 1989), the application of such a correction to every result in the study would be highly problematic (e.g., many analyses are repeated to address the robustness of the results to different clade ages). Therefore, we did not apply such a correction to every  $P$ -value in the study, but we do not discuss results with  $P > 0.01$ . Furthermore, our major result is that the relationship between niche breadth and rate is either absent or positive, and so our results do not support a relationship between narrower breadths and faster rates, regardless of whether there is a Bonferroni correction.

## Results

For each clade, estimates of the multivariate rate of climatic-niche evolution, the multivariate mean and variance in climatic-niche breadth, and the mean proportional climatic-niche breadth are summarized in Table 2. Estimates for each individual PC and the individual climatic variables are summarized in Tables S1 and S2, respectively. Results of all PGLS analyses for each root age are reported in Table S3.

There is no significant relationship between the mean climatic-niche breadth of species in a clade and the clade's rate of climatic-niche evolution, in either the multivariate analysis ( $r^2 = 0.002$ ,  $P = 0.864$ ) or for individual PCs ( $r^2 = 0.027$ – $0.195$ ,  $P \geq 0.087$ ). Similarly, the relationship between variance in multivariate climatic-niche breadth of a clade and the multivariate rate of climatic-niche evolution is also not significant ( $r^2 = 0.177$ ,  $P = 0.105$ ). The variance in climatic-niche breadth for PC2 is positively related to the rate of climatic-niche evolution for PC2 ( $r^2 = 0.302$ ,  $P = 0.027$ ), but is not significant ( $P < 0.01$ ) for any root age (see Table S3). PC1, PC3, and PC4 have no significant relationship between variance in climatic-niche breadth and rate of climatic-niche evolution ( $r^2 = 0.149$ – $0.256$ ,  $P \geq 0.046$ ). These results are robust across all three root ages (see Table S3).

The rate of climatic-niche evolution for both temperature seasonality (BIO4) and annual precipitation (BIO12) is positively related to both mean climatic-niche breadth (BIO4:  $r^2 = 0.324$ ,  $P = 0.021$ , Fig. 3A; BIO12:  $r^2 = 0.440$ ,  $P = 0.005$ , Fig. 3C) and variance in climatic-niche breadth for these variables (BIO4:  $r^2 = 0.442$ ,  $P = 0.005$ , Fig. 3B; BIO12:  $r^2 = 0.544$ ,  $P = 0.001$ , Fig. 3D). There are no significant relationships between rates of climatic-niche evolution and climatic-niche breadth (mean or variance) for the remaining individual climatic variables (BIO1, BIO5–BIO7, BIO15; see Table S3). Mean proportional climatic-niche breadth is not significantly related to the rate of climatic-niche evolution for the multivariate analysis ( $r^2 = 0.060$ ,  $P = 0.359$ ), or for any of the single variable analyses across all root ages (see PGLS results in Table S3).

Multivariate climatic niches of tropical species are generally similar in width to those of temperate species. PGLS analysis was not significant for any root age (Fig. 4; Table S3). One temperate species, *Ensatina eschscholtzii*, is an outlier, with a very wide multivariate climatic-niche breadth (8.89; Fig. 4). Nevertheless, the ranges of climatic-niche breadths are very similar for temperate species (range: 0.00–8.89; mean = 2.18; without outlier range: 0.00–7.25; mean = 2.13) and tropical species (range: 0.00–7.26; mean = 2.31). A Wilcoxon rank-sum two-sample test shows that mean multivariate climatic-niche breadth for temperate species is not significantly different from that for tropical species ( $W = 7989.5$ ,  $P = 0.676$ ; includes outlier; Table S4).

