# LETTER

# Evolutionary constraints on regional faunas: whom, but not how many

**Adam C. Algar, Jeremy T. Kerr and David J. Currie***
*Department of Biology, University of Ottawa, 30 Marie Curie, Ottawa, ON K1N 6N5, Canada*
*Correspondence: E-mail: dcurrie@uottawa.ca

## Abstract

The latitudinal diversity gradient has been hypothesized to reflect past evolutionary dynamics driven by climatic niche conservation during cladogenesis, i.e. the tropical conservatism hypothesis. Here we show that the species diversity of treefrogs (Hylidae) across the western hemisphere is actually independent of evolutionary niche dynamics. We evaluated three key predictions of the tropical conservatism hypothesis that relate to the relationships between climate, species richness and the phylogenetic structure of regional treefrog faunas across the continental Americas. Species composition was dependent on the inability of some lineages to evolve cold tolerance, but the actual number of species in a region was strongly predicted by precipitation, not temperature. Moreover, phylogenetic structure was independent of precipitation. Thus, species in low-richness areas were no more closely related than species in highly diverse regions. These results provide no support for the tropical conservatism hypothesis. Instead, they show that regional species composition and richness are constrained by different climatic components, demonstrating that global biodiversity gradients can be independent of niche stasis during cladogenesis.

## Keywords

Climate-richness relationships, community relatedness, latitudinal diversity gradient, niche conservatism, niche dynamics, path analysis, phylogenetic clustering, species richness, tropical conservatism hypothesis.

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## INTRODUCTION

Climate plays a key role in the distribution of global biodiversity and in the evolution of individual species' niches during cladogenesis (Hawkins *et al.* 2003; Smith *et al.* 2005; Wiens *et al.* 2006). The well-known latitudinal diversity gradient is a global phenomenon (Orme *et al.* 2005; Grenyer *et al.* 2006; Buckley & Jetz 2007) that is nearly ubiquitous across all major taxonomic groups in terrestrial environments (Hillebrand 2004). This increase in species richness from the poles to the tropics is highly collinear with climate, producing some of the strongest correlations in any ecological field ($r = 0.7$–$0.9$; Hawkins *et al.* 2003). Phylogenetic correlations of climatic tolerances are similarly high, demonstrating that even across diverse clades, niches are often strongly conserved (Smith *et al.* 2005; Wiens *et al.* 2006). It is generally thought that the latter produces the former: the latitudinal diversity gradient is a result of niche dynamics during cladogenesis, specifically the conservation of climatic niche components (the tropical conservatism hypothesis; Hawkins *et al.* 2005, 2006; Ricklefs 2006; Wiens *et al.* 2006).

Climatic niche conservatism is central to the idea that evolutionary niche dynamics create the latitudinal diversity gradient. Simply put, niche conservatism is the maintenance of ancestral niche characteristics in daughter species (Wiens & Graham 2005). Niche characteristics could encompass any number of abiotic or biotic interactions. The tropical conservatism hypothesis relies most clearly on Hutchinson's concept of the fundamental niche (Wiens & Graham 2005). In this context, climatic niche components define a species' abiotic tolerances and, consequently, its fundamental niche. At regional scales, these limits are the most extreme value of a given climatic component experienced by a species (Wiens & Graham 2005).

As an explanation of low temperate diversity, the tropical conservatism hypothesis integrates the phylogenetic correlation of species climatic tolerances with the observation

that many clades originated in the tropics (Ricklefs 2006). After such a clade arises, the hypothesis suggests that during subsequent cladogenesis, niche conservatism maintains climatic barriers to dispersal and range expansion that result in a build-up of species close to the area of origin. Rarely, an evolutionary event produces a species that is able to survive and reproduce in novel climatic conditions (Wiens & Donoghue 2004; Wiens & Graham 2005; Ricklefs 2006), for example by evolving the ability to tolerate freezing. This derived lineage can then continue to diversify, with descendent species eventually invading even more challenging environments. Under such a process, relatively few clades will escape the tropics, resulting in decreasing species richness from the tropics to the poles: the latitudinal diversity gradient.

