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Phylogeny, ecology, and the origins of climate–richness relationships

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Abstract. Many studies show that species richness is correlated with climate, especially among local sites within a region. However, few studies have addressed how these climate–diversity relationships actually arise. Only a few processes can directly change species richness (i.e., speciation, extinction, dispersal), and these processes may be best studied by incorporating a phylogenetic perspective. Here, we used a phylogenetic approach to address the causes of climate–diversity relationships in plethodontid salamanders by combining data on richness, climate, and phylogeny for 250 species. Our results suggest that species richness patterns in plethodontids are explained primarily by how long each region and climatic zone has been occupied, rather than by the effects of either area, species density (i.e., ecological limits), or climate on the rates of speciation or extinction. Across regions, diversity is related to time rather than climate. Within regions, significant climate–diversity relationships are also related to time, with higher richness in climatic regimes that have been occupied longer. Although some might think that phylogeny is unimportant at local scales and when climate and diversity are strongly correlated, we show that niche conservatism and phylogenetic history (time) combine to create species pools of different sizes in different habitats (climatic regimes), leading to variation in local species richness across these habitats within a region.

Key words: climate; diversity; phylogeny; Plethodontidae; speciation; species richness.

INTRODUCTION

A long-standing challenge in ecology is to explain why species richness varies among regions and among local communities (reviewed in Ricklefs 2004). Across many plant and animal taxa, patterns of species richness are often correlated with spatial variation in climatic conditions (e.g., Waide et al. 1999, Francis and Currie 2003, Hawkins et al. 2003, Willig et al. 2003, Buckley and Jetz 2007, McCain 2010). Surprisingly, despite the ubiquity of these climate–diversity relationships, the factors that ultimately generate correlations between climate and diversity remain poorly understood.

What processes might generate these strong relationships between climate and species richness across disparate taxa? Ultimately, such correlations must arise because climatic variables impact patterns of speciation, extinction, and dispersal (Ricklefs 2004, Wiens and Donoghue 2004). These are the only processes that can directly change species numbers in a community or region. Yet, most explanations for climate–richness relationships do not make linkages between these three processes and climate. For example, some hypotheses posit that a specific set of climatic conditions (e.g., warm temperatures, high precipitation) increases carrying capacities, which in turn, allows more species to coexist locally and regionally (review in Currie et al. 2004). Similarly, other hypotheses propose that more species are physiologically capable of living in warm and wet habitats than in cool and dry habitats (Currie et al. 2004). Although these hypotheses are appealing because they make mechanistic connections between climate and species richness, they do not address the key question of why so many species have accumulated in a particular set of climatic conditions in the first place. In other words, they do not link climate–diversity relationships to the processes that ultimately explain species richness patterns.

Two general hypotheses may ultimately explain origins of climate–richness relationships. First, certain climates may be more species rich because they have been occupied longer, allowing more time for species to accumulate through speciation. Certain climatic zones may have been inhabited longer than others because those climates are ancestral for the group (e.g., Ricklefs 2004, Wiens and Donoghue 2004), have occupied a greater proportion of the earth's surface over time (e.g., Fine and Ree 2006), and/or have been more stable over time (Araújo et al. 2008). Under the time-for-speciation hypothesis, niche conservatism for particular climatic conditions (e.g., warm, wet) drives gradients in species richness by limiting dispersal to other climatic zones through time (Wiens and Donoghue 2004). Second, certain climatic regimes may have more species because they drive higher rates of net diversification (speciation

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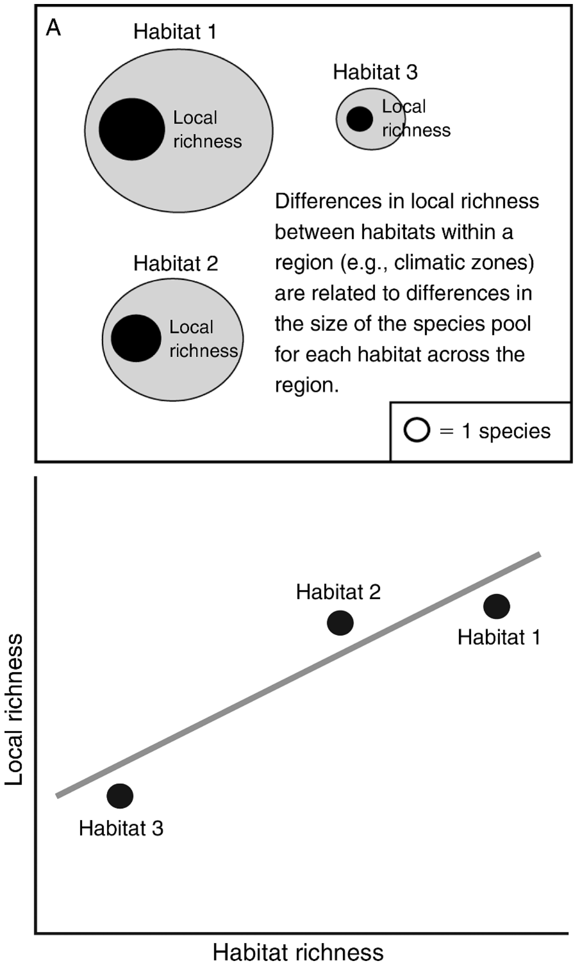

FIG. 1. (A) Conceptual diagram illustrating the idea that variation in local richness may be determined by the number of species in the region that are adapted to a particular habitat (e.g., set of climatic conditions). We found that in plethodontids, the number of species in each habitat (climatic band) is related to how long that habitat type has been occupied. Gray and black circles correspond to habitats and local communities, respectively. The sizes of the circles are proportional to the number of species. (B) The corresponding relationships between habitat richness and local richness produced by the processes described in panel (A).

minus extinction). Various mechanisms might lead to this pattern of higher diversification. For example, harsh or unstable conditions in some habitats might increase extinction rates. In addition, certain climatic regimes may have higher regional and local carrying capacities of species (Currie et al. 2004). If so, communities or regions that are "saturated" with species might have decreased opportunities for speciation or increased probability of local and regional extinction (Walker and Valentine 1984, Ricklefs 2007, Rabosky 2009, Vamosi and Vamosi 2011). Given this hypothesis, certain climates might only become saturated at higher levels of richness, leading to correlations between climate and richness. Some researchers have argued that such differences in carrying capacities (i.e., ecological limits) between regions and habitats offer an explanation for richness patterns that is fundamentally different from those based on time and net rates of diversification (e.g., Rabosky 2009). However, ecological limits can only influence species richness patterns by changing the number of species that accumulate over time (i.e., the net rate of diversification, or speciation minus extinction; Kisel et al. 2011, Wiens 2011). Phylogeny is critical to distinguishing among these potential causes of climate–diversity relationships, because time-calibrated phylogenies allow one to estimate the timing of colonization of different habitats, the diversification rates of the clades that these habitats contain, and whether some habitats might have become saturated with species over time.

Phylogeny is typically thought of as being relevant primarily for regional richness patterns (reviewed in Ricklefs 2004, Wiens and Donoghue 2004), but it may also be important for understanding richness patterns at smaller temporal and spatial scales (e.g., Harrison and Grace 2007, Wiens et al. 2011). Just as regional species pools may help determine variation in local richness across regions (review in Harrison and Cornell 2008), variation in timing and rate of diversification in different habitats within a region may lead to species pools of different size that are adapted to each habitat (Fig. 1), or set of habitats. The size of these within-region habitat-specific species pools may then determine the number of species that can populate local communities along a climatic gradient within a region (Fig. 1), resulting in correlations between richness and climate. Thus, patterns of local species richness may originate through processes that occur over evolutionary timescales (i.e., speciation, extinction, and dispersal), and that are best studied by incorporating a phylogenetic perspective (e.g., Wiens et al. 2011).