Similar to the multivariate results, the climatic-niche breadths based on single climatic variables (Table S2) either show no relationship with latitude (BIO1, BIO5, BIO12, BIO15), or a very weak positive relationship with latitude (BIO4, BIO6–7:  $r^2 = 0.023$ – $0.062$ ,  $P \leq 0.016$ ; Table S3). These results are generally similar across different root ages (Table S3). Wilcoxon tests for differences in mean tropical climatic-niche breadth versus mean temperate climatic-niche breadth are significant for BIO4 and BIO7 ( $P \ll 0.001$ ; Table S4), with mean tropical niches

**Table 2.** Summary of data for the 16 plethodontid salamander clades used in the multivariate analyses of climatic-niche rate and breadth.  $N_P$  refers to the number of species in the clade that are included in the phylogeny and  $N_C$  refers to the total number of species in the clade for which we have climatic data (note that all species in the phylogeny have climatic data). Rates and niche breadths are unweighted averages of individual values for PC1–PC4. Estimates from individual PCs and the weighted average are summarized in Table S1, and estimates from individual climatic variables are summarized in Table S2.

Clade	$N_P$	$N_C$	Multivariate rate of climatic-niche evolution	Mean multivariate climatic-niche breadth	Variance in multivariate climatic-niche breadth	Mean proportional climatic-niche breadth
Subgenus <i>Eladinea</i> ( <i>Bolitoglossa</i> )	12	24	0.53	1.95	4.32	0.17
Subgenera <i>Magnadigitata</i> , <i>Oaxakia</i> , <i>Pachymandra</i> ( <i>Bolitoglossa</i> )	20	22	0.26	2.98	6.98	0.31
Subgenera <i>Bolitoglossa</i> , <i>Mayamandra</i> , <i>Nanotriton</i> ( <i>Bolitoglossa</i> )	10	14	0.38	3.86	6.31	0.40
<i>Ixalotriton</i> , <i>Lineatriton</i> , <i>Parvimolge</i> , <i>Pseudoeurycea</i>	37	55	0.22	1.54	2.93	0.18
<i>Chiropterotriton</i>	7	11	0.06	1.84	3.89	0.24
<i>Oedipina</i>	13	16	0.27	1.89	5.17	0.23
<i>Nototriton</i>	6	8	0.12	1.60	5.38	0.24
<i>Batrachoseps</i>	17	26	0.08	2.80	3.26	0.33
<i>Gyrinophilus</i> , <i>Pseudotriton</i> , <i>Stereochilus</i>	4	4	0.03	3.38	3.35	0.62
<i>Eurycea</i>	24	30	0.07	1.30	2.50	0.16
Western <i>Plethodon</i>	7	8	0.20	3.03	3.51	0.43
<i>Plethodon cinereus</i> group	9	9	0.04	1.95	1.84	0.37
<i>Plethodon wehrlei-welleri</i> group	7	7	0.05	1.60	0.46	0.37
<i>Plethodon glutinosus</i> group	28	28	0.14	1.53	1.41	0.25
<i>Aneides</i>	5	7	0.08	4.46	7.12	0.49
<i>Desmognathus</i> , <i>Phaeognathus</i>	28	30	0.12	1.65	1.23	0.29

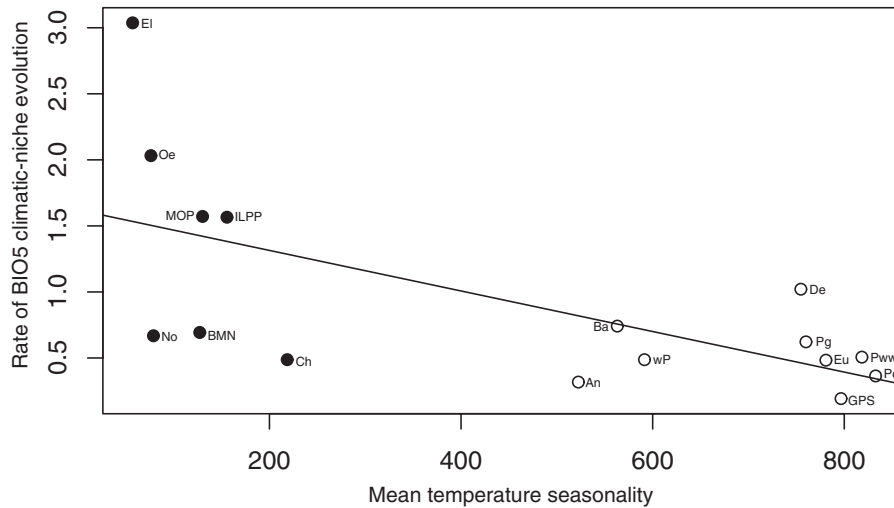
being narrower than mean temperate niches for those two variables. However, results from Wilcoxon tests are not significant for BIO1, BIO5–6, BIO12, or BIO15 ( $P = 0.151$ – $0.742$ ; Table S4).