Evolutionary-based hypotheses have considerable potential to explain the substantial increase in species diversity from polar to tropical regions; however, they are often hindered by the difficulty in generating testable predictions from their proposed processes (Currie et al. 2004). To be rigorously tested, evolutionary hypotheses must explicitly predict links between evolutionary patterns and species richness across broad spatial extents. Despite its prominence in recent literature (Wiens & Donoghue 2004; Hawkins et al. 2005, 2006; Wiens & Graham 2005; Ricklefs 2006; Wiens et al. 2006), studies of niche conservatism and diversity gradients have not tested such predictions. Most research to date has focused primarily on establishing whether any evidence consistent with phylogenetically conserved niches can be identified (Hawkins et al. 2006; Wiens et al. 2006). Such investigations have revealed some intriguing patterns: Hawkins et al. (2006) showed increased evolutionary derivedness towards polar regions for birds, while Wiens et al. (2006) and Smith et al. (2005) both found phylogenetic evidence of climatic niche conservatism in hylid frogs. However, these studies have left the critical prediction untested: if climatic niche conservatism during cladogenesis determines global diversity gradients, then regional diversity must be directly linked to the phylogenetic signature of niche conservatism.

Here, we examine data on both treefrog (Hylidae) species richness and phylogeny (Faivovitch et al. 2005) to provide a novel test of the link between climatic niche conservatism and the latitudinal diversity gradient in the western hemisphere. To spatially quantify the phylogenetic signature of niche conservatism, we utilized two recently developed fauna-wide metrics of phylogenetic structure (Kerr & Currie 1999; Helmus et al. 2007). Mean root distance (MRD) measures the evolutionary derivedness of species (Kerr & Currie 1999; Hawkins et al. 2005, 2006); it is the average number of nodes separating the species in a region from the root of their phylogenetic tree. Phylogenetic species variability (PSV; Helmus et al. 2007) is a measure of faunal

relatedness, or phylogenetic clustering (Webb 2000). PSV is calculated from the number of nodes between the tips and root of the tree that are shared by all pair-wise combinations of species in a fauna. It ranges from zero for highly clustered faunas to one for non-clustered faunas (Helmus et al. 2007).

Simple scenarios of niche conservatism during cladogenesis along an environmental gradient predict specific relations among environment, richness, MRD and PSV (Fig. 1). A simple simulation model indicates that these predicted relationships also apply to less-idealized scenarios that incorporate additional effects of extinction (Appendix S1; Fig. S1 in Supporting information). Three explicit relationships are predicted. First, geographical variation in MRD and PSV should be correlated with climate; as, the warm, wet tropics represent the clade's ancestral climatic conditions (Wiens et al. 2006), niche conservatism should cause phylogenetic clustering to be greater and MRD higher in areas of lower temperature and/or precipitation (or related variables; Fig. 1; Stevens 2006; Kraft et al. 2007). Second, richness should correlate positively with PSV and negatively with MRD (Fig. 1, Appendix S1, Fig. S1). Third, after accounting for the effect of evolutionary structure, little or no residual correlation between climate and richness should remain. Treefrogs are an ideal model taxon on which to test these predictions: they are diverse (492 species were used in our analysis), they originated in the tropics, and they display no latitudinal trends in absolute diversification rates that could obscure the effects of niche conservatism (Wiens et al. 2006). The latter point is important as latitudinal variation in absolute diversification rate (diversification events in a region per unit time, as compared to diversification events per species per unit time) could confound measures of root distance and phylogenetic clustering.
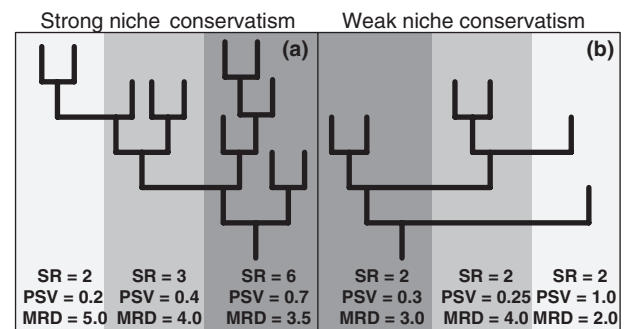


**Figure 1** Idealized scenarios of cladogenesis along an environmental gradient when niche conservatism is strong or weak. When niche conservatism is strong (a), phylogenetic species variability (PSV) decreases and mean root distance (MRD) increases along the environmental gradient as species richness (SR) decreases. No pattern in MRD or PSV is expected when niche conservatism is weak (b). See also Ricklefs (2006).