In this study, we illustrate how an integrative phylogenetic approach can help reveal the ecological and evolutionary processes that create climate–richness relationships and underlie patterns of local and regional richness. We use lungless salamanders (Plethodontidae) as a model system to examine the relationships between climatic variation, the rate and timing of species diversification, and species richness at regional and local scales. Plethodontidae includes 419 of 615 of the world's salamander species (AmphibiaWeb, *available online*).[4] The group is primarily distributed in the New World, shows strong variation in species richness within and among regions (Fig. 2), and is the only salamander family to have radiated extensively in the tropics. Recent studies have yielded a well-resolved, time-calibrated phylogeny that includes the majority of plethodontid species (Wiens et al. 2007, Adams et al. 2009, Kozak et al. 2009), which is critical for examining the relationship

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[4] http://amphibiaweb.org

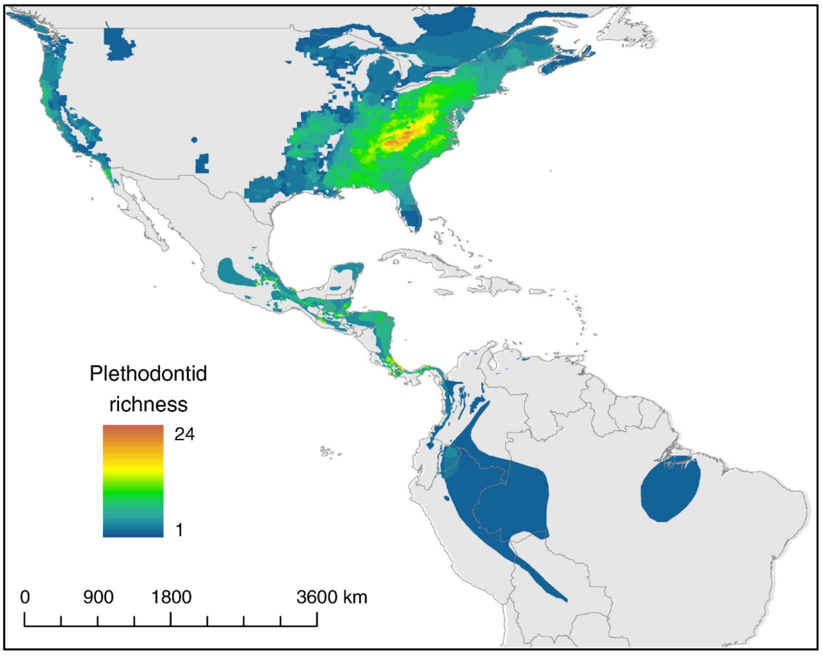

FIG. 2. Species richness (number of species) of plethodontid salamanders across the New World. Europe and Asia are omitted for illustrative purposes.

between climate and the timing and rate of species diversification. Previous studies have addressed the evolutionary and ecological factors that drive elevational variation in plethodontid species richness at regional scales (e.g., Wiens et al. 2007, Kozak and Wiens 2010*b*) and that influence their rates of diversification (e.g., Adams et al. 2009, Kozak and Wiens 2010*a*). However, no studies have addressed how climate, species richness, and evolutionary history are related at regional and local scales.

METHODS

Regional and local richness

To explore the relationship between climate and species richness, we first quantified the number of species that occur within each of nine major areas of plethodontid endemism: (1) Eastern North America (including the Appalachian Highlands and adjacent lowlands, or all of North America east of the Mississippi River), (2) the Interior Highlands region (including the Ozark and Ouachita Mountains of Missouri, Arkansas, and Oklahoma), (3) the Edwards Plateau region of Texas, (4) Western North America (including California, the Pacific Northwest, Idaho, and New Mexico), (5) Mesoamerica, west (and north) of the Isthmus of Tehuantepec (given that most Mesoamerican salamanders are montane, most occur on one side or the other of this low-lying region), (6) Mesoamerica, east (and south) of the Isthmus of Tehuantepec, (7) South America, (8) Europe, and (9) Asia. Very few species are shared between these regions (e.g., a maximum of four shared species for the Interior Highlands and Eastern North America). We estimated the species richness for each region by counting the number of species with geographic distributions that fell within each area of endemism (based on distribution maps from the Global Amphibian Assessment; *available online*).[5] For eastern North America, we also included 18 undescribed phylogeographic lineages in the species richness count, given that most or all of them clearly represent distinct species (see Kozak et al. 2009). Note that these estimates of regional richness include all described species, regardless of whether they were included in our phylogenetic and climatic databases.

We used georeferenced locality data to estimate local species richness within each of the nine areas of endemism. In total, we plotted 19 915 georeferenced species records representing 316 of the 416 species of plethodontids (most missing species were tropical species that are known from only a few localities and from only a few specimens). We estimated local richness by counting the number of species with georeferenced locations that occurred within the same 1 × 1 km grid cell. This approach likely underestimates local species richness, especially at sites that are embedded within larger regional species pools. Nevertheless, we found that the richness of our inferred communities was very similar to that of geographically proximate locations where local species diversity is well studied (Kozak et al. 2009). In contrast, we found that the alternative

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[5] http://www.iucnredlist.org/initiatives/amphibians

approach of counting the number of species whose range maps overlap (e.g., within a 1-km grid cell) often overestimates the local richness of these well known plethodontid communities by a factor of two. However, given the potential of our preferred approach (i.e., counting species in grid cells) to underestimate local richness in some cases, we generally focused on the maximum local richness of regions and climatic zones, rather than the mean, to avoid including sites with underestimated richness.

Regional-scale biogeography and richness

We estimated the relationship between the time that plethodontids have been present in each region and the species richness of that region (at the local and regional scales). We estimated the time in each region using likelihood-based ancestral-area reconstructions on the time-calibrated phylogeny of Kozak and Wiens (2010*a*) using LAGRANGE version 20110117 (Ree and Smith 2008). The chronogram contains 232 of the 419 recognized species of plethodontids (AmphibiaWeb 2011), along with 18 lineages in *Desmognathus* and *Eurycea* that are as yet undescribed, but should be recognized as distinct species (Kozak et al. 2009). It is based primarily on a time-calibrated phylogeny from nuclear and mitochondrial genes for higher level plethodontid relationships and almost all eastern North American plethodontids (Kozak et al. 2009), but also includes segments of the tree estimated separately for some clades (e.g., *Batrachoseps*, Kozak et al. 2009; tropical bolitoglossines, Wiens et al. 2007). The branch lengths for these clades were estimated using penalized likelihood in r8s (Sanderson 2003), with root ages inferred from dates in a time-calibrated phylogeny of all salamander families (Wiens 2007). Although there is some uncertainty in the estimated ages of plethodontid clades (based largely on different assumptions about the root age for the group), the relative ages of these clades are largely robust to these different assumptions (e.g., Wiens 2007, Kozak and Wiens 2010*a*, *b*). In our study, the relative ages of clades are important, but not the absolute ages. Note also that recent analyses of salamander divergence dates (Zheng et al. 2011) using multiple nuclear loci and alternate dating methods (e.g., BEAST, Drummond et al. 2006) estimate ages for major clades within Plethodontidae (e.g., *Aneides*, *Desmognathus-Phaeognathus*, *Plethodon*, Spelerpinae) that are very similar to those estimated by Kozak et al. (2009).

