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ORIGINAL ARTICLE

Climatic niche breadth and species richness in temperate treefrogs

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ABSTRACT

Aim Patterns of species richness are often closely linked with climate, but the specific mechanisms by which species' climatic niches underlie large-scale richness patterns remain poorly understood. It has been hypothesized that reduced temperature seasonality in the tropics promotes the evolution of species with narrow temperature niche breadths, and that this hypothesis helps explain high tropical richness. However, the relationship between species' climatic niche breadths and species richness has yet to be tested. We have addressed this issue using treefrogs (Hylidae) in eastern North America.

Location Eastern North America.

Methods We characterized climatic niches and niche breadths for all 24 hylid species in eastern North America using temperature and precipitation variables. We then examined the relationships between species richness, climatic niche positions and climatic niche breadths using phylogenetic comparative methods.

Results Species richness was negatively associated with mean climatic niche breadth, such that high-richness climates had species with narrower climatic niches. Our results also supported the roles of niche conservatism and the time-for-speciation effect in generating the relationship between climate and species richness in the region (more species in warm, wet regions that have been inhabited longer). Importantly, we show that the invasion of low-richness climates has occurred primarily through recent intraspecific niche expansion into these climates rather than evolution of species that are narrowly specialized for these conditions (although the two hylid clades studied showed somewhat different patterns).

Main conclusions We found that climatic zones with high species richness contain more species with narrower climatic niche breadths. Our results suggest that this pattern arose because narrow climatic niche breadths restricted the dispersal of most hylid species out of the ancestral, warm, moist climatic zones, allowing more time for speciation to build up higher species richness in these zones.

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Keywords

Amphibians, dispersal, eastern North America, Hylidae, niche conservatism, niche evolution, niche expansion, speciation, species richness, time-for-speciation effect.

INTRODUCTION

Patterns of species richness are often strongly correlated with large-scale variation in climate (e.g. Hawkins *et al.*, 2003) but the mechanisms underpinning these relationships remain unclear. The species climatic niche is a fundamental concept that can link climate with the mechanisms that directly influence species richness (e.g. Kozak & Wiens, 2012), specifically speciation, extinction and dispersal (e.g. Ricklefs, 1987, 2004; Wiens & Donoghue, 2004). Similar to the Grinnellian niche

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(Grinnell, 1917; Soberón, 2007), the species realized climatic niche comprises the set of large-scale climatic conditions (e.g. temperature and precipitation) that prevail where a species occurs (Soberón, 2007). Most species are limited to a particular range of climatic conditions, and whether these ranges (climatic niche breadths) are large or small may have important implications for species richness along climatic gradients. For example, if climatic niche widths are uniformly very wide (e.g. every species can occur everywhere) there should be little relationship between climate and richness. However, it remains highly uncertain how exactly patterns of species richness and patterns of climatic niche widths are related.

A negative relationship between species climatic niche widths and species richness has been suggested in many papers but not explicitly tested. In a landmark paper, Janzen (1967) hypothesized that the reduced temperature seasonality of tropical regions promotes the evolution of species with narrow climatic tolerances for temperature. These narrow tolerances would increase the effectiveness of topographical barriers, limiting dispersal across climatic gradients (e.g. along elevational transects). Although Janzen (1967) emphasized that he did not intend this hypothesis to explain richness patterns, many subsequent authors have explicitly suggested that narrow climatic niche widths in the tropics are related to large-scale richness patterns (e.g. Huey, 1978; Mittelbach *et al.*, 2007; Cadena *et al.*, 2012). Researchers have suggested that, as species track optimal environmental conditions during periods of climate change, narrower climatic niche breadths favour population fragmentation and reduced gene flow, accelerating allopatric speciation (see Ghalambor *et al.*, 2006, for a review). In temperate regions, greater seasonal variability of temperature would instead lead to species with broad climatic tolerances and reduced potential for range fragmentation and allopatric speciation. These differences could, in theory, lead to higher tropical speciation rates and thus higher tropical species richness (Mittelbach *et al.*, 2007). Although previous research has compared species climatic niche breadths between regions (i.e. tropical versus temperate; Cadena *et al.*, 2012; Fisher-Reid *et al.*, 2012), we are not aware of any study that has linked climatic niche breadth directly to species richness patterns.

A relationship between climatic niche breadth and species richness might also arise through the interplay of time, speciation, niche conservatism and niche evolution. In general, invasion of novel climatic regimes may be restricted by the tendency of a species' niche to resemble that of its ancestor, i.e. niche conservatism (see Wiens & Graham, 2005, and Wiens *et al.*, 2010a, for reviews). For example, evidence from various clades suggests that niche conservatism limits invasion of temperate regions by tropical lineages (e.g. frogs, Wiens *et al.*, 2006; bats, Stevens, 2006; birds, Hawkins *et al.*, 2007; mammals, Buckley *et al.*, 2010; vertebrates, Smith *et al.*, 2012). This mechanism may then lead to a build-up of richness within the ancestral climatic zone over time (e.g. Wiens & Donoghue, 2004). Thus niche conservatism is often associated with the 'time-for-speciation effect' (*sensu* Stephens & Wiens, 2003). Under this latter hypothesis, the richness of a given clade is higher in areas (or climatic zones) that have been colonized longer by that clade, because there has been more time for speciation to generate new species and richness to accumulate.

Based on this hypothesis of time and niche conservatism, we postulated that patterns of species richness within temperate or tropical regions could be driven (at least in part) by the evolution of niche breadths. Specifically, some climatic zones may have low richness because they have only recently been colonized by species that have evolved wide niche breadths that allow them to occur under many conditions, whereas climatic zones that have been inhabited for longer have species with narrower niche breadths that can tolerate only a limited range of conditions. This pattern of species niche breadths along environmental gradients might occur within both temperate regions (e.g. cold regions colonized by temperature generalists) and tropical regions (e.g. dry regions colonized by species that can tolerate both wet and dry conditions). Alternatively, species in more extreme environments on a given niche axis for a given clade might have narrower niche breadths on that axis (e.g. Wiens *et al.*, 2013), such that, for example, deserts are inhabited only by desert specialists and cold regions only by cold-climate specialists.