Our analysis revealed that the latitudinal diversity gradient is independent of niche conservatism during cladogenesis. Faunal phylogenetic structure (PSV and MRD) was strongly related to minimum annual temperature, indicating the evolutionary conservation of cold tolerance. However, species richness was best predicted by precipitation, not temperature, and was independent of phylogenetic structure, a direct contradiction of tropical conservatism's predictions. These results demonstrate the strong role of climate in determining regional faunal structure, but they provide no support for clear evolutionary control of regional diversity gradients via niche conservatism. Instead, for the diverse treefrogs, the latitudinal diversity gradient is dominated by a strong relationship with precipitation.

## MATERIALS AND METHODS

### Indices of phylogenetic structure

We examined two measures of phylogenetic structure that are indices of niche conservatism: MRD, which is a measure of average evolutionary derivedness (Kerr & Currie 1999; Hawkins *et al.* 2005, 2006), and PSV, which is a measure of phylogenetic clustering (Helmus *et al.* 2007). MRD is easily calculated by tallying the number of nodes separating each species in a fauna from the root of the phylogenetic tree, and then taking the mean over all species in any given assemblage. PSV ranges from zero to one, where the latter indicates that species in a region are unrelated (all species are from disparate parts of the tree), and values of zero indicate perfect relatedness. PSV is calculated from a matrix, **V**, whose diagonal elements give the evolutionary divergence of each species from the root to the tips of the tree, and the off-diagonal elements represent the degree of shared evolutionary history among species. **V** can thus be thought of as a variance–covariance matrix of neutral trait values, where elements on the diagonal represent variance in the neutral trait, and off-diagonal elements covariance in trait values among species (Helmus *et al.* 2007). Though Helmus *et al.* (2007) formulated their metric in the context of a neutral trait, they noted that no actual information on trait values is necessary to compute or interpret the index.

Helmus *et al.* (2007) presented the following equation (their eqn 1), for the expected variance in trait values among species in an assemblage, for a tree with contemporaneous tips:

$$E\left\{(X_i - \bar{x})^2\right\} = \frac{\sigma^2}{n^2}\left(n\mathrm{tr}(\mathbf{C}) - \Sigma\mathbf{C}\right), \tag{1}$$

where $\sigma^2$ is the average rate of evolutionary divergence for all species, **C** is the matrix **V** scaled to have ones on the diagonal (i.e. a correlation matrix), $\mathrm{tr}(\mathbf{C})$ is the trace of **C**, $\Sigma\mathbf{C}$ is the sum of all elements in **C** and $n$ is the number of

species. Equation 1 can then be converted to PSV by standardizing by the maximum possible variance among species, which occurs when the underlying phylogeny is a star (eqn 2 in Helmus *et al.* 2007):

$$\mathrm{PSV} = \frac{n\mathrm{tr}(\mathbf{C}) - \Sigma\mathbf{C}}{n(n-1)}. \tag{2}$$

In a tree lacking branch lengths, tips are not contemporaneous; instead species are separated from the root of the tree by differing numbers of nodes and thus the matrix **V** cannot be scaled to a correlation matrix with ones on the diagonal. Fortunately, eqn 2 can be easily modified to account for these differences, by replacing **C** with **V** in the numerator of eqn 2, and replacing the *n* term in the denominator [which in eqn 2 represents tr(**C**) because **C** is a correlation matrix] with tr(**V**). Replacing tr(**C**) with tr(**V**) accounts for the differences in root distance among species:

$$\mathrm{PSV} = \frac{n\mathrm{tr}(\mathbf{V}) - \Sigma\mathbf{V}}{\mathrm{tr}(\mathbf{V})(n-1)}. \tag{3}$$

Equation 3 gives identical results as eqn 2 when the tree is ultrametric. Note that MRD can also be easily calculated from the matrix **V**, where MRD = tr(**V**)/$n$.