We coded the nine regions for analysis in LAGRANGE. We restricted potential dispersal events between regions to those between areas that are geographically contiguous (Appendix A). This eliminates many potentially nonsensical inferences, such as dispersal between North and South America without passing through Mesoamerica. Almost all extant species are confined to a single region, and we therefore restricted ancestors to occur in no more than two regions simultaneously. Nevertheless, extant and ancestral species occurring in two or more regions are easily accommodated in LAGRANGE.

For some nodes, more than two biogeographic scenarios were considered nearly equally likely (i.e., within two log-likelihood units of the reconstruction with the highest likelihood). A region was only considered unambiguously supported at a given node if it was supported in all of the most likely scenarios. So, for example, a branch in which the most likely ancestral-area reconstructions are D and DE would be considered unambiguous support for D and only ambiguous support for E. Only unambiguous inferences were used in our estimates of the colonization times of regions.

We used linear regression to examine the relationship between regional species richness and the amount of time that plethodontids have been present in each region. To estimate the amount of time that plethodontids have been in each region, we used two general approaches. First, we determined the earliest colonization of each region by plethodontids. However, because the latter approach ignores the potential contribution of multiple colonizations (and their ages) to the species richness of a region, we employed a second approach where we summed the ages of all inferred colonizations of that region by plethodontids. Our estimates of time are based on the crown group ages of clades; although it is not clear when exactly on a branch a region was colonized, we know that the colonization must be at least as old as the first split within an endemic clade (i.e., the crown group age). However, some colonizations of a region are represented by a single species, making it particularly unclear when the region was colonized. In these cases, we used the age when the species split from its sister taxon, divided by two (i.e., the middle of the branch). Although this approach is admittedly arbitrary, the impact of the uncertainty regarding the ages of these colonization events should be minor, since these cases generally involve relatively recent timescales and the full range of possible ages is therefore limited. We acknowledge that (in theory) this analysis could be impacted by the incompleteness of our phylogeny. However, all major clades are included, especially all groups that are species rich. Thus, even though we may miss some recent colonization events involving one or a few species, these should have limited influence on the overall estimates of colonization times (e.g., such events are completely ignored using the oldest colonization approach, and should have relatively limited impact on the summed ages approach).

We also examined the relationship between rates of diversification (speciation minus extinction) and regional variation in species richness. To estimate a diversification rate for a region, we determined the timing of colonization of each region from the chronogram and reconstructed ancestral areas in the LAGRANGE analysis. We then counted the number of species that arose *within* the region following the colonization event (note that a regional assemblage of species may be paraphyletic if a clade in the ancestral area gives rise to a lineage that subsequently disperses beyond the ancestral area). Finally, given the age of the colonization event and the number of species arising from it, we used the method-of-moments estimator for crown groups to estimate a net rate of diversification (Magallón and Sanderson 2001). We utilized a relative extinction rate (epsilon) of 0.45, but our previous analyses (e.g., Kozak and Wiens 2010*a*) strongly suggest that very different values of epsilon have little impact on comparisons of net diversification rates among plethodontid clades. When a region was colonized more than once, we calculated an average diversification rate across the inferred colonization events. For this analysis, it was necessary to rely only on the species included in the tree to estimate diversification rates, and we acknowledge that these rates may be underestimated somewhat in tropical regions.

Climate–richness relationships

We obtained data on 19 climatic variables for 19,915 locality records from the U.S. Museum of Natural History (Smithsonian, Washington, D.C., USA), Museum of Vertebrate Zoology (University of California, Berkeley, California, USA) and published systematic studies. Together, the data set characterizes climatic variation for 316 species of plethodontids distributed across all nine areas of endemism (mean = 54 locations/species, range = 1–2446). Climatic data were extracted from the WorldClim data layers with 1-km^2 spatial resolution (version 1.3; Hijmans et al. 2005). Given that prior studies of climate–richness relationships (in amphibians and other taxa) have often focused on annual precipitation and mean annual temperature (e.g., Currie et al. 2004, Buckley and Jetz 2007, Algar et al. 2009), our primary analyses employed these two climatic variables (Bio1 and Bio12 in the WorldClim data set, respectively; Hijmans et al. 2005). However, we also examined the relationship between multivariate measures of climate and patterns of species richness (Appendix B).

We tested whether regional variation in species richness covaries with climate and region area. We calculated the mean annual temperature and precipitation for each region (calculated by averaging the values of Bio1 and Bio12 across all locations where plethodontids have been recorded within each region). Sites where more than a single species was recorded were treated as a single location in our calculations of mean regional climate. The area of each region (in km^2) was calculated in ArcGIS (ESRI 2011), using cylindrical equal-area projection. We then used linear regression in R (R Development Core Team 2009) to quantify the relationship between richness, temperature, precipitation, and area across the nine regions of endemism.

We also examined whether local patterns of species richness within regions are correlated with climate. To quantify local climate–richness relationships, we calculated the mean values of Bio1 and Bio12 for communities containing 1 to *n* species. We then used linear regression to calculate the correlation between local communities containing different numbers of species, and the mean climatic conditions of those communities. For these analyses, we assigned local communities to one of three major regions: East (eastern North America + Interior Highlands + Edwards Plateau), Western North America (as defined above in *Regional-scale biogeography and richness*), and Mesoamerica + South America (Mesoamerica west and east of the Isthmus of Tehuantepec + South America). Aggregating areas of endemism was necessary because it is not possible to estimate a climate–diversity relationship at the local scale in areas that have low maximum local richness (e.g., maximum local richness is 2 for the Edwards Plateau and South America). We also excluded Asia and Europe from these analyses (maximum local richness = 1).

Diversification rates, climate, and species richness

If climate impacts species richness by increasing speciation and/or decreasing extinction, one would expect a relationship between the net diversification rates of clades and the climatic conditions that they occupy (given that diversification rates are relatively straightforward to estimate and reflect the joint influence of speciation and extinction, whereas disentangling the contribution of speciation and extinction rates to diversification rates is notoriously difficult; Ricklefs 2007). To test this possibility, we selected 16 nonoverlapping clades from the chronogram, corresponding to those used by Kozak and Wiens (2010*a*): (1) *Desmognathus*-*Phaeognathus*, (2) *Aneides*, (3) western *Plethodon*, (4) *Plethodon cinereus* group, (5) *Plethodon wehrlei*–*welleri* group, (6) *Plethodon glutinosus* group, (7) *Gyrinophilus*–*Pseudotriton*–*Stereochilus* clade, (8) *Eurycea*, (9) *Batrachoseps*, (10) *Nototriton*, (11) *Oedipina*, (12) *Chiropterotriton*, (13) *Pseudoeurycea* clade (including *Ixalotriton*, *Lineatriton*, *Parvimolge*, and *Pseudoeurycea*), (14) *Bolitoglossa* (subgenus *Eladinea*), (15) *Bolitoglossa* (subgenera *Magnadigitata*, *Oaxakia*, *Pachymandra*), and (16) *Bolitoglossa* (subgenera *Bolitoglossa*, *Mayamandra*, *Nanotriton*). Taken together, these clades collectively include most plethodontid genera and species (excepting a few genera that are too poorly sampled in phylogenies at present). Given that these clades generally correspond to traditional taxonomic groupings (e.g., genera), we were able to unambiguously assign species to these clades that were not included in the phylogeny. We also selected these clades because they are well supported, maximize the climatic disparity exhibited across plethodontids, and minimize among-species variation within clades (e.g., each clade is strictly tropical or temperate, but does not span both climatic zones). We used the method-of-moments estimator for crown groups to estimate the net diversification rate of each clade given its age and species richness (following

Magallón and Sanderson 2001). For these analyses, we again used a relative extinction rate (epsilon) of 0.45, but previous analyses showed that alternate values (e.g., 0 and 0.90) gave similar estimates (Kozak and Wiens 2010*a*). Previous analyses also showed that the diversification rates of these clades are strongly correlated with their richness, and that these rates do not simply reflect clade age or other confounding factors (Kozak and Wiens 2010*a*).

