

# Evolutionary and ecological causes of species richness patterns in North American angiosperm trees

Hong Qian, John J. Wiens, Jian Zhang and Yangjian Zhang

H. Qian ([hqian@museum.state.il.us](mailto:hqian@museum.state.il.us)), Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA. – J. J. Wiens, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721, USA. – J. Zhang, Dept of Renewable Resources, Univ. of Alberta, Edmonton, AB T6G 2H1, Canada. – Y. Zhang, Key Laboratory of Ecosystem Network Observation and Modelling, Inst. of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.

Climate and evolutionary factors (e.g. diversification, time-for-speciation, niche conservatism) are both thought to be major drivers of species richness in regional assemblages. However, few studies have simultaneously investigated the relative effects of climate and evolutionary factors on species richness across a broad geographical extent. Here, we assess their relative effects on species richness of angiosperm trees across North America. Species richness of angiosperm trees in 1175 regional assemblages were related to climate and phylogenetic structure using a structural equation modeling (SEM) approach. Climate was quantified based on the mean temperature of the coldest month and mean annual precipitation. Evolutionary factors (time-for-speciation vs diversification) were inferred from phylogeny-based measures of mean root distance, phylogenetic species variability, and net relatedness index. We found that at the continental scale, species richness is correlated with temperature and precipitation with approximately similar strength. In the SEM with net relatedness index and phylogenetic species variability and with all the 1175 quadrats, the total direct effect size of phylogenetic structure on species richness is greater than the total direct effect size of climate on species richness by a factor of 3.7. The specific patterns of phylogenetic structure (i.e. greater phylogenetic distances in more species rich regions) are consistent with the idea that time and niche conservatism drive richness patterns in North American angiosperm trees. We conclude that angiosperm tree species richness in regional assemblages in North America is more strongly related to patterns of phylogenetic relatedness than to climatic variation. The results of the present study support the idea that climatic and evolutionary explanations for richness patterns are not in conflict, and that evolutionary processes explain both the relationship between climate and richness and substantial variation in richness that is independent of climate.

Explaining patterns of species richness is a major goal of ecology, but recently, there has been growing appreciation for the idea that many richness patterns result from a combination of ecological, evolutionary, and biogeographic processes (Ricklefs 1987, 2004, Ricklefs and Schluter 1993, Wiens and Donoghue 2004, Mittelbach et al. 2007, Wiens 2011). Speciation is the ultimate source of species, and the only three processes that directly determine species richness in a region are speciation, extinction, and dispersal (Ricklefs 1987). Given this perspective, many of the factors and processes traditionally studied in ecology may ultimately drive richness patterns by influencing rates and patterns of speciation, extinction, and dispersal.

The idea that ecology, evolution, and biogeography must be integrated to explain richness patterns has met with some resistance, however. For example, Algar et al. (2009) used path analysis of spatial data on richness, climate, and phylogenetic relatedness to conclude that climatic variables drive richness patterns and that evolutionary factors are unimportant, using treefrogs (Hylidae) as a model system. In short, they found that patterns of species richness were related to climatic variables and not to patterns of phyloge-

netic relatedness in species assemblages (see below). Here, we utilize a similar approach in North American angiosperm trees and find that strong relationships between climate and richness are not an alternative explanation for richness but that these climate–richness relationships must themselves be explained by the ecological, evolutionary, and biogeographic processes of speciation, extinction, and dispersal (see also Ricklefs 2004, 2006a, Wiens and Donoghue 2004, Wiens 2011, Kozak and Wiens 2012).