The rate of climatic-niche evolution for BIO5 (maximum temperature of the warmest month) is significantly negatively related to the mean temperature seasonality for each clade ( $r^2 = 0.409$ ,  $P = 0.008$ ; Fig. 5). Interestingly, there is also an obvious geographic split, as seen in Figure 5. The seven tropical clades have the greatest range of rates for BIO5, and the most limited temperature seasonality. The three clades found primarily in western North America have intermediate temperature seasonality and rates for BIO5. The remaining six clades, with the slowest rates for BIO5 and greatest temperature seasonality, are found in eastern

North America. The relationship between temperature seasonality and rate of climatic niche evolution for BIO1 and BIO6 was also negative, but only significant for BIO1 for the 61 Myr root age (see Table S3 for PGLS results). There was no significant relationship between precipitation seasonality and rate of evolution for BIO12.

## Discussion

The rate of climatic-niche evolution is important to many topics, from responses to global climate change, to speciation, to large-scale patterns of biodiversity. It is often assumed that climatic-niche breadth and the rate of climatic-niche evolution are closely related (e.g., Smith and Beaulieu 2009; Kozak and Wiens 2010b).



**Figure 5.** The relationships between the rate of climatic-niche evolution for maximum temperature of the warmest month (BIO5) and the mean temperature seasonality of a clade. The solid line represents PGLS results for the 61 Myr root:  $r^2 = 0.409$ ,  $P = 0.008$ . Filled circles are tropical clades (BMN, subgenera *Bolitoglossa*, *Mayamandra*, *Nanotriton* (genus *Bolitoglossa*); Ch, *Chiropterotriton*; EI, subgenus *Eladinea* (genus *Bolitoglossa*); ILPP, *Ixalotriton*, *Lineatriton*, *Parvimolge*, *Pseudoeurycea*; MOP, subgenera *Magnadigitata*, *Oaxakia*, *Pachymandra* (genus *Bolitoglossa*); No, *Nototriton*; Oe, *Oedipina*); open circles are temperate clades (An, *Aneides*; Ba, *Batrachoseps*; De, *Desmognathus*; Eu, *Eurycea*; GPS, *Gyrinophilus*, *Pseudotriton*, *Stereochilus*; Pc, *Plethodon cinereus* group; Pg, *Plethodon glutinosus* group; Pww, *Plethodon welleri-wehrlei* group; wP, western *Plethodon*). See Table S2 for rate and mean seasonality values, and Table S3 for summary statistics from PGLS.

However, the relationship between these variables has not been explicitly tested and the expected relationship between them is uncertain.

We found that rate of climatic-niche evolution and mean climatic-niche breadths are generally unrelated among the 16 clades of plethodontid salamanders. For PC-based analyses, only results for PC2 approach were significant. Kozak and Wiens (2010b) found that PC1 largely accounts for the climatic variation between tropical and temperate species (see Fig. 1B in Kozak and Wiens 2010b), whereas PC2 largely accounts for within-region variation in climate among species. In both studies, climatic variables have similar loadings on these axes, with PC1 having stronger loadings for temperature variables than precipitation variables, and PC2 having stronger loadings for precipitation than temperature variables (but these axes are not solely temperature vs. precipitation; Table 1). Our results suggest that variance in climatic-niche breadth on PC2 is positively related to rates of climatic-niche evolution, suggesting that precipitation may be important in explaining within-region variation in the climatic-niches of plethodontid salamanders, although this result was not significant.