Furthermore, the potential relationships between niche breadths on different axes remain poorly explored. For example, do species with narrower niche breadths for temperature have wider niche breadths for precipitation (as might be predicted given contrasting patterns in tropical versus temperate seasonality for temperature versus precipitation; Vázquez & Stevens, 2004)? Alternatively, do species tend to be broadly or narrowly distributed on both axes simultaneously? This also raises similar questions about the relationship between niche position and niche breadth. For instance, are species that inhabit warmer or wetter climates more likely to have wider or narrower niche breadths compared with those occupying colder or drier conditions?

We used an integrative phylogenetic approach to test whether climatic zones with high richness tend to be inhabited by species with narrow climatic niche breadths, and to explore potential explanations for such a pattern. A negative relationship between species richness and climatic niche breadth has been implied by various studies (e.g. Cadena *et al.*, 2012; Fisher-Reid *et al.*, 2012) showing narrower temperature niche breadths of species inhabiting tropical (i.e. high-richness) regions compared with those occupying temperate (i.e. low-richness) regions, but has not been tested directly. Importantly, precipitation niche breadths may be broader in the tropics (Vázquez & Stevens, 2004), suggesting that a relationship between richness and climatic niche breadth cannot be inferred directly from greater tropical species richness alone. To reduce the potentially confounding effects of comparing tropical versus temperate regions, we focused on a group of temperate species. We analysed hylid frogs in temperate, eastern North America (24 species in the genera *Acris*, *Pseudacris* and *Hyla*; north of Mexico) for which both climatic and phylogenetic data were available for all species (Wiens *et al.*, 2011). We addressed the following questions. (1) Under what climatic conditions have eastern North American hylids attained the highest regional richness? (2) In high-richness climates, do species have narrow or wide climatic niche breadths for temperature and precipitation? (3) Do species with narrow temperature niche breadths have wider precipitation niche breadths, and vice versa? (4) How is climatic niche position (i.e. warmer/colder or wetter/drier) related to niche breadth (i.e. narrow or wide) for both climatic variables? (5) Is a pattern of narrower niche breadth in high-richness climates explained by greater time spent in these climatic zones, and by recent expansion of certain species' climatic niches into low-richness climates? Previous studies have addressed species richness, time and niche conservatism in hylids (e.g. Wiens *et al.*, 2006, 2011) but have not addressed the fundamental questions about niche breadth posed here, nor have they addressed what explains richness patterns within the temperate zone.

MATERIALS AND METHODS

Phylogeny, locality and climatic data

Phylogenetic and locality information were obtained from Wiens *et al.* (2011) for all 24 species in eastern North America (north of Mexico) and for 56 related species in the tribe Hylini (including all genera in the tribe). Most other genera of hylids occur in tropical Middle America (Mexico to Panama) and adjacent subtropical North America (i.e. *Smilisca* in extreme southern Texas and Arizona). Locality data included 2157 unique localities (means of 26.96 ± 65.21 localities species^{-1} for all 80 species and 49.33 ± 112.69 localities species^{-1} for the 24 species in our study area). Locality data were carefully vetted to ensure that no localities were outside known species' ranges (e.g. based on Conant & Collins, 1998) and that sampled localities spanned each species' full geographical range. The time-calibrated phylogeny for hylids, based on multiple nuclear and mitochondrial genes (Wiens *et al.*, 2011), was pruned to include only these 80 species. The phylogeny is relatively well supported (based on likelihood bootstraping), especially for the focal 24 species (Fig. 6 of Wiens *et al.*, 2010b).

For each locality, we extracted relevant climatic variables (see below) at *c.* 1-km^2 resolution from the WorldClim database (Hijmans *et al.*, 2005; http://www.worldclim.org/bioclim) using the 'raster' package (version 2.0–12; Hijmans & van Etten, 2012) in R 2.15.0 (R Development Core Team, 2011). Climatic data and sample sizes for each species are provided in Appendix S1 in Supporting Information (Tables S1–S3). Throughout the paper, specific bioclimatic variables are indicated with the prefix BIO.

In theory, narrow climatic niche breadths might represent an artefact of limited sampling of localities. However, this seems unlikely here, as hylid ranges are well known and well sampled in eastern North America. Furthermore, a previous study has shown that estimates of climatic niche breadth should be insensitive to limited sample sizes in hylids, because within-locality seasonal variation seems to drive species' overall climatic niche breadths (Quintero & Wiens, 2013). Climatic niche breadths might also be limited by a lack of access to more extreme climatic conditions. However, all hylid species in eastern North America have unimpeded terrestrial access to colder, warmer, drier and wetter climates to the north, south and west.

Climatic niche breadth

To analyse how climatic niche position and climatic niche breadth relate to species richness, only species occurring in eastern North America (defined as having a range that extends east of 100° longitude) were considered. For these 24 species, localities extending west of 100° were omitted (outside eastern North America). However, including these localities did not change our results (see Fig. S1 in Appendix S1). Almost all hylids in eastern North America are endemic there, and have western range limits that occur east of (or very close to) 100°. We also excluded *Smilisca baudinii* (occurring east of 100° but only in the subtropical southern tip of Texas, thus barely entering temperate North America) and the non-native *Osteopilus septentrionalis* of southern Florida (Conant & Collins, 1998).