There are two general explanations for both climate–richness relationships and richness patterns in general, which both integrate ecology and evolution (reviewed by Wiens 2011): 1) higher net diversification rates in certain climatic regimes, regions, or habitats, and 2) greater time for speciation to build up richness in certain climatic regimes, regions, or habitats relative to others. Under the first explanation, certain ecological conditions promote a higher net rate of diversification, where diversification is the balance of speciation and extinction over time (diversification = speciation – extinction). For example, many hypotheses about the latitudinal diversity gradient are ultimately based on how ecological conditions in tropical regions promote

speciation or buffer against extinction, including hypotheses based on greater ecological specialization, more intense species interactions, and faster rates of evolution in tropical regions (Mittelbach et al. 2007). Many studies have now demonstrated faster diversification rates in tropical regions in some clades (Ricklefs 2006b, Wiens 2007, Svenning et al. 2008, Condamine et al. 2012, Pyron and Wiens 2013). Note that based on first principles, 'ecological limits' are not an alternative explanation relative to diversification rates (as suggested by Mittelbach et al. 2007, Rabosky 2009), because these limits can only impact clade richness by influencing speciation and extinction, and clades that occur in regions with more limited resources that can support fewer species must have lower net diversification rates over time than clades of the same age that have higher richness because they occur in regions that can support more species (Wiens 2011). Thus, ecological limits are simply one of many explanations for how ecological conditions influence net diversification, and not an alternative explanation.

In contrast, under the time hypothesis, one or more areas (e.g. regions, habitats, or climatic regimes) are colonized before others, and these areas have more time to build up richness through speciation (time-for-speciation effect *sensu* Stephens and Wiens 2003). This explanation does not require that rates of speciation or extinction differ between regions, and diversity patterns can arise simply from different areas being occupied for different periods of time. Here, the important role of ecological processes is to prevent species dispersal between regions (i.e. through niche conservatism; reviewed by Wiens et al. 2010). A widely discussed example in the recent literature is the tropical conservatism hypothesis (reviewed by Wiens and Donoghue 2004). Under this hypothesis, richness is higher in a given group in tropical regions because the group originated in tropical regions, and dispersed to temperate regions only recently (with more groups ultimately originating in tropical climates due to the greater geographic area of these habitats in the past; Fine and Ree 2006). Under this hypothesis, ecological factors specifically limit dispersal from tropical to temperate regions. For example, species of tropical groups may be unable to disperse into temperate regions because they cannot tolerate freezing temperatures in winter (Latham and Ricklefs 1993, Wiens and Donoghue 2004, Donoghue 2008, Zanne et al. 2014). Many studies now support one or more predictions of the tropical conservatism hypothesis (Fine and Ree 2006, Stevens 2006, Wiens et al. 2006, Hawkins et al. 2011, 2014, Condamine et al. 2012, Smith et al. 2012, Pyron and Wiens 2013, Qian et al. 2013). Note that we consider the time-for-speciation effect to be a component of the tropical conservatism hypothesis (following Wiens and Donoghue 2004 and others), although some authors have considered these competing hypotheses instead (Stevens 2011).

In general, these two hypotheses for climate–richness relationships (diversification rates vs time) can be distinguished most directly by utilizing time-calibrated phylogenies with extensive species sampling. These phylogenies can be used to directly estimate and compare rates of diversification in clades inhabiting different climatic regimes and to estimate and compare the relative timing of colonization of these regimes and how this timing is related to richness

(Wiens et al. 2006, 2007, Kozak and Wiens 2010, 2012, Condamine et al. 2012, Wiens et al. 2013).

An alternative approach is to compare patterns of phylogenetic relatedness among species in different species assemblages, and to relate these patterns to climate and richness (Algar et al. 2009). Although this approach does not directly estimate parameters related to time-for-speciation and diversification, it can be used to test relevant predictions with limited phylogenetic information. For example, Algar et al. (2009) used species range maps to estimate New World hylid frog richness in  $100 \times 100$  km quadrats (regional assemblages hereafter), obtained climatic data (minimum annual temperature and mean annual precipitation) for these quadrats, and used incomplete phylogenies to estimate mean root distance (MRD) and phylogenetic species variability (PSV) as measures of phylogenetic relatedness. They then used path analysis to test the relationships among climate, phylogenetic relatedness, and richness. They considered the tropical conservatism hypothesis to be supported if: a) MRD is higher and PSV lower in areas of lower temperature and precipitation (suggesting that species in these cooler, drier environments evolved relatively recently and are more closely related to each other on average than to other species in the species pool), b) richness is correlated positively with PSV and negatively with MRD, and c) there is little residual correlation between climate and richness after accounting for PSV and MRD. The connection between these predictions and the relevant processes was supported by some simulations. They found that in treefrogs, richness was not strongly related to PSV or MRD, but was closely related to precipitation. They concluded that evolutionary history was therefore unimportant in explaining richness patterns.