For temperature seasonality (BIO4) and annual precipitation (BIO12), we find a strong positive relationship between the rate of climatic-niche evolution and both mean climatic-niche breadth and variance in climatic-niche breadth, even though previous analyses of plethodontids (Kozak and Wiens 2007, 2010b) predicted a negative relationship between mean climatic-niche

breadth and rate. In contrast, the remaining temperature variables (BIO1, BIO5–7) and precipitation seasonality (BIO15) show no relationship between niche breadth and rate. Finding the same pattern in both a temperature and precipitation variable suggests that the positive relationship is consistent across the two major climatic axes.

Why should rates of niche evolution be faster for clades in which species have broader climatic-niches? This may depend on the climatic variable. For precipitation, the seven clades with the fastest rates of precipitation niche evolution and the broadest, most variable precipitation niches (Fig. 3C–D) all inhabit the very wettest environments (the tropics and the Pacific northwest of North America), for which the distinction between the available moisture regimes is not wet versus dry, but rather wet versus very wet. This dichotomy is reflected in the maximum mean precipitation values among species of these seven clades (approximately 2500–4800 mm for the seven fastest clades vs. 1400–2150 mm in the nine slower evolving clades on this niche axis). Also, these seven clades have the greatest ranges of mean precipitation values among species within the clade (range among species of approximately 1900–3600 mm for the seven fast clades vs. approximately 260–1550 mm for the nine slow clades). This pattern suggests that these seven faster evolving clades live in generally wetter environments, with a much wider range of precipitation regimes compared to the nine slower evolving clades. It could be that in these seven faster evolving clades, the basic moisture requirements are generally met, and thus species are able to

spread into a variety of wet environments. Likewise, in the nine slower evolving clades, the species occur in drier environments that may be closer to the limits of their environmental tolerances, constraining both their evolution and the range of environments that individual species can tolerate. This hypothesis should be tested with more in-depth studies of plethodontid environmental tolerances, and with macroevolutionary studies similar to this one in other groups of organisms.

For temperature seasonality, the six plethodontid clades with the slowest rates of temperature seasonality niche evolution and the narrowest, least variable temperature seasonality niches (Fig. 3A–B) are all tropical clades. In general, the temperate zone has much greater temperature seasonality than the tropics (Janzen 1967; MacArthur 1972; Vázquez and Stevens 2004). In the tropics, all climatic regimes may have low-temperature seasonality, regardless of the absolute difference in mean temperature between them. Thus, given the similarity in seasonality values among species, the rate of evolution is expected to be very slow. Indeed, species in tropical clades show the lowest magnitude and narrowest range of absolute BIO4 values (raw BIO4 values for tropical species range from approximately 20–400), whereas species in temperate clades show a much higher magnitude and wider range of absolute BIO4 values (raw BIO4 values for eastern North American species: approximately 500–1200; for western North American species: approximately 190–950). Interestingly, the three clades with the fastest rates, and broadest, most variable temperature seasonality niches, all occur primarily in western North America, yet have intermediate absolute BIO4 values (but have the widest difference between maximum and minimum raw BIO4 values). This pattern suggests that there is some intermediate level of temperature seasonality that is related to faster rates and broader, more variable niches in plethodontid salamanders, and the very low or very high levels of temperature seasonality constrain evolution along this niche axis, resulting in slower rates.

We also found that the mean proportional climatic-niche breadths of species in a clade were generally not related to the rate of climatic-niche evolution of a clade. However, in the two instances for which the relationship between these two variables approached significance (for PC3 and BIO1), clades that have narrower proportional climatic-niche breadths have faster rates of climatic-niche evolution. BIO1 and other temperature-related variables load strongly onto PC3, and these results are consistent with predictions based on Janzen's (1967) hypothesis.

Contrary to our expectations, we find that multivariate climatic-niches are not strongly narrower in tropical plethodontids relative to temperate species (Fig. 4). Interestingly, Janzen's (1967) hypothesis and previous work on niche breadth in plethodontids and frogs (Kozak and Wiens 2007; Hua and Wiens 2010) are both based on temperature, rather than climatic-niches in general. Vázquez and Stevens (2004) suggest that because annual

precipitation is more temporally variable in the tropics, temperate precipitation-niche breadths should be narrower than tropical ones. Indeed, we do find that the mean climatic-niche breadth for BIO12 (annual precipitation) for temperate species is somewhat smaller than that for tropical species, but this difference is not significant (temperate mean: 543.01; tropical mean: 990.46;  $W = 6934.5$ ;  $P = 0.151$ ; see Table S4 for other variables). Additionally, there is no relationship between rate of climatic-niche evolution and climatic-niche breadth for BIO15 (precipitation seasonality). PGLS analyses of the relationship between latitude and climatic-niche breadth for the remaining individual variables were either nonsignificant (BIO1, BIO5, BIO12), or weakly positively related (BIO4, BIO6–7), also suggesting that climatic-niche breadth has no strong relationship with latitude.