We tested for a relationship between the mean climatic conditions occupied by each clade and its diversification rate using phylogenetic generalized least squares (PGLS) regression (in the R package APE; Paradis et al. 2004) to account for the phylogenetic nonindependence of clades. To generate a tree for the 16 clades, we simply pruned the chronogram to include a single species for each clade. For a given clade, the mean value for a climatic variable was based on the mean across all localities for each species, and then averaged across all sampled species within that clade. We also separated clades by which of the three major regions of endemism they occur in, and then conducted separate analyses of the relationship between climate and diversification with each major region. This analysis involved pruning the extralimital clades from the tree for each region and then repeating the PGLS analysis of climate and diversification rate, including only those clades occurring in that region (note that no clades occur in more than one of these three major regions).

A disadvantage of this approach is that it requires the delimitation of clades (which is somewhat arbitrary). Therefore, we also tested whether climate influences rates of diversification using the test of Freckleton et al. (2008). This test examines whether the number of nodes [log(N)] linking extant species to the root of a phylogeny (i.e., the net diversification rate of each root-to-tip lineage) is correlated with variation in a continuous trait. Following Freckleton et al. (2008), we used PGLS regression to calculate the correlation between log(N) and the mean temperature (Bio1) and precipitation (Bio12) values for species. This approach is potentially influenced by the absence of many species from the phylogeny, but the results show that this method corroborates those based on the estimated diversification rates of the 16 clades, with more complete sampling.

Time-for-speciation, climate, and species richness

Climate–richness relationships might also arise simply because a given climatic regime has been inhabited for a longer period of time during the evolutionary history of the group, allowing more time for species to accumulate under those climatic conditions in comparison to climatic zones that have been colonized more recently. Referred to as the time-for-speciation effect (Stephens and Wiens 2003), this potential cause of climate–richness relationships predicts a positive relationship between the amount of time that a given climatic regime has been occupied and the number of species currently occurring in those conditions.

To test for this association between time and richness of climatic regimes, we divided each of the three major regions of endemism into bands of annual mean temperature of 2°C width and bands of annual precipitation of 200 mm width. We then tallied the number of species that occur within each climatic band within each major region. The exact widths of the climatic bands were somewhat arbitrary, but were chosen to minimize difficulties associated with estimating time–richness relationships from a small number of climatic bands (e.g., <8) in regions that exhibit a more limited range of climatic conditions than others. To estimate the relative amount of time that each band has been occupied, we used species mean values for each climatic variable (i.e., Bio1 and Bio12) and PGLS ancestral-trait reconstruction for continuous characters (under a Brownian motion model) to reconstruct the climatic conditions occupied by each ancestral node in the chronogram for 250 species (using APE; Paradis et al. 2004). Prior to ancestral-state reconstruction, we used the GEIGER package in R (Harmon et al. 2008) to identify the best fitting model of continuous-trait evolution with which to reconstruct ancestral-trait values, based on comparison of AIC values calculated from the likelihood for each model. The best fitting model was a random walk model in which there is strong phylogenetic signal (maximum-likelihood estimate of Pagel's lambda = 0.74 for Bio1 and 0.92 for Bio12). This model is strongly preferred ($\Delta\text{AIC} > 10$) over a white noise model (species' traits evolve independently of phylogeny, lambda = 0), a Brownian motion model (species' traits are perfectly correlated with phylogeny, lambda = 1.0), and an Ornstein-Uhlenbeck model in which trait values have a tendency to return to a medial value. We used the estimates of lambda to derive the evolutionary variance-covariance matrix for PGLS reconstruction in APE (Paradis et al. 2004).

Given these ancestral-trait estimates, we first recorded the age of the oldest node occurring within each climatic band (this is our first index for how long each band has been occupied). Because a given climatic band might be colonized more than once during the evolutionary history of clade, we also summed the ages of all nodes that were inferred to represent independent colonization events of a given climatic band. We then used linear regression to examine the relationship between the relative amount of time that a climatic band has been occupied and the number of species currently occurring in that band, using each of the two indices for time and each of the two climatic variables. We acknowledge that these estimates of relative time of colonization could potentially be influenced by incomplete sampling of species in the phylogeny. However, this problem should only influence the Neotropical region, as our species sampling in temperate North America is nearly complete. Furthermore, given that we did find significant relationships between time and climate in all three regions (see *Results*), it appears that potential noise and error associated with incomplete species sampling does not obscure the patterns that are present (and that these relationships are not necessarily an artifact of incomplete sampling).

Finally, to assess the potential influence that colonization time has on the number of species that co-occur locally in each climatic band, we calculated the correlation between the relative amount of time that each climatic band as been occupied (as inferred above in the second paragraph of this section) and the maximum number of locally sympatric species in that band (i.e., the number co-occurring in a 1-km^2 grid cell). We focused here on the maximum number of locally co-occurring species because the carrying capacity hypothesis posits that climatic conditions place an upper limit on the number of species that can co-occur in a given location (and given problems with mean local richness mentioned previously). We also performed analyses using the mean number of species in each band, but these gave generally similar results (not shown).

We recognize that the mean climatic conditions occupied by each species and our reconstructed climatic conditions might not represent the precise climatic conditions that species inhabited in the past, nor the actual time at which a climatic band was occupied (climate changes over time). However, previous analyses suggest that plethodontid species and clades seem to track suitable climates and remain associated with particular climatic zones over millions of years (i.e., they show climatic niche conservatism; see Kozak and Wiens 2006, 2010*b*). Moreover, our present results also show strong phylogenetic signal in these climatic variables across the entire tree (lambda = 0.74 for Bio1 and lambda = 0.92 for Bio12). Therefore, we assume that present-day climatic conditions and ancestral reconstructions can reveal very broad patterns of relative colonization times (e.g., lineages that are predominantly distributed in wet habitats today gave rise to those lineage presently occurring in predominantly dry habitats, leaving less time for species to accumulate in dry climates) and rates of diversification (e.g., lineages that have tracked wet climates over time have diversified more rapidly than those that have occupied dry climates, resulting in higher species richness in wet habitats).

In theory, methods for reconstructing ancestral values for continuous traits (such as PGLS) might be biased toward reconstructing a climatic zone as being ancestral for the group simply because it harbors more species and not because it was occupied before those bands that are currently less species rich. To address this possibility, we used simulations to test whether the observed time-for-speciation effect could be explained by the random placement of species ranges along the available temperature and precipitation gradients (following Kozak and Wiens 2010*b*). If the observed relationship between time and diversity of climatic regimes is similar in magnitude to that from simulated data sets in which species are randomly distributed with respect to climatic variables, then this pattern would suggest that the observed relationship might simply be an artifact of the reconstruction methods. In brief, we used Mid-Domain null (McCain 2004) to simulate 1000 data sets in which species' ranges were randomly placed along the temperature and precipitation gradients in each region. For each simulated data set, we estimated the species richness and the timing of the first colonization of each climatic band (by reconstructing ancestral temperature and precipitation midpoints for each node in the chronogram), and tested for a relationship between them using linear regression. We then compared the observed relationship between time and richness to that from the simulations. If fewer than 5% of the simulated data sets had F values greater than the observed data, we rejected the hypothesis that the observed time-for-speciation effect was an artifact of the ancestral reconstruction. Ancestral reconstructions (using APE) and linear regressions of the relationship between time and species richness for each of the 1000 simulated data sets were conducted in R, version 2.7.1 (R development Core Team 2009).