An alternative explanation for deviations from these predictions is variation in diversification rates. Specifically, if climatic variables are strongly correlated with both richness and MRD in regional assemblages, then richness patterns may be explained by faster diversification rates associated with these climatic variables. In fact, a positive relationship between MRD and climatic variables is conceptually related to a test designed to address the relationship between diversification and quantitative variables (where species values for traits that promote diversification are significantly related to the number of nodes separating species from the root; Freckleton et al. 2008). An important difference, however, is that test uses entire phylogenies rather than regional assemblages. In theory, the use of regional assemblages might obscure patterns across clades, but it is also possible that patterns across clades in other regions might obscure the relevant patterns in a given regional assemblage.

Thus, it should be possible to use patterns of phylogenetic relatedness in species assemblages to test between the two major competing explanations for climate–diversity relationships (time-for-speciation vs diversification rates). Specifically, if time and niche conservatism drive richness patterns (as under the tropical conservatism hypothesis), species in low-richness climatic regimes should be relatively closely related to each other (with low phylogenetic distance), indicating that these regions have been colonized by few clades and relatively recently. In contrast, high-richness climate regimes should have more distantly related species (on average), indicating greater time for richness to build

up in these habitats. Alternately, if diversification rates explain the climate–richness relationship, then there should be a positive relationship between MRD and those climatic variables that are positively related to richness. Importantly, failing to support the time hypothesis does not necessarily mean that evolutionary factors were not involved in generating the observed richness patterns, and a different evolutionary hypothesis (diversification rates) may be supported instead. To our knowledge, no previous studies have used patterns of phylogenetic structure in regional assemblages to explicitly test hypotheses about the fundamental causes of richness patterns (time vs diversification), although this approach could potentially be applied to many regions and organisms.

Another potential explanation for climate–richness relationships is that climate controls richness directly without any role for evolutionary processes whatsoever (Currie and Paquin 1987, Algar et al. 2009). However, species richness ultimately arises from speciation, making a completely non-evolutionary hypothesis seem unlikely. Nevertheless, species richness patterns in a given region might be dominated by very recent and rapid assembly of species into different habitats in a pattern that is independent of their phylogenetic relationships (leading to no significant relationships between phylogenetic structure of species in habitats and the climate or species richness of those habitats). In this case, richness in different habitats might primarily reflect the number of species that can co-exist in local communities in that habitat type (see Chesson 2000 for a review of mechanisms of species maintenance).

Here, we test these predictions using the angiosperm trees of North America (north of Mexico) as a model system. Specifically, we combine range maps, climatic data, and time-calibrated phylogenies to test the causes of species richness patterns using path analysis. Using patterns of phylogenetic relatedness in regional assemblages, we test if richness patterns are related to time, diversification rates, or if they instead are related to climatic variables but unrelated to these evolutionary factors. North America offers an excellent setting for testing hypotheses about large-scale species richness patterns because it includes many major vegetation zones including subtropical forests, boreal forests, grasslands, warm and cold deserts, Mediterranean scrubland, and arctic tundra (Barbour and Billings 1988).