### Phylogeny

We used the phylogeny of Faivovitch *et al.* (2005) to evaluate faunal phylogenetic structure. This phylogeny includes the majority of Hylidae genera in the Americas and is resolved to the genus and species group level. Eleven of the 492 species in our analysis were not included in Faivovitch *et al.*'s (2005) lists; we placed these species in the phylogeny on the basis of their generic name and assigned them randomly to a species group within their genus. The Faivovitch *et al.* phylogeny is based on both morphological and molecular characteristics and has been broadly corroborated by Wiens *et al.* (2005). The phylogeny lacks branch lengths; therefore, we considered all branches to have a length of one. Nodes that involved branches to lineages not present in the study area were left in the phylogeny as these still represent potentially important branching events. Because the Faivovitch *et al.* phylogeny is resolved only to the generic and species group level, and our phylogenetic-structure measures required all species to be included in the phylogeny (Webb *et al.* 2002), we included species by grafting them onto the tips of the phylogeny as polytomies with branch lengths of zero. While not optimal, the grafting of polytomies is a common practice in studies of community phylogenetic structure (Webb 2000; Hawkins *et al.* 2005, 2006; Stevens 2006). Our method creates a tree in which species within species groups retain closer linkages to each other than to species in other groups, a reasonable

approximation. Unfortunately, phylogenies that are well resolved at the species level for all species in a clade are rare, and they are non-existent for widespread, diverse taxa that can be used to test broad-scale hypotheses. To limit biases generated by this uncertainty, we also performed our analysis using a phylogenetic tree in which the branch lengths within each polytomy were set to the average number of nodes separating a species from the root in randomly resolved trees of a given diversity (Webb 2000). In the resulting tree, two species that arise from a small polytomy are, on average, more closely related than two species arising from a large polytomy, a reasonable approximation.

## Species richness and environmental data

We obtained, from Natureserve (http://www.natureserve.org), range maps for all hylid species in the continental Americas represented in the Faivovitch *et al.* (2005) phylogeny. Natureserve did not have ranges for the genus *Dendropsophus*, therefore we excluded this genus from our analysis. To sample richness, we overlaid these maps on a grid of $100 \times 100$ km equal area quadrats covering the continental Americas. To reduce the potential effects of small land areas of coastal quadrats, we removed all quadrats that contained $< 50\%$ land. The species richness of a quadrat was considered to be the number of individual ranges that overlap the quadrat. As our goal was to analyse patterns in faunal relatedness, we also removed all quadrats that contained less than two species, since a fauna that contains only a single species is, by definition, perfectly related. This left us with 2244 equal area quadrats.

Environmental data were sampled for the same 2244 quadrats. Climatic measures were obtained from Worldclim (http://www.worldclim.org) at 30 s resolution. For each quadrat we sampled the mean annual temperature, mean minimum temperature (MINT) (the average minimum temperature of the coldest month), mean annual precipitation (MAP) and mean minimum precipitation. We also obtained the mean net primary production from the MODIS satellite (http://www.disc.sci.gsfc.nasa.gov/MODIS/), and we considered two measures of heterogeneity: the number of landcover classes per quadrat, generated from Global Mosaic SPOT VGT 2000 data (http://www-tem.jrc.it//Processed_Satellite_Data_Sets/glc2000_vegetationmosaic.htm), and the range in elevation within a quadrat, which was also obtained from Worldclim.

## Regression and path analysis

To guide our path analysis, and to ensure that we were including the strongest environmental predictors of species richness, PSV and MRD, we first performed a series of regressions. We examined univariate relationships between our three response variables and each of the environmental predictors. We next tested whether these relationships were better described by a curvilinear model by including a quadratic term in each regression. Testing for curvilinearity was especially important as path analysis requires linear relationships between variables (Shipley 2000; Grace 2006). Lastly, we tested models that included temperature and precipitation (the strongest univariate predictors of all response variables) and an interaction term between the two (a model that is commonly considered in macroecological analysis; the interaction term is also highly collinear with actual evapotranspiration). For all analyses, mean minimum precipitation, MAP and net primary productivity were log-transformed to improve normality. Species richness and MRD were square-root and log-transformed respectively to maximize normality in regression residuals. It was not necessary to transform PSV. As our goal was simply to identify predictors for our path analysis, we did not yet consider potential effects of spatial autocorrelation or null models of phylogenetic structure.