Finally, if rates of diversification vary with respect to climate, the reconstruction of climatic variables on ancestral nodes may be influenced (Maddison 2006). We addressed this possibility by testing whether climatic distributions of clades and species influence rates of diversification (see above in *Diversification rates, climate, and species richness*). Such biases do not appear to drive our results, as we found no or weak relationships between diversification rates and climate (see *Results*), suggesting that our reconstructions of ancestral-climatic values are not influenced by the effects of climate on diversification.

Ecological limits and species richness

The idea that differences in carrying capacities drive variation in species richness leads to two key predictions. First, if regions and communities differ in the number of species that they can sustain and have reached those limits to diversity, then no relationship should exist between the amount of time that a region or climatic zone has been occupied and its regional or local species richness (with local richness being particularly important). Second, the rate at which species accumulate should be diversity dependent, with net rates of diversification slowing as regions and communities become "saturated" with species. To test whether variation in diversity is independent of the time available for diversification, we used linear regressions to test whether there is a positive correlation between the amount of time that regions and climatic zones have been occupied and their corresponding estimates of species richness (at regional and local scales). We used the gamma statistic of Pybus and Harvey (2000) to test

TABLE 1. For nine biogeographic regions where plethodontids occur, we show the species richness, regional area, mean values for two climatic variables across the sites, diversification rate, and two measures for the timing of colonization for each region.

Region	Regional richness	Local richness (maximum)	Area (km^2)	Annual mean temperature (°C, mean ± SD)	Annual precipitation (mm, mean ± SD)
Middle America (East)	85	9	32 471	15.0 ± 4.1	2354 ± 947
Middle America (West)	96	12	162 911	16.6 ± 5.3	1478 ± 640
South America	25	2	1 585 245	19.3 + 6.3	2227 ± 1185
Western North America	46	5	479 291	12.7 ± 2.6	974 ± 464
Eastern North America	103	12	2 959 922	10.6 ± 2.5	1325 ± 302
Edwards Plateau	14	2	186 644	18.9 ± 0.7	757 ± 71
Interior Highlands	16	4	346 192	14.7 ± 0.8	1264 ± 121
Europe	5	1	32 019	13.2 ± 1.8	812 ± 166
Asia	1	1	3 378	11.6 ± 0.0	1316 ± 0

Notes: When a region was colonized repeatedly, diversification rates were calculated separately for each clade associated with each colonization event, and the average value among clades is reported (when applicable, the range of diversification rates among clades is shown in parentheses). Values of the gamma statistic that are significantly negative (implying declining rates of diversification through time) are marked with an asterisk ($P < 0.05$). Abbreviations are: myr, millions of years ago; N/A, data not available.

for diversity-dependent diversification within regions. We estimated gamma for a region by pruning the chronogram to include only divergence events that unambiguously occurred within the region of interest (e.g., Eastern North America). We conducted 1000 simulation replicates to evaluate the significance of gamma values given incomplete taxon sampling within regions (implemented in the R package LASER; Rabosky 2006).

RESULTS

Species richness, mean climate, diversification rates, gamma statistics, and the timing of colonization for each of the nine regions of plethodontid endemism are shown in Table 1.

Our analyses provide little support for the idea that climatic conditions influence species richness by increasing the number of species that can coexist, or by increasing rates of net diversification. Differences in regional and local species richness among areas of plethodontid endemism are not associated with regional variation in mean annual temperature, precipitation, area (Table 2), or multivariate measures of climate (Appendix B). We detected no association between the mean climatic values (for temperature and precipitation) occupied by clades and clade diversification rates ($r^2 = 0.07–0.17$, $P = 0.13–0.46$). Similarly, using the test of Freckleton et al. (2008), we found little evidence to support the hypothesis that variation in temperature or precipitation regimes among species strongly effects rates of diversification (temperature, $r^2 = 0.04$, $P = 0.001$; precipitation, $r^2 = 0.0001$, $P = 0.27$). Although this latter test shows a weak but significant relationship between diversification rate and temperature, this relationship is positive, whereas the relationship between richness and temperature is negative (Fig. 3), strongly reinforcing the idea that climatic influences on diversification rates do not drive richness patterns in this system.

We found little evidence to support the hypothesis that diversity regulation drives differences in species richness at regional or local scales. Regional and local richness are very strongly correlated with each other across areas, and both are strongly correlated with the relative amount of time that each area has been occupied, and there are no obvious signs of "saturation" (i.e., plateaus in richness over time; Fig. 4). Moreover, after accounting for taxa missing from the chronogram, only one of the nine regions was found to have a significantly negative value for the gamma statistic (Middle America, East of the Isthmus of Tehuantepec; Table 1). Thus, we found little support for the hypothesis that the accumulation of species is diversity dependent, that regions or local communities have reached their "ecological limits" on species richness, or that our estimates of net diversification rates are

TABLE 2. Results of linear-regression analyses testing for relationships between species richness and climate, diversification rate, and timing of colonization across nine regions of endemism.

	Temperature (Bio1)		Precipitation (Bio12)		Area (km^2)		Diversification rate (species/myr)		Time (oldest)		Time (summed)	
Richness	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*
Regional richness	−0.15	0.699	0.44	0.351	0.48	0.183	0.37	0.324	**0.87**	**0.002**	**0.74**	**0.02**
Maximum local richness	−0.16	0.673	0.45	0.226	0.39	0.290	0.27	0.561	**0.85**	**0.003**	**0.75**	**0.01**
Mean local richness	−0.01	0.984	0.43	0.239	0.03	0.946	0.14	0.712	**0.67**	**0.04**	0.58	0.096

Notes: Values are standardized regression coefficients, β, followed by *P* values. Statistically significant relationships ($P < 0.05$) are shown in boldface.

TABLE 1. Extended.

Diversification rate (species/myr)	Gamma statistic	Time (myr, oldest colonization)	Time (myr, summed colonizations)
0.09	−2.40*	40.0	40.0
0.09	−2.41	39.2	62.7
0.17	−1.31	13.3	13.3
0.04 (0.03–0.05)	−1.42	44.7	111.7
0.09 (0.07–0.10)	−1.40	55.9	119.9
0.11	0.97	10.7	12.2
0.03	−0.49	20.5	51.2
0.07	N/A	10.7	10.7
0	N/A	19.6	19.6

uninformative because rates of diversification within regions have changed over time. Together, these analyses show that time explains variation in species richness across regions, climatic bands, and local communities.

Within each of the three major regions of plethodontid endemism, local richness is generally correlated with either annual mean temperature or precipitation (Fig. 3). Across all three regions, local richness shows an inverse relationship with temperature. Local richness is positively associated with precipitation in Eastern and Western North America, but shows a weak tendency to decline with mean annual precipitation across Mesoamerica + South America (seemingly because precipitation is typically higher at lower elevations in these regions, where plethodontid richness is lower; Wiens et al. 2007). However, these patterns do not appear to be explained by climatic effects on ecological limits (i.e., certain climates increasing rates of speciation and/or lowering rates extinction), as we found no relationship between climate and rates of diversification within any of the three focal regions ($r^2 = 0.01–0.20$, $P = 0.37–0.91$).