We calculated temperature and precipitation niche breadths (Fig. 1) by pooling localities for each species and subtracting minimum from maximum values among localities for both annual mean temperature (BIO1) and annual precipitation (BIO12). As an alternative approach, niche breadths for temperature were calculated by pooling the localities for each species and subtracting the minimum value among localities of the minimum temperature of the coldest month (BIO6) from the maximum value of the maximum temperature of the warmest month (BIO5). For precipitation, niche breadths were calculated by subtracting the minimum value of driest quarter precipitation (BIO17) from the maximum value of wettest quarter precipitation (BIO16) among localities (see Fig. S2 in Appendix S1). We assumed that quarterly values for precipitation were more relevant than short-term monthly extremes, but yearly values may also be more relevant than quarterly extremes for survival in a given habitat. For example, deserts and rain forests are defined based on differences in yearly rainfall values, not on a few wet or dry months.

Species richness

We plotted hylid richness with respect to annual mean temperature (BIO1) and annual precipitation (BIO12). Species richness was measured by dividing the range of annual mean temperature and annual precipitation values across all localities for all species (the *x*-axis in Fig. 1) into bands. Sixteen bands of 2 °C each were used for temperature. Similarly, precipitation was divided into 14 bands of 100 mm year^{-1}. These widths were arbitrary but sufficient in number to allow for (potentially) statistically significant results. Results were similar using narrower and wider bands (see Fig. S3 in Appendix

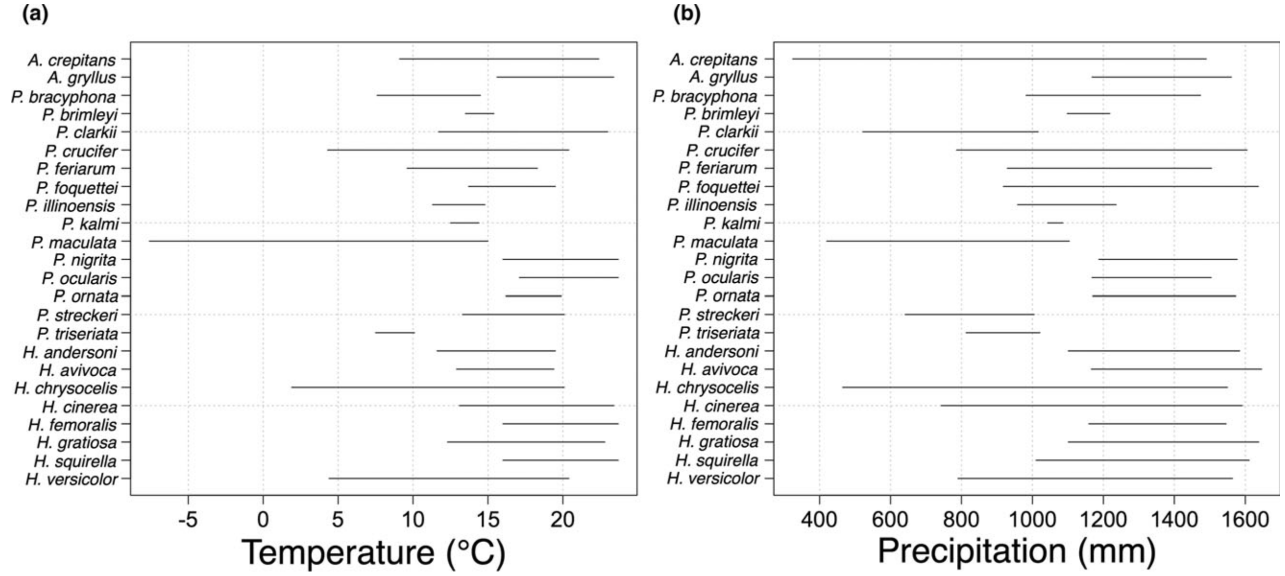

Figure 1 Distribution of 24 eastern North American treefrog species (Hylidae, genera *Acris*, *Pseudacris* and *Hyla*) on (a) temperature and (b) precipitation niche axes using annual mean temperature (BIO1) and annual precipitation (BIO12). Each line indicates the range of values among sampled localities across the species' geographical range for these variables, and the species temperature and precipitation niche breadths.

S1). Regional richness for each band was the number of species with values within that band. It could be argued that, if two species occur under similar climatic conditions but are not sympatric (e.g. in southern Texas and Florida), our estimations of richness may be inaccurate. However, we focused on richness at a regional scale, and the majority of eastern North American hylids do have partially overlapping ranges, especially in the south-eastern USA (e.g. Conant & Collins, 1998; Smith *et al.*, 2005).

To address the relationship between climatic niche breadth and species richness, we calculated the mean climatic niche breadth of each climatic band by averaging the niche breadths of all species occurring in that band. We first used both climatic bands and niche breadths based on BIO1 (temperature) and BIO12 (precipitation). We also used niche breadths measured from seasonal climatic extremes (BIO5 and BIO6 for temperature, and BIO16 and BIO17 for precipitation). We then used standard linear regression (in R) to test the significance of these relationships. As the units of analysis were climatic bands (which lack phylogeny) and not species, we did not use phylogenetic methods in the analyses. We did not estimate species richness based on the ranges of climatic extremes (BIO5, BIO6, BIO16 and BIO17) because these ranges do not have an obvious geographical interpretation that would allow calculation of species richness.

The relationship between climatic niche breadth and niche position

We used phylogenetic generalized least squares (PGLS; Martins & Hansen, 1997) with the R package 'caper' version 0.5 (Orme *et al.*, 2012) to test the relationship between niche breadth and niche position. For PGLS, we used a random walk (estimated lambda) model of continuous trait evolution (see 'Ancestral reconstruction and the time-for-speciation effect' for details on model testing and selection). For temperature and precipitation niche positions, we used the midpoint between the maximum and minimum values for BIO1 and for BIO12 across the localities for each species (Table S1 in Appendix S1). Alternative measurements of niche position were calculated as the midpoint between the minimum value of BIO6 and the maximum value of BIO5 for temperature, and between the minimum value of BIO17 and the maximum value of BIO16 for precipitation (Table S2 in Appendix S1). An interesting alternative measure of niche position would be to use climatic values corresponding to the highest species abundance. However, range-wide data on relative abundance of these species were not available. Nevertheless, as an approximation, we also calculated niche positions using mean values of BIO1 for temperature and BIO12 for precipitation (Table S3 in Appendix S1). These mean values may reflect conditions where each species is collected more frequently (possibly because of, among other things, higher abundance). Niche breadths were calculated from both standard (i.e. BIO1 and BIO12) and alternative (i.e. BIO5/6 and BIO16/17) measurements. We tested the relationship between species niche breadths for temperature and precipitation, between niche positions for temperature and precipitation, between temperature niche breadth and temperature niche position, and between precipitation niche breadth and precipitation niche position.