## Methods

We used the Lambert Azimuthal Equal Area projection to divide North America into equal area quadrats of 12100 km<sup>2</sup> (110 × 110 km or approximately equivalent to a 1° × 1° latitude–longitude square near the equator). We determined the presence or absence of each angiosperm tree species in each quadrat by superimposing range maps on the grid system and then generated species lists for each quadrat. Range maps were obtained from <<http://esp.cr.usgs.gov/data/atlas/little/>>. This database or its original data source was used in previous studies (e.g. Montoya et al. 2007, Qian et al. 2013). We excluded all quadrats with land covering <75% of the quadrat area. In addition, species-poor assemblages may have extreme values for some metrics of phylogenetic

structure (Fritz and Rahbek 2012) and assemblages with few species may produce results that are unreliable due to a large number of ties (Kamilar and Guidi 2010). Therefore, we followed Hortal et al. (2011) in excluding quadrats with five or fewer species to avoid spurious effects of low sample size. As a result, a total of 1175 quadrats were used in this study, 91% of which each have >95% of their area on land.

We used the phylogeny of Hawkins et al. (2014) for North American angiosperm trees, which includes 500 species and is resolved at the species level. This phylogeny combines topological information from the APG III (Angiosperm Phylogeny Group 2009), Smith et al. (2011), and additional phylogenetic studies of lower-level groups, and is time-calibrated using information from Bell et al. (2010). There are some angiosperm tree species that occur in North America north of Mexico (based the angiosperm tree range map source available at <<http://esp.cr.usgs.gov/data/atlas/little/>>) but are absent from this phylogeny. We added these species to the phylogeny manually. Specifically, for each added species, we identified its closest relative in the phylogeny of Hawkins et al. (2014) based on the phylogenies of Smith et al. (2011) or Zanne et al. (2014). We then (somewhat arbitrarily) added the new species to the middle of the branch of its closest relative in the phylogeny of Hawkins et al. (2014). Although the lengths of these branches may be less accurate than those based on including these species with sequence data and a new dating analysis, we emphasize that only 8.2% of the species in our study were not included in the phylogeny of Hawkins et al. (2014). These species with suboptimal branch lengths were closely related to species already included in the phylogeny and so seem very unlikely to affect our results qualitatively.

We standardized botanical nomenclature according to Hawkins et al. (2014). For those species that were absent from the tree of Hawkins et al. (2014), we followed The Plant List (available at <[www.theplantlist.org](http://www.theplantlist.org)>) in standardizing nomenclature. In summary, our phylogeny and distributional database included all 512 angiosperm tree species present in the study area.

Algar et al. (2009) used path analysis to estimate the effects of minimum temperature (MINT), mean annual precipitation (MAP), mean root distance (MRD) and phylogenetic species variability (PSV) on species richness. We initially used the same model and the same variables in our study to make our analyses directly comparable to their analyses. The relative importance of evolutionary versus ecological effects on species richness was determined by comparing the total direct effect size of phylogenetic structure on species richness (i.e. sum of absolute values of coefficients of paths leading from phylogenetic variables to species richness) with the total direct effect size of climatic variables on species richness (i.e. sum of absolute values of coefficients of paths leading climatic variables to species richness). MRD has been used in several studies but a recent study (Fritz and Rahbek 2012) concluded that species-poor assemblages may have extreme values of MRD, making this metric potentially problematic in some cases. Furthermore, MRD does not take into account evolutionary time. Therefore, we also performed a set of

supplementary analyses in which we replaced MRD with the net relatedness index (NRI) of Webb (2000).

The climatic variables used in Algar et al (2009) and our study seem to be among the most important factors predicting tree distributions (Wang et al. 2011). Other climatic or climate-derived variables that are considered to be important in trees are generally strongly correlated with these two climatic variables and can be less strongly correlated with tree species richness, compared to MINT and MAP. For example, potential evapotranspiration (strongly correlated with temperature) was the most important predictor of woody plant species richness in southern Africa (O'Brien 1993) and potential evapotranspiration and water deficit (a measure of water availability) were considered the most important predictors of angiosperm family richness globally (Francis and Currie 2003). However, in our North American data set, potential evapotranspiration is correlated with tree richness as strongly as MINT ( $r = 0.68$  for both variables) and water deficit is uncorrelated with tree richness ( $r = 0.003$ ).