Our regression analysis identified MINT and MAP as the strongest predictors of richness, PSV and MRD (see Table S1 in Supporting information for details). To test whether richness was primarily affected by climate via evolutionary processes, we constructed a path model that included direct effects of MINT and MAP, as well as indirect effects via PSV and MRD. We analysed our model using the SEM library (Fox 2007) in R v. 2.6.0 (R Development Core Team 2007). All variables were first standardized to a mean of zero and a variance of one to allow for the comparison of path coefficients connecting variables with different initial units.

Spatial patterns in MRD and PSV can arise simply as a result of sampling effects due to differences in species richness between regions; therefore it is necessary to compare the results to a null model (Webb 2000; Hawkins *et al.* 2005, 2006; Stevens 2006; Helmus *et al.* 2007). A variety of null models have been used in ecological analysis, therefore it is important to utilize a model that provides an appropriate null hypothesis. Our hypotheses about the processes that produce spatial patterns of richness made predictions about where co-occurring species would occur on the phylogenetic tree, which were quantified using PSV and MRD. We therefore generated a null distribution in which species were randomly shuffled on the tips of the phylogeny. Our primary interest was not in the statistical significance of MRD and PSV for individual faunas, but rather the gradients of MRD and PSV along climatic gradients (see Stevens 2006, for further justification). Therefore, for each of 999 randomly shuffled phylogenies, we computed MRD and PSV for all 2244 quadrats. We next recalculated our path model 999 times to generate null

distributions of path coefficients for paths that involved either MRD or PSV for comparison to the actual coefficients. Because we had specific expectations as to the direction of these effects, we considered one-tailed tests with $\alpha = 0.05$. Spatial autocorrelation remained in the residuals of our path analysis. To account for this, we adjusted the degrees of freedom and re-performed statistical tests of path coefficients to ensure that our analysis were not prone to inflated Type I error rates (Fortin & Dale 2005). Geographically effective degrees of freedom were calculated using the observed spatial autocorrelation in model residuals, following the procedure described in detail by Dale & Fortin (2002). This procedure left 432 degrees of freedom to evaluate paths linking climate and PSV, 321 for MRD and 299 for paths leading to species richness. This approach has been used successfully in other studies that have used path analysis to examine richness gradients (Harrison & Grace 2007).

Our analysis could be confounded by the effects of widespread species if they also have high root distances (Prinzing *et al.* 2004). As widespread species occur in more quadrats than narrow-ranged species, then if they are consistently highly evolutionarily derived, they will disproportionately increase the MRD of multiple regions. We tested for this effect by computing the correlation between the number of quadrats occupied by a species (i.e. range size) and root distance for all species.

## RESULTS

Species richness, PSV and MRD all displayed substantial geographic variation (Fig. 2). Of a wider set of environmental variables, including net primary productivity and two measures of environmental heterogeneity, the hemispheric variation in MRD and PSV was most strongly related to minimum temperature ($r^2 > 0.45$ in both cases) and to a lesser extent, to mean annual precipitation (Table S1;

Fig. S2). Spatial variation in species richness was strongly related to both precipitation ($r^2 = 0.57$) and minimum temperature ($r^2 = 0.51$).

Our path analysis clearly shows that geographical patterns of faunal phylogenetic structure show a strong direct relationship with minimum temperature (Fig. 3a). Also, the sign of the path coefficients leading to PSV matched our predictions. The coefficient leading from minimum temperature to MRD also matched our prediction; although adjusting branch lengths to account for differing polytomy sizes suggests that this result may not be robust to phylogenetic uncertainty (Appendix S2; Fig. S3). Paths leading to PSV remained consistent after applying this correction. These results held even after we adjusted the degrees of freedom of statistical tests to account for spatial autocorrelation and randomly shuffled species on the phylogeny's tips to account for constraints of overall tree structure (Fig. 3). These results are not confounded by an effect of widespread species as range size was not correlated with species' root distances (Pearson's $r = 0.02$, $P > 0.33$).