Climatic niche overlap and niche conservatism

Eastern North American hylids consist of two clades (*Acris*–*Pseudacris* and *Hyla*). We compared these clades for potential differences in climatic niche breadth overlap, given the seemingly greater overlap among geographical ranges in *Hyla* (e.g. Conant & Collins, 1998). First, we conducted pairwise comparisons of niche overlap between all species within each clade. Second, for each species pair and for each climatic variable, we divided the length of niche breadth overlap by the niche breadth of the species with the larger breadth, producing values between 0 (no overlap) and 1 (complete overlap). Finally, the mean overlap for each clade for each niche axis was calculated from the average of all pairwise comparisons of species in that clade. This method parallels similar metrics quantifying climatic niche conservatism among sister species (e.g. Cadena *et al.*, 2012). This analysis, in conjunction with the testing of different evolutionary models described below, addressed whether climatic niches are conserved evolutionarily within these clades.

Ancestral reconstruction and the time-for-speciation effect

We reconstructed the timing of colonization of different climatic regimes to test the potential role of time in driving climate–richness relationships. The *Acris–Pseudacris* clade in eastern North America is monophyletic except for a single clade of two species endemic to western North America. Similarly, *Hyla* in eastern North America is paraphyletic with respect to a single clade of species that occurs in western North America, Middle America and Asia. We used all species within the tribe Hylini for which both climatic and phylogenetic data were available (i.e. 80 species), to obtain ancestral values for climatic variables for nodes associated with eastern North American species. All other analyses were limited to the 24 species in eastern North America. Given that only a single clade was excluded from *Acris–Pseudacris* and *Hyla*, these excluded species should have minimal impact on the results. For these analyses, climatic niche breadths were based on all the localities for each species (i.e. not excluding western localities) and included both standard and alternative measurements of niche breadth.

Before ancestral reconstruction, we found the best-fitting model of evolution for each variable. Four models were tested on each climatic variable (standard measurements: the midpoint and average of BIO1 and BIO12 for each species across localities, and temperature and precipitation niche breadths based on the ranges of BIO1 and BIO12 values across localities; alternative measurements: the midpoint of BIO5/6 and BIO16/17 for each species, and temperature and precipitation niche breadths based on BIO5/6 and BIO16/17) for the 80 species in Hylini using the R package 'geiger' (Harmon *et al.*, 2008). Models included white noise (WN; lambda = 0, trait evolution is independent of phylogeny), Brownian motion (BM; lambda = 1, trait evolution is completely dependent on phylogeny), random walk (RW; another BM model using the maximum likelihood estimate of lambda, intermediate between WN and BM), and Ornstein–Uhlenbeck (OU; trait evolution is constrained by stabilizing selection around an optimal trait value). The best model was determined by comparing corrected Akaike information criterion ($\mathrm{AIC_c}$) values, with $\mathrm{AIC_c}$ differences > 4 considered to show strong support (Burnham & Anderson, 2004). We found strong support (i.e. $\Delta\mathrm{AIC_c} > 20$) for the RW model for all traits excluding temperature niche breadth, for which OU had similar support (i.e. $\Delta\mathrm{AIC_c} = 0.44$; see Table S4 in Appendix S1). We used the RW model in all subsequent analyses. We reconstructed values for each node for each variable using maximum likelihood with the R package 'ape' (Paradis *et al.*, 2004). Note that significant support for a model with a phylogenetic signal (RW) over one without (WN) can also be considered support for phylogenetic niche conservatism in these climatic variables (e.g. Wiens *et al.*, 2010a).

To test the time-for-speciation hypothesis, we reconstructed the breadths and positions (i.e. midpoints) of BIO1 and BIO12 on the tree and then recorded the age of the oldest node occurring within each climatic band (2 °C for temperature; 100 mm year^{-1} for precipitation), as a measure of the relative time of first colonization for that band for that variable. This time of first colonization was then regressed (ordinary least squares; OLS) against that band's current richness. Alternatively, richness may be better explained as the result of multiple colonization events, rather than only the initial colonization of a climatic zone. Thus we also regressed richness with the summed ages of all colonization events. However, previous studies have shown that this approach gives similar results to using just the first colonization time (e.g. Stephens & Wiens, 2003; Kozak & Wiens, 2010b; Hutter *et al.*, 2013). Climatic bands occupied by only extant species (i.e. not ancestral species) were given colonization times equal to half the age of the oldest species found within that band (assuming that the extant species in that band did not necessarily colonize that band immediately at their time of splitting nor in the last few years). Again, we did not correct for phylogeny because climatic bands were the units of analysis and not species (and 'correcting' for phylogeny here might remove the phylogeny-based effect that we were trying to test).

We recognize that phylogenetic reconstructions of ancestral climatic variables have many uncertainties. For example, our reconstructions may be inaccurate if climatic niches change very rapidly across the tree. However, we have found that these climatic variables show significant phylogenetic conservatism (see above). Although there has been rapid climate change in eastern North America (e.g. as a result of recent glacial cycles), this does not mean that climatic niches have changed rapidly, and many species may have simply tracked their climatic niches over space as climates changed (i.e. the fact that north-eastern North America was glaciated does not mean that species occurring there today were adapted to living under ice). Note that all species seem to pre-date Pleistocene climatic fluctuations (see time-calibrated tree in Results).