We did find a significant negative relationship between mean temperature seasonality (BIO4) of species in a clade and the rate of climatic-niche evolution of the maximum temperature of the warmest month (BIO5). This result, and the marginally nonsignificant results for the other temperature variables (BIO1, BIO6), suggests that limited temperature seasonality in the tropics is weakly associated with faster rates of temperature-niche evolution, despite the general lack of significant relationships between climatic-niche breadth and rate of climatic-niche evolution and the positive relationship between the rate of evolution of BIO4 (temperature seasonality) and its breadth. There is no relationship between precipitation seasonality and climatic-niche rate for annual precipitation, which suggests that even though the seasonality pattern of precipitation is opposite to that of temperature (the tropics have more seasonal precipitation than the temperate zone; MacArthur 1972; Vázquez and Stevens 2004), precipitation seasonality is not related to rates of precipitation niche evolution.

Overall, we make several caveats regarding these analyses and results. First, these analyses address the realized climatic niche of the species involved (i.e., the conditions where species occur, given both abiotic and biotic factors), and not necessarily the fundamental climatic-niche (i.e., the actual physiological tolerances of species to climatic conditions; Hutchinson 1957). Behavioral or plastic responses to climate may also be important in determining climate niche breadths (e.g., Huey et al. 2003). Kozak and Wiens (2010b) showed that rates of climatic-niche evolution are likely influenced by species interactions in plethodontids: the amount of geographic overlap between clades is negatively related to rates of climatic-niche evolution within clades. This suggests that more spatially isolated clades have faster rates of climatic-niche evolution. Their results raise the possibility that climatic-niche breadth may also be influenced by species interactions, especially for the variables (temperature seasonality and annual precipitation) showing a significant relationship between niche breadth and rate. However, PGLS analysis using our climatic-niche breadth data and data on clade overlap (from Table 2

in Kozak and Wiens 2010b) reveals no significant relationships between climatic-niche breadth (for mean, variance, and mean proportional) and clade overlap for all variables across all root ages, including for annual precipitation (results not shown). Furthermore, analyses of individual plethodontid species suggest that climatic variables are generally important in limiting their geographic ranges relative to species interactions (e.g., Kozak and Wiens 2006, 2010a) but this may depend on the particular part of the range limits being considered (e.g., Gifford and Kozak 2012). Thus, our results are not necessarily an artifact of species interactions on climate niche breadths.

Nevertheless, the climatic niche as analyzed here (based on climatic conditions in known localities) may still be only a subset of the fundamental niche, even without the impact of biotic interactions. Peterson et al. (2011) define this as the “existing fundamental niche” based on the idea that climatic tolerances of a species may be underestimated because some climatically distinct (but tolerable) locations are not accessible to individuals of the species due to nonclimatic limitations on dispersal (see also Barve et al. 2011). For example, for a species found only on an island, some parts of the mainland may have climatic conditions that do not occur on the island but are nevertheless within the range of tolerances of species on the island, leading to underestimation of the actual climatic tolerances of the island species. A similar situation can be envisioned for species on different continents, or separated by a geographic barrier on the same continent. The existing fundamental niche may be further influenced by changes in climate over time. Thus, the differences we observe in mean climatic-niches between species (used to calculate rate) and climatic-niche breadths may be influenced by nonevolutionary processes such as the differences in accessible environments (locally, regionally, and temporally) for each individual species (e.g., Godsoe 2010; Soberón and Peterson 2011).