Instead, our analyses suggest that the time available for speciation within a given set of climatic conditions drives these climate–richness relationships in plethodontids. Within each region, climatic bands that are inferred to have been occupied for longer periods of time tend to have more species than those that were colonized more recently (Table 3, Fig. 5; Appendix B). In turn, this time-for-speciation effect seemingly generates the observed negative correlations between temperature and species richness, and the positive correlations between precipitation and species richness. The maximum number of species that co-occur locally in a given climatic band is strongly associated with the band's total species richness (Table 3). Moreover, climatic band richness and the maximum local richness of climatic bands are both generally strongly associated with the amount of time that the band has been occupied (Table 3, Fig. 5). Thus, climatic bands that have been occupied longer have a larger pool of species in the region that can occur in those bands, which then translates into higher local richness in sites that are within those climatic bands. Our simulations indicate that it is highly unlikely that the observed correlations between time and richness could arise from data sets in which species ranges are randomly placed along the available temperature ($P = 0.0001$) and precipitation gradients ($P = 0.036$). Thus, these time-for-speciation effects are not artifacts of bias in reconstruction methods toward more species-rich climatic zones.

DISCUSSION

In this paper, we used a phylogenetic approach to evaluate the causes of the relationship between climate and species richness. We argue that even a perfect relationship between climate and diversity must still be explained in terms of the processes that directly change species numbers (speciation, extinction, dispersal; see also Ricklefs 2004, 2006, Wiens 2011, Wiens et al. 2011). These processes may be best studied using an integrative approach that incorporates both phylogeny and climate.

Given this perspective, there are two general hypotheses that can explain the climate–diversity relationship: time (i.e., climatic regimes that have been occupied longer have more time to accumulate species through speciation) and variation in diversification rates (i.e., some climatic regimes promote speciation and/or decrease extinction). Despite the widespread hypothesis that climate and richness are related, few previous studies have explicitly tested the importance of these two factors in directly explaining the climate–richness relationship (but see Wiens et al. 2011). For example, some studies have addressed whether time or diversification rates explain latitudinal (e.g., Wiens et al. 2006, 2009) and elevational patterns of richness (e.g., Smith et al. 2007, Wiens et al. 2007, Kozak and Wiens 2010*b*). However, these studies did not directly address the climate–richness relationship. Other studies have addressed relationships between diversification rate and latitude, without directly considering time or climate (e.g., Cardillo et al. 2005, Ricklefs 2006, Wiens 2007, Svenning et al. 2008).

Our results strongly suggest that in plethodontid salamanders, the climate–diversity relationship is ultimately explained by time rather than by variation in diversification rates. In fact, comparing all nine regions where plethodontids occur (and all local communities), we found that time was significantly correlated with both regional and local richness (Fig. 4), whereas climate was not (Table 2). Thus, in plethodontids, time seems to "trump" climate at this scale. Ultimately, it appears that species richness may take millions of years to develop, even in the most optimal climate. However, we did find significant relationships between climate and richness when considering diversity patterns within the three major regions where plethodontids occur, especially in the two regions in North America (Fig. 3). These relationships appear to be explained by time rather than diversification rates. Specifically, we found

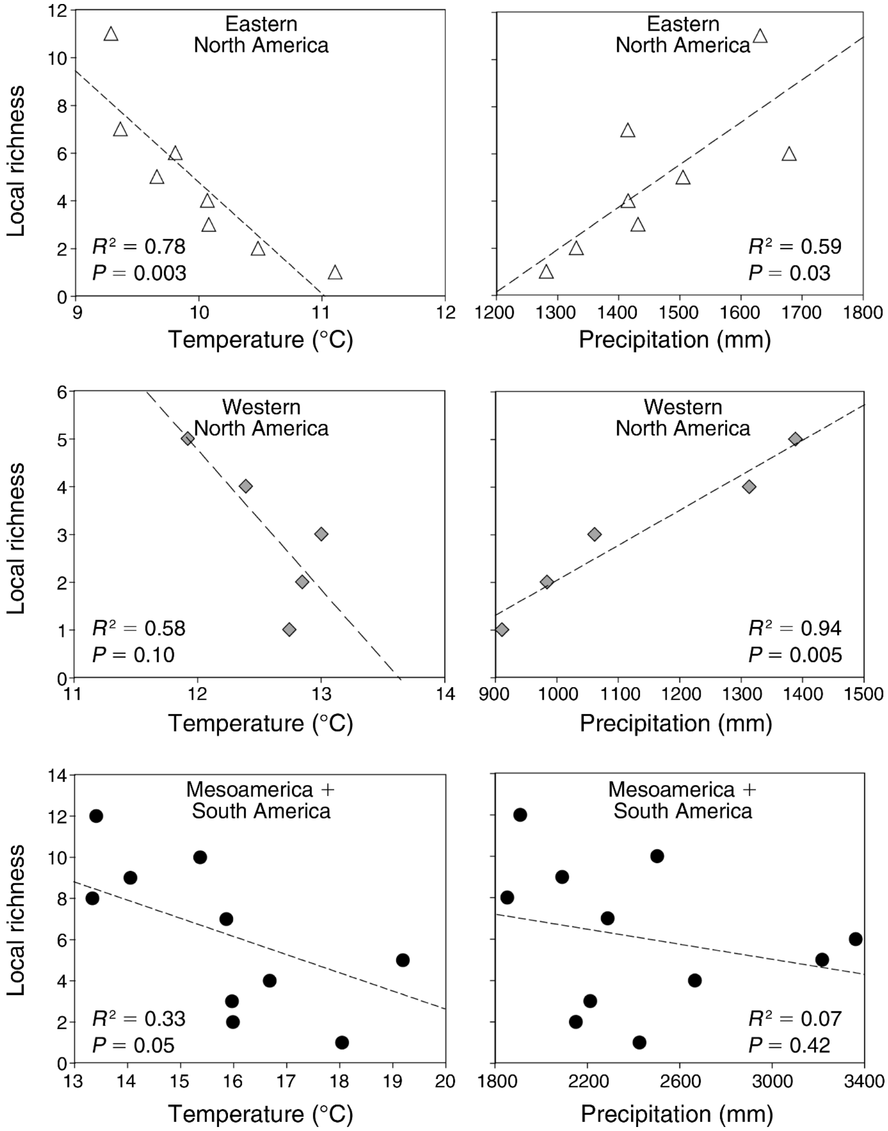

FIG. 3. Relationship between local species richness and mean annual temperature (Bio1) and mean annual precipitation (Bio12) within three large-scale regions of plethodontid endemism (Eastern North America, Western North America, and Mesoamerica + South America). Each data point represents the mean value for a climatic variable across localities having a given number of species. Samples sizes, mean climatic values, and standard errors for each set of communities (i.e., communities sharing the same number of species) are reported in Appendix C.

generally strong relationships between the timing of colonization of climatic zones and their local richness (Table 3), and we found little evidence that climate strongly influences net diversification rates.