MINT was measured as mean coldest month (January) temperature, which should be related to frost and freezing tolerance. MINT and MAP data were obtained from the WorldClim database (ver. 1.4, available at <[www.worldclim.org](http://www.worldclim.org)>). The WorldClim database includes climate data at a spatial resolution of 30 arc seconds (1 km at the equator; Hijmans et al. 2005). We calculated the averages of MINT and MAP for each quadrat, using all data points located within the quadrat.

MRD is a measure of how distant species in an assemblage are from the root of the tree (Kerr and Currie 1999, Algar et al. 2009). MRD was quantified by first tallying the number of nodes separating each species in an assemblage from the root of the angiosperm tree, and then taking the mean over all species in the assemblage (Algar et al. 2009), using MRD.R (available at <[www.umsl.edu/~emmq7/Menu/Rphylo/MRD.R](http://www.umsl.edu/~emmq7/Menu/Rphylo/MRD.R)>). A strong relationship between mean MRD and a given climatic variable and between that climatic variable and richness may indicate that the climatic variable promotes higher diversification rates, and that these higher diversification rates may explain the relationship between climate and richness among regional assemblages.

PSV is a measure of phylogenetic clustering (Helmus et al. 2007). It is defined by Helmus et al. (2007) as follows:  $PSV = (ntrC - \Sigma C) / n(n - 1)$  where  $n$  is the number of species,  $C$  is a covariance matrix that summarizes the correlation structure of the community phylogeny,  $trC$  is the trace (sum of the diagonal elements) of  $C$ ,  $\Sigma C$  is the sum of all elements in  $C$ . PSV is standardized to vary from zero, indicating maximum relatedness (clustering), to one, indicating that species in the assemblage are maximally unrelated (evenness), such that all species are from disparate parts of the phylogenetic tree (Algar et al. 2009). This metric is independent of species richness (Helmus et al. 2007, Savage and Cavender-Bares 2012). PSV was calculated with Picante (Kembel et al. 2010). Time-calibrated branch lengths were incorporated into calculation of PSV. A strong relationship between a given climatic variable and both PSV and richness should support the time-for-speciation hypothesis, assuming that climatic regimes that are occupied longer will have greater time to build up both richness and phylogenetic distance

than climates that have only been colonized more recently (on average).

NRI, which is a commonly used metric of phylogenetic relatedness (Cardillo 2011), measures the standardized effect size of mean phylogenetic distance (MPD), which estimates the average phylogenetic relatedness between all possible pairs of taxa in an assemblage. NRI is defined as (Webb 2000):  $NRI = -1 \times (MPD_{\text{observed}} - MPD_{\text{randomized}}) / (sdMPD_{\text{randomized}})$ , where  $MPD_{\text{observed}}$  is the observed MPD,  $MPD_{\text{randomized}}$  is the expected MPD of randomly generated assemblages ( $n = 1000$ ) generated by drawing a number of species randomly from across the phylogeny equal to the observed number of species in the assemblage, and  $sdMPD_{\text{randomized}}$  is the standard deviation of the MPD for the randomized assemblages. A positive NRI value indicates that MPD is lower than expected by chance (i.e. species more closely related than expected) and that phylogenetic clustering of species is occurring. Conversely, a negative NRI value results when the observed MPD is greater than expected by chance (i.e. species more distantly related than expected by chance) and thus indicates phylogenetic evenness or overdispersion. NRI was calculated with Phylocom (<<http://phylodiversity.net/phylocom>>). Time-calibrated branch lengths were incorporated into NRI. As with PSV, a strong relationship between a given climatic variable and both NRI and richness should support the time-for-speciation hypothesis.

To generate randomized (null) assemblages, species in each quadrat are treated as random draws from the overall pool of all species in the phylogeny across the region (i.e. model 2 of Phylocom. This null model has been considered as an appropriate null model for phylogenetic community studies and is commonly used in the recent literature (Santos et al. 2010, Ding et al. 2012, Pontarp et al. 2012). To test the robustness of our results to the choice of null model, we also used the other three null models available in Phylocom (i.e. model 0, model 1, and model 3) for calculating NRI. We then compared the main results using NRI calculated with null model 2 to those calculated with the other three null models.