However, it seems unlikely that these differences in accessibility explain our results on climatic-niche breadth and rate of climatic-niche evolution, considering our observations on patterns of proportional climatic-niche breadth. Given that the clades we use tend to each be confined to a single, relatively circumscribed geographic region (e.g., eastern North America, western North America, southern Mexico, lower Central America), the proportional climatic niche breadth addresses the climatic-niche breadth of a species in relation to the total climate space occupied by the clade in the region where they occur. We find that most of the 299 species in our analyses have relatively small multivariate proportional niche breadths (mean: 0.26, range: 0.00–0.94), and most clades have mean proportional climatic niche breadths among species of less than 0.50 (Table 2; excepting the *Gyrinophilus* clade, with only four species). This pattern suggests that the observed climatic niche distributions and breadths are determined more by the limited tolerances of species to climatic conditions

within the regions where they occur, rather than by their inability to reach novel climatic conditions in other geographic regions. In fact, it is hard to imagine why species would be adapted to novel climatic conditions in other regions that they are never exposed to, given that natural selection should favor adaptation to present or recent climates. Finally, it is unclear why there should be strong, nonrandom relationships between variables such as niche breadth, niche rate, clade overlap, and species diversification, if the estimated climatic niches of plethodontids are simply artifacts of limited dispersal caused by nonclimatic factors.

A second major caveat is that there may be substantial variation in which climatic variables limit geographic ranges, both within clades and within species. For example, within a clade, different variables may be important to different species in limiting their geographic ranges. Further, different parts of the geographic range of a single species could be limited by different climatic variables (e.g., northern vs. southern range limits, upper vs. lower elevational range limits; MacArthur 1972). If there is extensive variation within species and clades as to which climatic variables limit their geographic ranges, it may be difficult to detect patterns at the scale of species and clades. Nevertheless, we do find significant relationships between niche breadth and rate for two biologically important variables (temperature seasonality and annual precipitation).

Third, plethodontids are ectotherms that may be particularly sensitive to the two main axes of climatic variation we examined (temperature and precipitation). Different patterns may occur in other groups, depending on their physiology and other factors.

Fourth, analyses of climatic-niche distribution are potentially influenced by species-level taxonomy. For example, *E. eschscholtzii* may have a wide multivariate climatic-niche breadth because it is “undersplit” by current taxonomy and may actually be multiple species (e.g., the subspecies *croceater*, *eschscholtzii*, *klauberi*, and *xanthoptica* are considered potential “genealogical entities” and the subspecies *oregonensis* and *platensis* may represent multiple lineages; p. 992 of Kuchta et al. 2009). In general, temperate plethodontids have been more thoroughly studied for patterns of genetic variation within named species than tropical species, revealing several unnamed lineages that seem to represent distinct species (e.g., in *Desmognathus* and *Eurycea*; Kozak et al. 2005, 2006, 2009). Hence, there may be concern that tropical plethodontids are “undersplit,” biasing our estimates of climatic-niche breadth in tropical taxa to be wider on average than more narrow climatic-niche breadths of the more finely split temperate taxa. However, we find no evidence that climatic niche breadths are consistently narrower in either temperate or tropical taxa. Instead, most tropical species are narrowly distributed and therefore tend to be represented by relatively few localities (for 197 species, range: 1–68, mean: 7 localities) compared to temperate species (for 157 species, range: 1–2287, mean: 98 localities). Thus,

tropical species do not have significantly wider niches, and there is little evidence that tropical species are widely distributed and undersplit (or that temperate species are oversplit).

Finally, our analyses involve comparisons among clades, a practice that assumes that there are consistent differences among clades that can be detected. Our results (see also Kozak and Wiens 2010b) show that there are substantive differences in the rate of climatic-niche evolution among clades, and that clades also differ considerably in climatic-niche breadth (Table 2). However, it is possible that within-clade variation might swamp between-clade variation, at least in some cases. For example, if many or most clades showed a broad range of within-species niche breadths, from very narrow to very wide, we might not expect any relationship in our between-clade comparisons of within-clade rates of niche evolution and mean species niche breadths. In addition, given only 16 clades, our power to detect weaker relationships between rates of climatic-niche evolution and climatic-niche breadth may be limited.