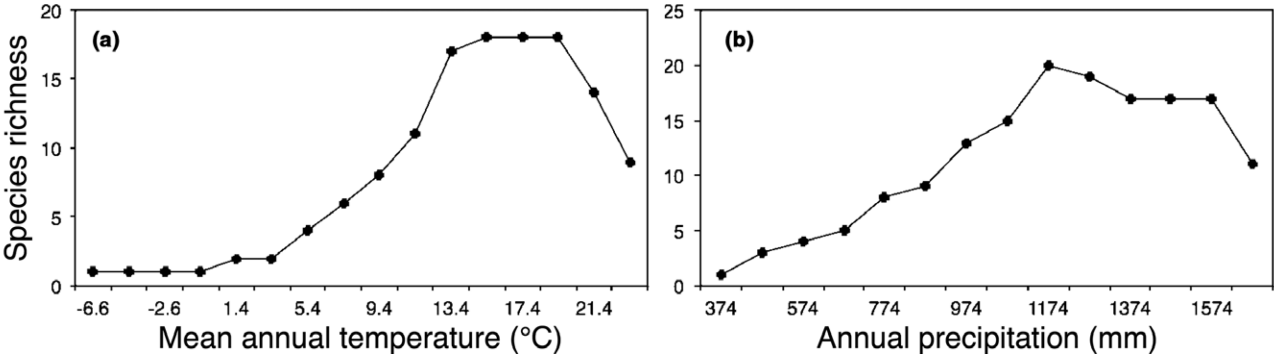

Figure 2 Species richness of 24 eastern North American treefrog species (Hylidae) with respect to (a) annual mean temperature (BIO1) and (b) annual precipitation (BIO12).

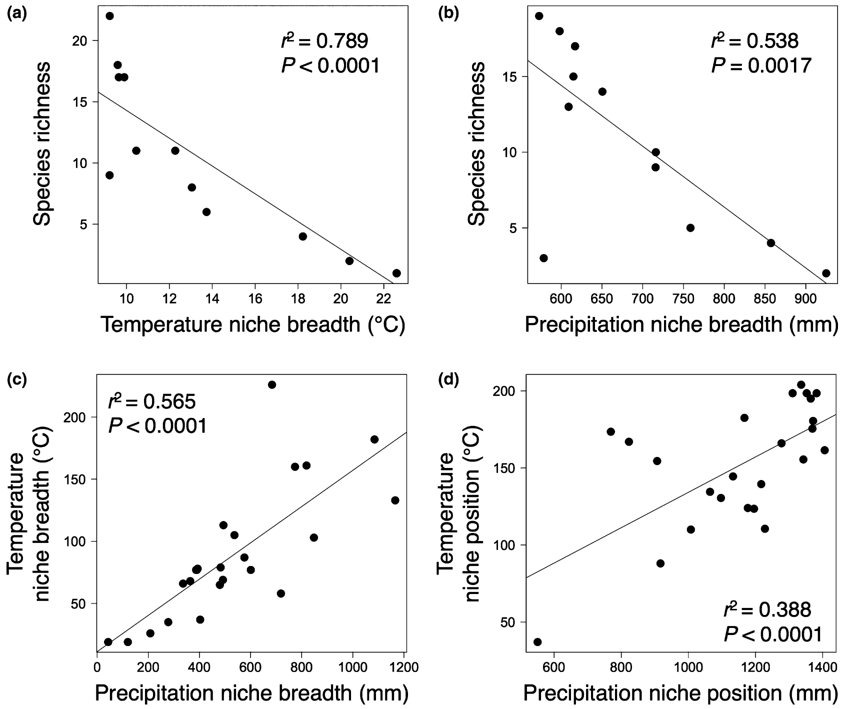

Figure 3 Relationships between mean climatic niche breadth and species richness per climatic band for 24 eastern North American treefrog species (Hylidae) for both (a) temperature and (b) precipitation, and relationships between species' (c) niche breadths and (d) niche positions for temperature and precipitation. Niche breadths and positions (c, d) were regressed using phylogenetic generalized least squares (PGLS), but the raw data are plotted here for illustrative purposes. For these analyses, species niche breadths and niche positions were based on annual mean temperature (BIO1) for temperature and annual precipitation (BIO12) for precipitation (using the range of values among localities for each species).

RESULTS

Climatic niche breadth and species richness

Species richness was distributed unimodally with respect to annual mean temperature and precipitation (Fig. 2). Species richness was high in regions with relatively high temperature and high precipitation values, but not the highest values, resulting in highly left-skewed distributions.

Climatic niche breadths for both temperature and precipitation were significantly narrower among species from climatic zones with high species richness (Fig. 3a,b; temperature, $r^2 = 0.789$, $P < 0.0001$; precipitation, $r^2 = 0.538$, $P = 0.0017$; using BIO1 and BIO12 for niche breadth and species richness). This negative relationship was upheld using an alternative measurement of temperature niche breadth (BIO5 – BIO6; $r^2 = 0.735$, $P < 0.0001$) but not precipitation niche breadth (BIO16 – BIO17; $r^2 = 0.130$, $P = 0.1124$; see Fig. S4 in Appendix S1), although the alternative measure of precipitation niche breadth may be less relevant.