Species richness was effectively independent of faunal phylogenetic structure (Fig. 3). Richness was only weakly related to PSV and MRD; these constituted only 14% of the total effect of all factors on richness (Fig. 3b). Instead, species richness was strongly and directly related to precipitation with a path coefficient of 0.48, comprising 51% of the total effect on richness. However, precipitation had no role in determining either PSV or MRD (Fig. 3), revealing an almost complete climatic decoupling of species richness and niche dynamics during cladogenesis. Minimum temperature did have a smaller direct effect on species richness, but this was also independent of phylogenetic structure of the assemblages present in any given location (Fig. 3). These conclusions were unaffected by applying the polytomy branch length correction (Appendix S2; Fig. S3).
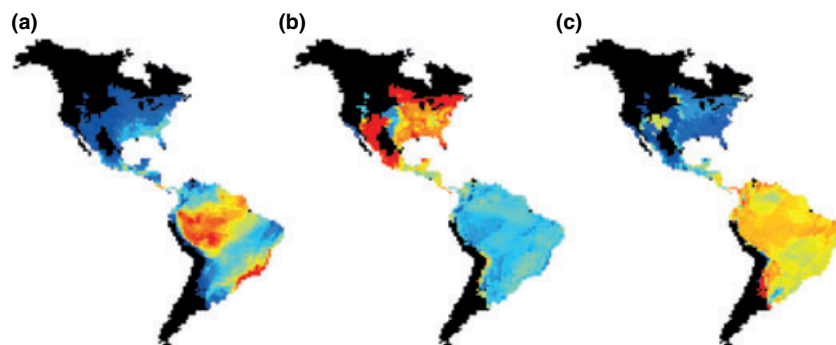


**Figure 2** Spatial variation in species richness (a), mean root distance (b) and phylogenetic species variability (c). Black areas are those with less than two species in which PSV cannot be calculated. Hot (reds) and cold (blues) colours indicate high and low values respectively. Colour values are not comparable between maps.
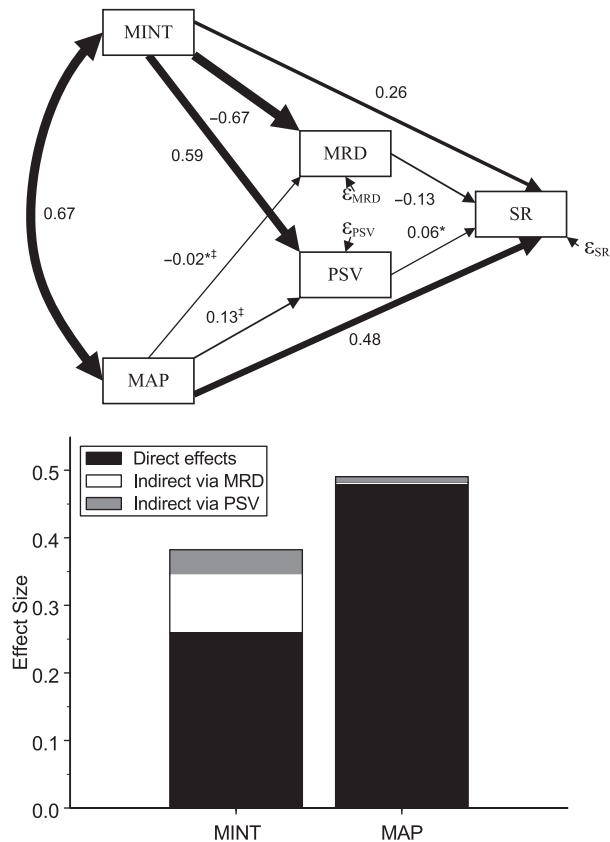
**Figure 3** Direct and indirect effects of climate on species richness (SR). (a) Values are standardized path coefficients; line width is proportional to the strength of the effect. * and ‡ indicate coefficients that were not statistically significant ($\alpha = 0.05$) after accounting for spatial autocorrelation or randomizing species on the phylogeny's tips respectively; all other paths had $P < 0.05$. (b) The total effects of mean annual precipitation and minimum temperature on SR. PSV, phylogenetic species variability; MRD, mean root distance; MINT, minimum temperature; MAP, mean annual precipitation; $\varepsilon$, unexplained variation.