In summary, we find no strong relationships between the rate of multivariate climatic-niche evolution and the breadth of multivariate climatic-niches in plethodontid salamanders. However, we do find significant positive relationships between rate and breadth for temperature seasonality and annual precipitation. We also find a significant negative relationship between temperature seasonality and rate of climatic-niche evolution for maximum yearly temperature. Overall, our results show that there is not necessarily a tendency for clades of species with relatively narrow niche breadths to have faster rates of niche evolution. Nevertheless, it will be important to test the generality of these results in other clades.

## ACKNOWLEDGMENTS

We thank X. Hua, J. Levinton, G. Mayer, A.T. Peterson, J. Soberón, J. True, and two anonymous reviewers for helpful comments on the manuscript.

## LITERATURE CITED

- AmphibiaWeb: Information on amphibian biology and conservation [web application]. 2011. Berkeley, California: AmphibiaWeb. Available at <http://www.amphibiaweb.org>. Accessed October 19, 2011.
- Adams, D. C., C. M. Berns, K. H. Kozak, and J. J. Wiens. 2009. Are rates of species diversification correlated with rates of morphological evolution? *Proc. R. Soc. B. Lond.* 276:2729–2738.
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222:1810–1819.
- Baselga, A., E. Recuero, G. Parra-Olea, and M. García-París. 2011. Phylogenetic patterns in zopherine beetles are related to ecological niche width and dispersal limitation. *Mol. Ecol.* 20:5060–5073.
- Blankers, T., D. C. Adams, and J. J. Wiens. 2012. Ecological radiation with limited morphological diversification in salamanders. *J. Evol. Biol.* 25:634–646.
- Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling rees. *BMC Evol. Biol.* 7:214.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4:e88.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Syst.* 19:207–33.
- Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.* 46:5–17.
- Gifford, M. E., and K. H. Kozak. 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* 35:193–203.
- Godsoe, W. 2010. Regional variation exaggerates ecological divergence in niche models. *Syst. Biol.* 59:298–306.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. The WorldClim interpolated global terrestrial climate surfaces version 1.3. Available at <http://www.worldclim.org>.
- Hua, X., and J. J. Wiens. 2010. Latitudinal variation in speciation mechanisms in frogs. *Evolution* 64:429–443.
- Huey, R. B., and J. G. Kingsolver. 1993. Evolution of resistance to high temperature in ectotherms. *Am. Nat.* 142:S31–S46.
- Huey, R. B., P. E. Hertz, and B. Sinervo. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161:357–366.
- Hutchinson, G. E. 1957. A treatise on limnology. Wiley and Sons, New York.
- Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* 74:2204–2214.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101:233–249.
- Kozak, K. H., and J. J. Wiens. 2006. Does niche conservatism drive speciation? A case study in North American salamanders. *Evolution* 60:2604–2621.
- . 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. *Proc. R. Soc. Lond. B* 274:2995–3003.
- . 2010a. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *Am. Nat.* 176:40–54.
- . 2010b. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecol. Lett.* 13:1378–1389.
- Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution* 59:2000–2016.
- Kozak, K. H., R. A. Blaine, and A. Larson. 2006. Gene lineages and eastern North American palaeodrainage basins: phylogeography and speciation in salamanders of the *Eurycea bislineata* species complex. *Mol. Ecol.* 15:191–207.
- Kozak, K. H., R. W. Mendyk, and J. J. Wiens. 2009. Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in co-existing clades of North American salamanders. *Evolution* 63:1769–1784.
- Kuchta, S. R., D. S. Parks, R. L. Mueller, and D. B. Wake. 2009. Closing the ring: historical biogeography of the salamander ring species *Ensatina eschscholtzii*. *J. Biogeogr.* 36:982–995.
- MacArthur, R. H. 1972. Geographical ecology. Harper and Row Publishers, Inc., New York.
- Mandle, L., D. L. Warren, M. H. Hoffmann, A. T. Peterson, J. Schmitt, and E. J. von Wettberg. 2010. Conclusions about niche expansion in introduced *Impatiens walleriana* populations depend on method of analysis. *PLoS ONE* 5:e15297.

- Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149:646–667.
- McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecol. Lett.* 12:550–560.
- O'Meara, B. C., C. Ané, M. J. Sanderson, and P. C. Wainwright. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* 60:922–933.
- Orme, D. 2007. The CAIC package: comparative methods using independent contrasts. Available at <http://r-forge.rproject.org/projects/caic/>.
- Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78:419–433.
- . 2011. Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr.* 38:817–827.
- Peterson, A. T., and D. A. Vieglais. 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* 51:363–371.
- Peterson, A. T., J. Soberón, R. P. Anderson, R. G. Pearson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. *Ecological niches and geographic distributions*. Princeton Univ. Press, Princeton, New Jersey.
- Petranka, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, DC.
- R Development Core Team. 2010. R: a language and environment for statistical computing, v. 2.11.1. R Foundation for Statistical Computing. Available at <http://cran.R-project.org>, Vienna, Austria.
- Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and R. K. Colwell. 2007. Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *Am. Nat.* 170:602–616.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:222–225.
- Roelants, K., D. J. Gower, M. Wilkinson, S. P. Loader, S. D. Biju, K. Guillaume, L. Moriau, and F. Bossuyt. 2007. Global patterns of diversification in the history of modern amphibians. *Proc. Natl. Acad. Sci. USA* 104:887–892.
- Smith, S. A., and J. M. Beaulieu. 2009. Life history influences rates of climatic niche evolution in flowering plants. *Proc. R. Soc. Lond. B* 276:4345–4352.
- Soberón J., and A. T. Peterson. 2011. Ecological niche shifts and environmental space anisotropy: a cautionary note. *Rev. Mex. Biodivers.* 82:1348–1355.
- Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Roguet. 2005. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biol.* 11:2234–2250.
- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. USA* 106:19637–19643.
- Vázquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: Concepts and evidence. *Am. Nat.* 164:E1–E19.
- Vieites, D. R., M. S. Min, and D. B. Wake. 2007. Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proc. Natl. Acad. Sci. USA* 104:19903–19907.
- Vieites, D. R., S. Nieto Roman, M. H. Wake, and D. B. Wake. 2011. A multi-genetic perspective on phylogenetic relationships in the largest family of salamanders, the Plethodontidae. *Mol. Phylogenet. Evol.* 59:623–635.
- Wake, D. B., and J. F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Sci. Bull. Nat. Hist. Mus. Los Angeles Co.* 25:1–65.
- Whitlock, M. C. 1996. The Red Queen beats the jack-of-all-trades: The limitations on the evolution of phenotypic plasticity and niche breadth. *Am. Nat.* 148:S65–S77.
- Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. *Am. Nat.* 170:S86–S306.
- Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.* 36:519–539.
- Wiens, J. J., and M. C. Morrill. 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Syst. Biol.* 60:719–731.
- Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168:579–596.
- Wiens, J. J., G. Parra-Olea, M. García-París, and D. B. Wake. 2007. Phylogenetic history underlies elevational patterns of biodiversity in tropical salamanders. *Proc. R. Soc. B. Lond.* 274:919–928.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J.-A. Grytnes, S. P. Harrison, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13:1310–1324.
- Zheng, Y., R. Peng, M. Kuro-o, and X. Zeng. 2011. Exploring patterns and extent of bias in estimating divergence time from mitochondrial DNA sequence data in a particular lineage: a case study of salamanders (Order: Caudata). *Mol. Biol. Evol.* 28:2521–2535.

Associate Editor: G. Mayer

## *Supporting Information*

The following supporting information is available for this article:

**Table S1.** Rates of climatic-niche evolution, mean climatic-niche breadths, variances in climatic-niche breadth, and proportional climatic-niche breadths for each PC score for each clade.

**Table S2.** Rates of climatic-niche evolution, mean climatic-niche breadths, variances in climatic-niche breadth, and proportional climatic-niche breadths for BIO1, BIO4–BIO7, BIO12, and BIO15 for each clade.

**Table S3.** PGLS results for all analyses for all root ages.

**Table S4.** Tropical and temperate mean climatic-niche breadths and Wilcoxon test results.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.