The relationship between climatic niche breadth and niche position

PGLS regression showed a strong positive relationship between species temperature and precipitation niche breadths using BIO1 and BIO12 (Fig. 3c; $r^2 = 0.565$, $P < 0.0001$) but was not significant using alternative measurements of niche breadth (i.e. BIO5/6 and BIO16/17; $r^2 = 0.040$, $P = 0.9181$). Thus, for the standard measurements of niche breadth, species tended to have narrow or wide niche breadths on both axes simultaneously, rather than trading off breadth on one axis for narrowness on another. The relationship between temperature and precipitation niche positions (i.e. midpoints of temperature and precipitation niche breadths) was also positive for both standard (i.e. BIO1/12; Fig. 3d; $r^2 = 0.388$, $P < 0.0001$) and alternative (i.e. BIO5/6 and BIO16/17; $r^2 = 0.360$ $P = 0.0001$) measurements of niche position, such that species tended to occur either in relatively warm and wet, or cold and dry, environments. The relationship between temperature and precipitation niche positions based on the means of BIO1 and BIO12 (i.e. an alternative measure of niche position) was also significantly positive ($r^2 = 0.494$, $P < 0.0001$). Species occupying warmer regions had significantly narrower temperature niche breadths (i.e. temperature midpoint versus temperature niche breadth) for both standard (i.e. BIO1; $r^2 = 0.200$, $P = 0.0052$) and alternative measurements (i.e. BIO5/6; $r^2 = 0.824$, $P < 0.0001$). The relationship between precipitation niche position and precipitation niche breadths was not significant using standard niche breadths (i.e. BIO12; $r^2 = 0.049$, $P = 0.1357$) but was significantly positive with alternative measurements (i.e. BIO16/17; $r^2 = 0.247$, $P = 0.0018$). Niche positions (as BIO1 and BIO12 means) were positively related to niche breadth (the range of BIO1 and BIO12 values across localities) for temperature ($r^2 = 0.178$ $P = 0.0085$) but not for precipitation ($r^2 = 0.045$ $P = 0.1483$; see Table S5 in Appendix S1 for a complete list of PGLS results).

Climatic niche overlap and niche conservatism

The mean overlap of species' temperature niches was 0.543 for *Hyla* and 0.279 for the *Acris–Pseudacris* clade. The overlap of precipitation niches for *Hyla* was 0.647 and for the *Acris–Pseudacris* clade was 0.292. Thus *Hyla* showed greater climatic overlap among species for both temperature and precipitation niche axes, with most species nested within the distribution of other, more broadly distributed species (Fig. 1). In contrast, the *Acris–Pseudacris* clade contained several species that occurred on different, largely non-overlapping portions of each of these axes (Fig. 1).

Ancestral reconstructions, climatic niche evolution and time-for-speciation effect

Ancestral reconstructions of climatic variables using 80 species of Hylini inferred occurrence in relatively warm (BIO1 = 18.3 °C) and wet (BIO12 = 1745 mm year^{-1}) climates in the ancestor of Hylini. This finding was consistent with the tropical origin of Hylini inferred from biogeographical analyses (Wiens *et al.*, 2006, 2011), although the values were more similar to those of tropical montane species than tropical lowland species (Appendix S1; consistent with elevational reconstructions in Smith *et al.*, 2007). Additionally, this ancestor was inferred to have had a narrow temperature niche breadth (using BIO1, 7.6 °C) and a wide precipitation niche breadth (using BIO12, 1236 mm), as expected for a tropical species. Phylogenetic reconstructions among species in eastern North America (Fig. 4) indicated a recent invasion of cooler and drier environments, along with an expansion of temperature niche breadths and a contraction of precipitation niche breadths over time. Reconstructions using alternative measurements of niche breadth (BIO5/6 and BIO16/17) yielded similar trends (see Fig. S5 in Appendix S1).

Using these ancestral reconstructions, we found strong support for the time-for-speciation hypothesis for both temperature and precipitation (Fig. 5). Specifically, there was a significant positive relationship between the age of the oldest node and current richness within each band for both annual mean temperature (BIO1: $r^2 = 0.844$, $P < 0.0001$) and annual precipitation (BIO12: $r^2 = 0.553$, $P = 0.0014$). Results obtained by summing the ages of all colonization events were also significant for both temperature ($r^2 = 0.821$, $P < 0.0001$) and precipitation ($r^2 = 0.444$, $P = 0.0055$; see Fig. S6 in Appendix S1)

DISCUSSION

How is climatic niche width related to species richness? There has been much speculation about a potential (negative) relationship between these variables but, to our knowledge, this relationship has not been tested explicitly. We tested this hypothesis in hylid frogs in eastern North America. Based on Janzen (1967), it is sometimes assumed that tropical species have narrower climatic niche breadths. However, this is only expected for temperature, as tropical species are thought to have wider precipitation niche breadths (Vázquez & Stevens, 2004). We have found that, among eastern North America hylids, there are significant relationships between climatic niche breadth and species richness, such that climatic zones with the highest richness tend to have species with narrower climatic niche breadths. These results are surprising for two reasons. First, our results are based on comparing species within a temperate zone, not between tropical and temperate regions. Second, we found a negative relationship between niche breadth and richness for both temperature and precipitation. From Janzen's (1967) hypothesis, we might have expected this negative relationship for temperature but we would actually have expected to see the opposite relationship for precipitation (wider niches in tropical regions with higher richness).

Our results also offer potential insights into the mechanisms underpinning this relationship. Patterns of species richness must ultimately be explained in terms of the processes that directly change species numbers (speciation, extinction, dispersal; e.g. Ricklefs, 1987, 2004; Wiens & Donoghue, 2004). Our results show a strong relationship between how long each climatic zone has been occupied and the number of species it contains today (i.e. the time-for-speciation effect). Ancestral reconstructions suggest that both hylid clades in eastern North America occurred ancestrally in relatively warm and wet habitats (e.g. mesic tropical forests), and this is where the highest richness occurs today, in the mesic, subtropical forests of south-eastern North America (Fig. 5 of Smith *et al.*, 2005). Occupation of drier and colder environments occurs primarily as a result of species with relatively wide niches (Fig. 1). Intriguingly, in the genera *Acris* and *Hyla,* occupation of cool, dry habitats seems to occur largely through expansion of the precipitation and temperature niches of some species to