## DISCUSSION

The tropical conservatism hypothesis posits that evolutionary niche dynamics, coupled with the tropical origin of many clades, produce the latitudinal diversity gradient (Wiens & Donoghue 2004; Wiens & Graham 2005; Ricklefs 2006; Wiens et al. 2006). If climate affected phylogenetic structure, which in turn determined richness, then richness should be most strongly related to phylogenetic structure, and only indirectly related to climate. Our analysis reveals that minimum temperature predicts faunal phylogenetic structure very well, indicating that cold tolerance (or lack thereof) is phylogenetically conserved. This result is consistent with the first prediction of the tropical conservatism hypothesis and with purely phylogenetic analysis of niche correlations

in temperate hylids (Smith et al. 2005). However, the correlation between phylogenetic structure and climate represents only the first half of the evolutionary conservatism hypothesis; the second half is the correlations between species diversity and phylogenetic structure. Here, the tropical conservatism hypothesis fails. Contrary to the hypothesis's predictions, the hemispherical diversity gradient in hylid frogs is independent of niche conservatism's effects on faunal phylogenetic structure. Instead, richness is best predicted by precipitation.

We suggest that the constraints that evolutionary niche dynamics place on regional faunal structure determine the species composition in a region, but not the number of species that persist there. Previous work on hylid frogs revealed a strong phylogenetic signature of niche conservatism: Smith et al. (2005) found a strong phylogenetic correlation of minimum temperature tolerance in temperate hylids, while Wiens et al. (2006) found that temperature seasonality predicted northern range limits of six tropical hylid species. Our analyses of entire hylid assemblages across the Americas are consistent with these findings but clarify niche conservatism's role in determining ecological patterns along environmental gradients. Our findings indicate that phylogenetically constrained niche components, such as cold tolerance, relate to broad patterns of species co-occurrence. An extension of this finding is that phylogenetic information can increase our ability to predict which species will occur where (Peterson et al. 1999). However, niche conservatism during cladogenesis does not constrain the species diversity of a region: species inhabiting low-richness areas are no more likely to be closely related than those in species-rich regions. While evolutionary history has left an indelible imprint on regional species composition, its influence over the latitudinal diversity gradient, at least for hylid frogs, is minimal.

Although our study focused solely on hylid frogs, several consistencies suggest that our results may apply more broadly; however, further tests are necessary to test this conjecture. First, global variation in the species richness of amphibians as a whole is strongly related to precipitation (Buckley & Jetz 2007), a somewhat intuitive relationship given this class's obvious water requirements. For amphibians there is evidence that absolute diversification rates are higher in tropical regions, although the hylids are an exception (Wiens 2007); explicit tests of whether variation in absolute diversification rate can account for the amphibian climate-richness relationship are still lacking. The strong relationship between precipitation and species richness is also shared by a wide variety of other taxa in warm regions, including both ectotherms and endotherms, vertebrates and invertebrates, and plants (Hawkins et al. 2003). We do not know if evolutionary niche dynamics in these other groups are more strongly related to temperature than to

precipitation, as in hylids, as phylogenies of broad clades over hemispheric extents are not generally available. As these phylogenies are generated, they will allow for the generality of our findings to be tested in additional clades and geographical domains.

It is still unknown what mechanism(s) produce(s) the broad-scale correlation between richness and precipitation. The lack of correlation between precipitation and phylogenetic structure indicates it is not a result of niche constraints with respect to precipitation regimes. It is also unlikely to be due to systematic variation in absolute diversification rates as hylid absolute diversification rate does not vary with latitude (Wiens *et al.* 2006). Our analysis also eliminates a response to primary productivity or habitat heterogeneity as potential dominant explanations as both predicted less variation in diversity than precipitation. One remaining possible explanation is suitable habitat area: regions with high precipitation may contain large amounts of habitat that is sufficient for hylid persistence, or have increased coincidence of pre- and post-metamorphic habitats in wetter regions, both of which can predict richness at local scales (Becker *et al.* 2007; Werner *et al.* 2007). Tests of this possibility at a global scale are still lacking. Alternatively, perhaps the population densities at which species can persist vary inversely with precipitation, leading to increased richness when the total number of individuals in a region is constant. Finally, we also cannot exclude the possibility that some complex set of evolutionary and ecological factors combine to produce the precipitation-richness correlation.