How exactly might time explain the climate–richness relationship? We assume that each species occupies only a limited portion of the climatic gradient within a region, and that shifts between climatic regimes over time are limited (at least relative to the rate of speciation). Given that these assumptions are met, a relationship between species richness and climate in a given clade and region can develop simply by species accumulating at the end of the gradient that was first colonized, without postulating any differences in the rate at which species arise and go extinct in different environments, or even any asymmetries in the rate at which species disperse between different environments. Simply put, those climatic regimes that were colonized first will have more species simply because the group in question has been present and speciating in those habitats for a longer amount of time than in the other habitats. This model will explain higher regional diversity in some habitats than others, but this should also lead to higher local richness in these climatic regimes as well. Just as regions that are more species-rich will tend to have higher local richness due to a

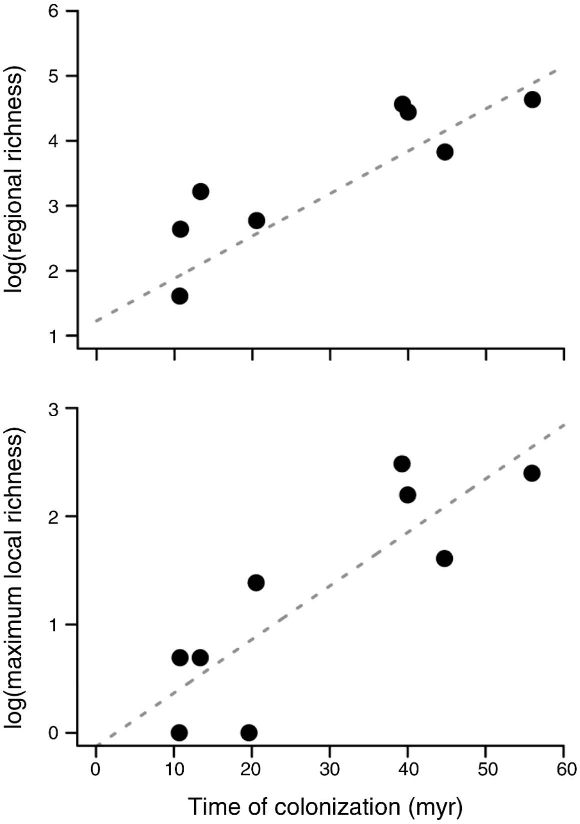

FIG. 4. Relationship between species richness (regional and maximum local) for nine biogeographic regions vs. the time (millions of years ago, myr) that these regions have been occupied. Correlation coefficients and P values are presented in Table 2.

larger regional species pool, different climatic regimes within a region should have higher or lower local richness depending on the size of the regional pool of species that are adapted to tolerate those climatic conditions (Fig. 1). We find some evidence for this hypothesis in plethodontids, in that climatic bands with more species across a region tend to be the same climatic bands with higher maximum local richness (Table 3).

Under the time-for-speciation hypothesis, the critical pattern to explain is not differences in rates of speciation and extinction between clades in different climatic zones, but rather the limited dispersal between climatic regimes. The two important assumptions of this hypothesis for explaining the climate–diversity relationship are that species are typically specialized to a limited portion of a range of climatic regimes and that dispersal between these regimes over time is generally limited. There is some support for these assumptions in plethodontids. We have previously shown that most plethodontid species are confined to relatively narrow climatic regimes, especially in the tropics (e.g., Kozak and Wiens 2010*a*, *b*). The idea of limited dispersal between climatic regimes is related to the broader concept of niche conservatism (reviews in Wiens and Graham 2005, Wiens et al. 2010). Our previous studies strongly support climatic niche conservatism in eastern North American plethodontids (Kozak and Wiens 2006, 2010*b*), and show that it plays an important role in generating elevational species richness patterns. In addition, our current results show strong phylogenetic signal in both temperature and precipitation, which can be taken as evidence for niche conservatism (review in Wiens et al. 2010). Nevertheless, much additional work is needed on the underlying mechanisms that cause climatic niches to be conserved over evolutionary timescales (e.g., stabilizing selection on physiological tolerances vs. species interactions). Furthermore, there are some cases in which climatic niches evolve rapidly among plethodontid species, such as in the South American clade of *Eladinea* within the genus *Bolitoglossa* (Kozak and Wiens 2010*a*).

TABLE 3. Relationships between the regional and maximum local richness of climatic bands vs. the time that climatic bands have been occupied.

Regression	Eastern North America		Western North America		Mesoamerica + South America	
	β	P	β	P	β	P
Temperature (Bio1)						
Climatic-band richness vs. maximum local richness	**0.90**	**0.002**	**0.94**	**0.0006**	**0.83**	**0.003**
Climatic-band richness vs. time (oldest colonization)	**0.85**	**0.007**	**0.70**	**0.053**	**0.69**	**0.025**
Climatic-band richness vs. time (summed time of colonization)	**0.80**	**0.016**	**0.75**	**0.051**	**0.81**	**0.004**
Maximum local richness vs. time (oldest colonization)	**0.70**	**0.049**	0.62	0.134	0.42	0.424
Maximum local richness vs. time (summed time of colonization)	**0.93**	**0.0005**	**0.70**	**0.054**	**0.67**	**0.032**
Precipitation (Bio12)						
Climatic-band richness vs. maximum local richness	**0.93**	**0.002**	−0.25	0.512	**0.70**	**0.0002**
Climatic-band richness vs. time (oldest colonization)	**0.77**	**0.039**	−0.36	0.331	**0.54**	**0.003**
Climatic-band richness vs. time (summed time of colonization)	**0.79**	**0.033**	−0.19	0.622	**0.69**	**0.0001**
Maximum local richness vs. time (oldest colonization)	0.67	0.065	0.15	0.691	**0.68**	**0.0003**
Maximum local richness vs. time (summed time of colonization)	**0.74**	**0.052**	0.39	0.287	**0.72**	**0.0001**

Notes: Values are standardized regression coefficients, β, followed by P values. Statistically significant relationships ($P < 0.05$) are shown in boldface.

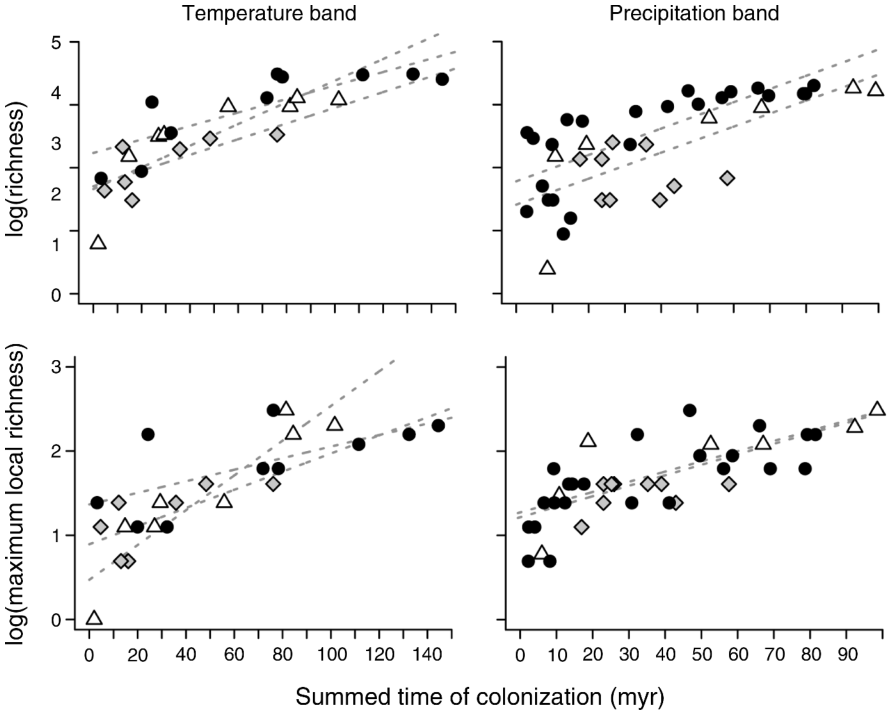

FIG. 5. Relationship between the species richness of climatic bands (regional and maximum local) vs. the time that climatic bands have been occupied. Major regions are coded with symbols as in Fig. 3: open triangles, Eastern North America; gray diamonds, Western North America; and black circles, Mesoamerica + South America. The least-squares regression line is shown for each major region where a significant relationship between richness and colonization time was detected. Correlation coefficients and P values are presented in Table 3.