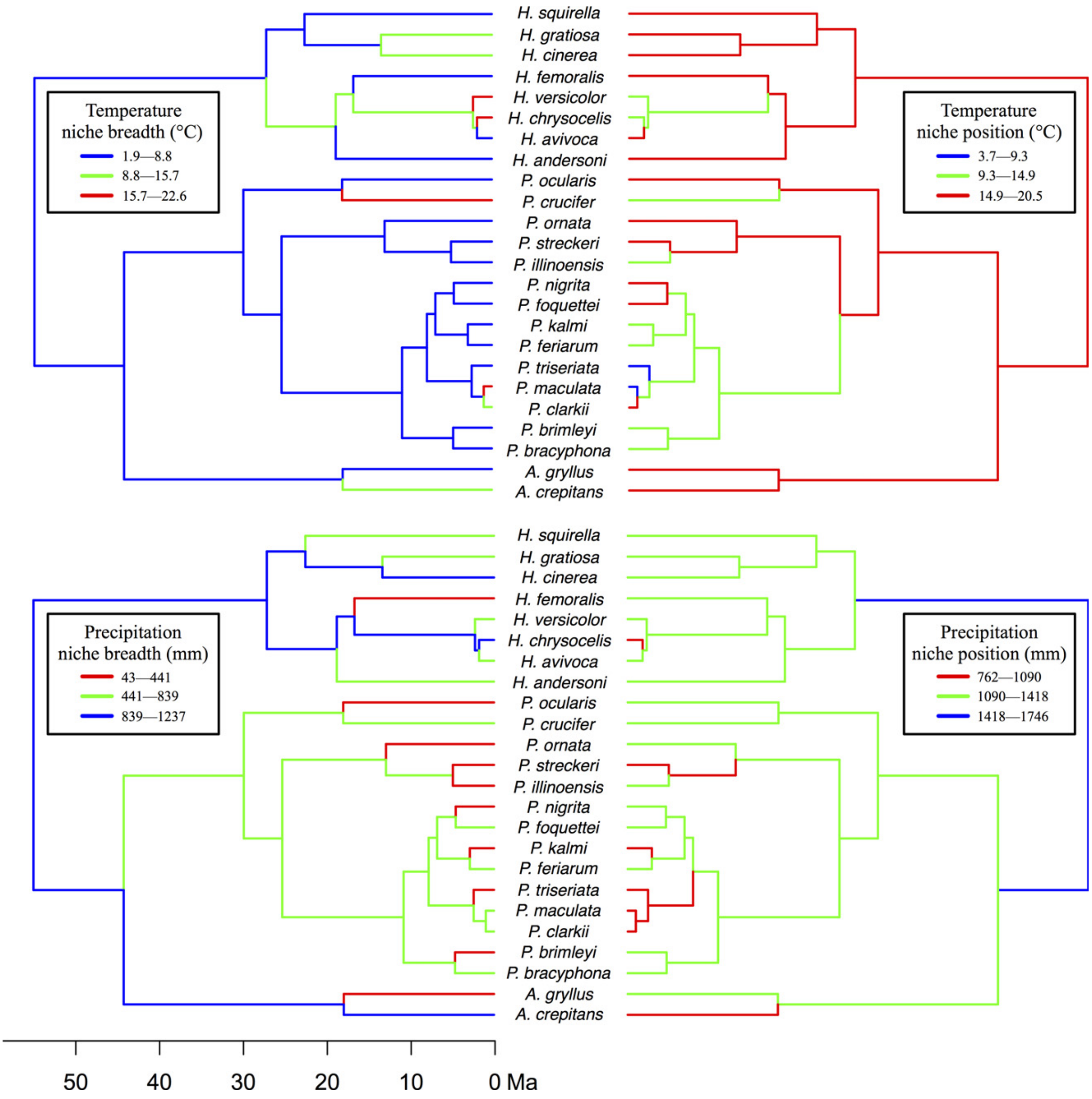

Figure 4 Climatic niche evolution in eastern North American treefrog species (Hylidae, genera *Acris*, *Pseudacris* and *Hyla*) based on ancestral reconstruction of climatic niche breadth (range of values across the species' ranges) and climatic niche position (midpoint of maximum and minimum values across the species' ranges) for annual mean temperature (BIO1) and annual precipitation (BIO12). For illustrative purposes, the range of values across all nodes was divided into three bins of equal size for each variable (but reconstructions were based on continuous values).

encompass these novel environments (Fig. 4), even though these species still retain populations in the warm, mesic, ancestral environment. Thus there are no species specialized for cooler and drier environments in these two groups (Fig. 1). We also found no tendency for narrower niches in species occurring in harsher, lower richness environments (cooler, drier), suggesting that there are no trade-offs leading to greater specialization in more extreme environments, contrary to some expectations (Wiens *et al.*, 2013). In contrast, in *Pseudacris*, some species occur only at the drier end of the precipitation niche gradient (although patterns for temperature are similar to those in *Hyla*, with species in the coolest environments also occurring in warmer environments; Fig. 1). Thus these two clades of hylid frogs in eastern North America illustrate two general (non-exclusive) pathways by which clades may diversify along an environmental niche gradient: either by expansion of the climatic niche within individual species (as in *Hyla*) or occupation of new environments by species that occur only under those conditions (as in *Pseudacris*). In both groups, there has been

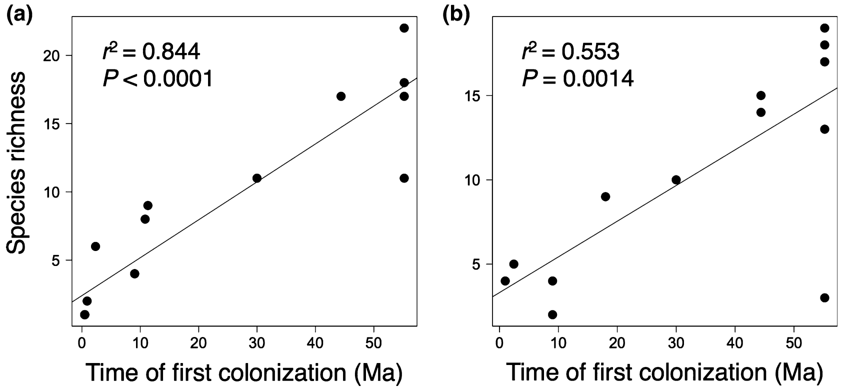

Figure 5 Relationship between time of first colonization (millions of years ago; Ma) and species richness for 24 eastern North American treefrog species (Hylidae) for both (a) temperature and (b) precipitation, using annual mean temperature (BIO1) and annual precipitation (BIO12). Climatic bands occupied only by extant species (i.e. not ancestral species) were given colonization times half the age of the oldest species in that band.

evolution of wider temperature niche breadths and narrower precipitation niche breadths over time (Fig. 4), and both patterns seem to reflect a general trend for temperate species to have wider temperature niche breadths and narrower precipitation niche breadths relative to tropical species (e.g. Vázquez & Stevens, 2004).