Phylogenetic information can contribute substantially to our understanding of the processes structuring ecological communities (Webb *et al.* 2002). Tests of evolutionary explanations for the latitudinal diversity gradient have been historically rare due to the difficulty of deducing quantitative predictions that can be explicitly linked to the macro-ecological pattern (Currie *et al.* 2004). However, we have shown that incorporating faunal phylogenetic metrics into macroecological analyses allows for rigorous tests of evolutionary hypotheses. Such tests require substantial information on species distributions and phylogenetic relationships (Webb *et al.* 2002). Unfortunately, well-resolved species-level phylogenies do not exist for any diverse, broadly distributed clade. Therefore, it is necessary to make assumptions with respect to final tree structure, especially with respect to intrageneric relationships. Our analysis appears to be relatively robust to these assumptions; correcting branch lengths to account for differing polytomy size had no effect on our conclusions. Despite these corrections, we cannot completely eliminate potential effects of phylogenetic uncertainty, especially the influence of poorly supported or incorrectly resolved nodes. However, changes in tree topology would have to be very substantial to destroy the correlation we observed with temperature and

to yield one with precipitation instead. Such a major reorganization seems unlikely. It is more likely that phylogenetic uncertainty introduced noise into observed relationships. Nevertheless, the development of well-resolved trees for diverse clades will undoubtedly allow for increasingly precise evaluation of faunal phylogenetic patterns and the processes that generate them.

To be considered strong, tests of evolutionary hypotheses about the latitudinal diversity gradient must not only evaluate explicit predictions, but must quantify evolutionary and diversity patterns at comparable spatial resolutions. Past studies of niche conservatism have relied on taxonomically coarse paleo-data that count orders instead of species (Martin *et al.* 2007), or have been limited to binary comparisons at coarse geographic resolution, comparing the tropics to extratropics (Jablonski *et al.* 2006). Studies of contemporary patterns have suffered from similar limitations, focusing on tropical or temperate areas in isolation (Kerr & Currie 1999; Smith *et al.* 2005; Wiens *et al.* 2006), or phylogenies with only family level resolution (Hawkins *et al.* 2005, 2006). Our study is not free from these limitations, as we used generalized range maps and a species group-level, not a species-level, phylogeny; however, our study does have the advantage of having examined the entire hemispherical gradient with a large number of degrees of freedom. Additionally, our measures of phylogenetic structure allowed us to quantify the effects of niche conservatism at the same spatial scale at which the latitudinal diversity gradient is strongly apparent. It remains to be determined whether our findings not only apply to other taxonomic groups, but also at other spatial scales, especially with respect to local communities where species interactions are expected to play a greater role than in the $100 \times 100$ km regions that have been our focus.

In conclusion, our study is not consistent with the hypothesis that niche conservatism from a tropical ancestor has produced the latitudinal diversity gradient in hylid frogs. This hypothesis postulates links between environment, niche dynamics, cladogenesis and diversity. Our tests showed that several of these links were missing. Instead, we found that species diversity and faunal phylogenetic structure are related to different climatic niche axes. Therefore, evidence of phylogenetic conservatism should not be taken as evidence that niche conservatism necessarily controls the latitudinal diversity gradient. For hylid frogs, the evolutionary constraints on regional faunas are limited to which species co-inhabit a region, but do not influence the number of species that persist there: whom, but not how many.

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## SUPPORTING INFORMATION

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

**Figure S1** Predicted relationships between environment, phylogeny and richness from simulation model.

**Figure S2** Relationships between precipitation, temperature, richness and phylogenetic structure.

**Figure S3** Effects of climate on species richness after applying the branch length correction.

**Table S1** Model fit parameters for regressions of richness and phylogenetic structure on environment.

**Appendix S1** Simulation model structure and results.

**Appendix S2** Results using alternate polytomy branch lengths.

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