The major alternative to time is that net diversification rates (speciation – extinction) explain differences in richness between environments with different climates, leading to strong relationships between climate and diversity. Some evidence from other systems suggests that climate may indeed influence diversification rates (e.g., Jansson and Davies 2008, Svenning et al. 2008). Nevertheless, we do not find a relationship between climate and diversification rates in plethodontids. This is somewhat surprising, especially given that plethodontids have higher regional richness in the tropics (206 vs. 185 species; Table 1), and that tropical plethodontid clades generally have higher diversification rates (e.g., Kozak and Wiens 2010*a*). Why then is there no relationship between climate and diversification in plethodontids? We previously showed that high diversification rates in some tropical clades are associated with rapid shifts in climatic regimes among species, as opposed to particular climatic regimes (Kozak and Wiens 2010*a*). For example, the most rapidly diversifying clade of plethodontids (*Bolitoglossa*, subgenus *Eladinea*) occurs from sea level to >3600 m, rather than being centered in the lowland tropics. Indeed, the relationships between climate and richness in the tropical plethodontids are only marginally significant at best (Fig. 3). Furthermore, unless diversification rates are extremely high, a high rate may need to be maintained for relatively long periods of time in order to generate large numbers of species. For example, tropical bolitoglossines have somewhat higher diversification rates, but are also a relatively old clade among plethodontids (~40 million years ago [myr]). Thus, both time and diversification rates may contribute to their higher richness. In general, both time and diversification rates might act concomitantly in a given system to help drive the climate–diversity relationship. For example, habitats that have been colonized longer may be those that have been buffered from extinction, whereas habitats that are colonized more recently may have suffered from extinction in these habitats in the past. However, in general, the influence of certain environments on diversification (including extinction) should be reflected by a relationship between climate and net diversification rates.

Despite the demonstrated importance of time to regional and local richness patterns in this and other studies (e.g., Stephens and Wiens 2003, Stevens 2006, Wiens et al. 2006, 2007, 2009, 2011, Kozak and Wiens 2010*b*), many authors tend to ignore or downplay time as a potential explanation for richness patterns (e.g., Mittelbach et al. 2007, Rabosky 2009). For example, there is a substantial literature documenting how diversification rates vary with latitude, but most studies did not consider time as well (e.g., Cardillo et al. 2005, Svenning et al. 2008). Yet, our results (and others) suggest that time can be critically important to the buildup of species richness at both regional and local scales.

Why do researchers often not consider time as a cause of species richness patterns? One explanation may be that incorporating time requires reconstructions of regional biogeography and habitats on a time-calibrated phylogeny, procedures that some ecologists may be unfamiliar or uncomfortable with (e.g., estimating phylogenies, divergence times, and ancestral-trait values). Indeed, we acknowledge that analysis of time as a factor in explaining richness patterns is not always straightforward. For example, we employed different indices for determining how long regions and climates have been occupied, based on different ways of dealing with multiple colonizations of a region or a climatic regime. Nevertheless, little in ecology is truly straightforward, including the estimation of local and regional richness (although few would use this ambiguity as an excuse to simply ignore richness patterns altogether). Furthermore, methods for reconstructing ancestral traits (for continuous variables) and ancestral biogeographic regions have been extensively tested using simulations and found to be generally accurate, given some assumptions (e.g., Martins 1999, Ree and Smith 2008). Therefore, any claim that the relationship between time and richness should not be considered based on the belief that these reconstruction methods are inherently inaccurate is unsupported by the available evidence. Overall, based on our results and those of other neontological and paleontological studies, we see no excuse for not considering time as a potential explanation for species richness patterns. In fact, the majority of studies that have explicitly considered both time and diversification rate as explanations for richness patterns have supported time over diversification rate (e.g., Wiens et al. 2006, 2007, 2009, Kozak and Wiens 2010*b*) or have supported both (e.g., Jablonski et al. 2006, Smith et al. 2007).

Our results also have important implications for the idea that "ecological limits" drive species richness patterns. Some authors have suggested that regions and clades can "fill-up" with species over time, due to ecological limits on how many species a regions and communities can contain when there is competition for finite resources (e.g., Walker and Valentine 1984, Rabosky 2009, but see Wiens 2011). The hypothesis of ecological limits assumes that the number of species in a clade or region will initially rise to a given limit and then remain constant over millions of years (although the ecological mechanisms underlying this predicted pattern are not entirely clear). Indeed, previous studies have revealed that rates of lineage accumulation have declined over time in many subclades of plethodontids (e.g., Kozak et al. 2005, 2006, Kozak and Wiens 2010*a*). Similarly, our analyses suggest that some climatic bands that have been occupied for very long periods of time may not be as species rich as expected under a model of exponentially increasing species richness through time (i.e., in some regions, the age–diversity relationship appears to "plateau" across climatic bands; Fig. 5). Nevertheless, these apparent slowdowns do not appear to reflect variation in the "saturation" points of regional and local communities, nor do they appear to drive gradients in plethodontid richness. For example, in contrast to the hypothesis that differences in carrying capacities drive variation in diversity, we found that regional and local richness are both strongly related to time. Moreover, our results using the gamma statistic suggest that the overall rate at which lineages have accumulated within regions has been relatively constant over time (Table 1). Thus, we found little evidence to support the idea that regions or local communities differ in richness because they have different upper limits on how many plethodontid species they can sustain. Similar patterns of increasing local richness over time have been found in other phylogenetic studies (e.g., Stephens and Wiens 2003, Stevens 2006, Wiens et al. 2011) and in paleontological studies (e.g., Bambach 1977, Knoll 1986).

Intriguingly, combining our observations of increasing local and regional richness over time with that of seemingly decreasing diversification over time within many plethodontid clades (Kozak and Wiens 2010*a*) suggests that these widespread apparent slowdowns in the rate of accumulation of species in clades over time (e.g., Phillimore and Price 2008) should not necessarily be taken as evidence that regional variation in ecological limits drives variation in species richness. Regions and communities may indeed have fewer species than the number that might be expected if all the clades inhabiting them had undergone constant rates of diversification. However, as we demonstrate here, those regions and communities that have been occupied the longest may still often be the most species rich (slowing is not the same as stopping; see also Wiens et al. 2011). Indeed, a study of 289 plant and animal clades suggests that speciation rates typically decline over time within clades, but that diversity nevertheless continues to accumulate (Morlon et al. 2010).

CONCLUSIONS

In this study, we show how climate–richness relationships can arise as a result of the time-for-speciation effect: particular climatic zones exhibit greater local species richness not because they have higher ecological carrying capacities, but simply because they have been inhabited longer, allowing more time for speciation and the accumulation of species richness. More generally, our study illustrates the power of using phylogenetic methods to test alternative evolutionary and ecological explanations for local-scale species richness patterns, and how time-calibrated phylogenies can link climate–richness relationships to the processes that produce them. Our findings challenge the conventional wisdom that phylogeny and biogeography are primarily relevant to regional scales (not the local scale) and that the observed relationships between climate and richness overturn or are an alternative to explanations based on time and history (e.g., Algar et al. 2009).

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Supplemental Material

Appendix A

Regions and adjacency matrix for likelihood-based ancestral-area reconstructions in LAGRANGE (*Ecological Archives* E093-184-A1).

Appendix B

Analyses of the relationships between species richness patterns and multivariate measures of climatic variation (*Ecological Archives* E093-184-A2).

Appendix C

Samples sizes, mean climatic values, and standard errors for the local communities of different sizes illustrated in Fig. 3 (*Ecological Archives* E093-184-A3).