We realize that we have not tested whether there is an association between higher richness and narrower niche breadths as a result of less competitive exclusion or faster diversification rates in some climatic regimes. However, neither hypothesis seems likely to explain our results. First, narrower climatic niches in eastern North American hylids do not seem to foster allopatry among these species. In fact, most species show some sympatry in parts of south-eastern North America (e.g. Fig. 5 of Smith *et al.*, 2005), and this high-richness region is where climatic niches are seemingly narrowest. Second, it seems unlikely that there are higher diversification rates in warmer and wetter climates in eastern North American hylids because analyses across all hylid genera do not support a relationship between climate and diversification rates (Wiens *et al.*, 2011). Although it is theoretically possible that there are still some differences in diversification rates within the region, this would be difficult to support given the few species that occur there. Specifically, methods for estimating relationships between diversification rates and climate would have little statistical power (e.g. without > 50 species; FitzJohn, 2010).

Our results also raise many unanswered questions about the mechanisms underlying these patterns. First, what mechanisms allow some species to occupy colder and drier environments? For example, some hylids have evolved a biochemical ‘antifreeze’ that seemingly allows them to tolerate cold conditions (e.g. *Pseudacris crucifer* and *Hyla versicolor*, Schmid, 1982; *Pseudacris triseriata*, Storey & Storey, 1985; *Hyla chrysocelis*, Costanzo *et al.*, 1992). It is possible that similar evolutionary innovations allow some of these species to tolerate drier conditions as well, but the specifics remain unclear. It is also unclear why the two North American hylid clades show somewhat different patterns of niche evolution (more overlapping versus distinct). An important caveat about our results is that *Pseudacris* has been the focus of more intensive phylogeographical studies than have *Hyla* in eastern North America (e.g. Lemmon *et al.*, 2008). In theory, climatic distributions of *Hyla* might differ if molecular studies subdivided current species into cryptic species with smaller geographical ranges (and narrower climatic niches). The role of speciation in determining climatic niche breadths and the richness–breadth relationship also remains uncertain. For example, certain environments might both increase speciation rates and lead to narrower climatic niches (e.g. the tropics; Mittelbach *et al.*, 2007). However, previous analyses across hylids do not show a significant relationship between climate and diversification rates among genera (Wiens *et al.*, 2011). In salamanders, previous studies have shown higher diversification rates (speciation–extinction) in clades with higher rates of niche evolution (Kozak & Wiens, 2010a) but have not found higher rates of niche evolution in clades of species with narrower niches (Fisher-Reid *et al.*, 2012). Another important but unresolved question is what actually determines species’ climatic niche breadths for these variables. An earlier study suggested a strong role for within-locality seasonality in driving both temperature and precipitation niche breadths in hylids (Quintero & Wiens, 2013); thus the factors that set geographical range limits may be of lesser importance in determining their niche breadths. We acknowledge that we have implicitly assumed that climatic tolerances set the climatic distributions of these species. Still, our analyses are focused on realized climatic niches, and our conclusions do not depend on climatic tolerances setting range limits (nor do they require that species distributions be at equilibrium with climate; Munguía *et al.*, 2012). Instead, it may be that the realized climatic niche reflects biotic interactions rather than limits to the fundamental climatic niche, or interactions between biotic and abiotic factors (e.g. Soberón, 2007; Sexton *et al.*, 2009; Sunday *et al.*, 2012; Cahill *et al.*, 2014). We note that most hylid species in eastern North America have partially overlapping rather than abutting geographical ranges (i.e. most species in both clades occur sympatrically in parts of south-eastern North America), suggesting that interactions among species in these groups might not set their range limits. Hylids are also the only arboreal anurans in North America (Wiens *et al.*, 2006). Of course, other species interactions might also be important (e.g. predation and parasitism), but it is unclear what those would be. We also note that we have focused on two standard measurements of climatic distributions, based on yearly totals (precipitation) and averages (temperature). It may be that climatic extremes are more important in driving patterns of climatic distribution (e.g. the coldest and hottest yearly temperatures), but using these measurements for niche breadth generally gave similar results, at least for temperature.

In this study, we tested the relationship between climatic niche breadth and species richness, focusing on the hylid frogs of eastern North America. We have shown, for the first time, that higher species richness is associated with narrower climatic niche breadths, for both temperature and precipitation. Our results suggest that this occurs because of narrower niche breadths in species occurring in the warmer, wetter environments that seem to be ancestral for the group, leading to a strong time-for-speciation effect and higher species richness in these climatic zones. These results also highlight the role that climatic niche expansion within single species may play in generating richness patterns along an environmental gradient, as opposed to species that specialize for more extreme conditions. We acknowledge that these results are only for one group of organisms in one geographical region. However, the generality of these patterns can be readily tested in other clades and regions.

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SUPPORTING INFORMATION

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

Appendix S1 Climatic data for the hylid species from North America used in phylogenetic ancestral reconstruction, results of evolutionary model testing, and supplementary analyses of climatic niche breadth versus species richness, phylogenetic generalized least squares and the time-for-speciation effect (Tables S1–S5 and Figs S1–S6).

BIOSKETCHES

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