We analyzed our data using the SEM library (<[cran.r-project.org/web/packages/sem/](http://cran.r-project.org/web/packages/sem/)>) in R (R Development Core Team). In addition to using path analysis, we also used Pearson's correlation coefficients to assess correlations between pairs of variables. To improve normality and linearity, we  $\log_{10}$  transformed species richness, and square-root transformed MAP (mm) and MINT (in Kelvin scale). Although the goal of our study is to determine relative importance of climate variables vs. phylogenetic metrics in determining patterns of species richness, rather than determining the significance of each variable per se, we examined whether observed values of each of the three phylogenetic metrics differ from expected values from a null model. For each of the 1175 quadrats, we generated 1000 null assemblages in each of which species were randomly shuffled on the tips of the phylogeny. For each of 1000 randomly shuffled assemblages for the quadrat, we computed MRD, PSV, and NRI. We calculated the average of values of MRD, PSV, and NRI derived from the 1000 null assemblages for each quadrat. We related the averages of the phylogenetic metrics derived from the null model to species richness, MINT, and MAP. These analyses were conducted using customized coding in R.

In each SEM, pairwise climatic and phylogenetic variables were correlated to each other to some degree. Differences in the degree of multicollinearity between different pairs of variables may influence a conclusion drawn from analyses using SEM. To determine the robustness of the results of SEM analyses to multicollinearity, we conducted a set of analyses that accounted for the effect of multicollinearity between paired variables on the variation in species richness explained by the paired variables. Specifically, we regressed each pair of variables on species richness and comparing coefficients of determination from different regressions. To account for nonlinear relationships between the variables, we included the quadratic terms of the variables in the regressions. We compared the results of SEM analyses with those from these regression analyses.

In addition to conducting analyses including all quadrats in North America, we also conducted analyses for three longitudinal bands (western, central, and eastern; Supplementary material Appendix 1, Fig. A1) because geographical setting, geological history, and floristic history differ substantially among these regions (Brouillet and Whetstone 1993, Graham 1999).

Spatial autocorrelation may inflate the rate of type I error in significance tests using large-scale ecological data. Therefore, we used SAM (spatial analysis in macroecology, Rangel et al. 2010) to recalculate *p*-values based on geographically effective degrees of freedom. The latter were determined using the approach of Dutilleul (1993). For path analysis, we used the same approach to determine geographically effective degrees of freedom for testing the significance of the coefficient of determination ( $R^2$ ) of each model. Specifically, we used Dutilleul's method to correlate the observed and estimated species richness and to test for the statistical significance of the model based on geographically effective degrees of freedom (gedf; Qian 2008). We did not perform statistical tests for significance of path coefficients because our primary interest was in the relative importance of the two groups of variables (climate vs phylogenetic relatedness) in influencing tree species richness, by assessing their direct effect sizes (effect strengths). These analyses were done using SAM ver. 4.0 (Rangel et al. 2010).

## Results

The two climatic variables (MINT and MAP) both varied substantially across North America. The range of MINT values was about 50°C, whereas that for MAP was 2080 mm (Supplementary material Appendix 1, Table A1). PSV, NRI, and species richness also varied greatly across North America (Supplementary material Appendix 1, Table A1). The number of angiosperm tree species in the sampled quadrats ranged from 6 to 138. Species richness generally decreased with latitude, and the gradient was steeper in eastern than western North America (Fig. 1).

Species richness was significantly correlated with both MINT and MAP after accounting for spatial autocorrelation, and was correlated with MAP more strongly than with MINT (Table 1). However, values of the three phylogenetic metrics (MRD, PSV, and NRI) were more strongly correlated with MINT than with MAP (Table 1). The cor-

relation of species richness with MRD, PSV, and NRI was  $-0.731$ ,  $0.742$ , and  $-0.488$ , respectively. All the correlations were significant ( $p < 0.001$ ) using raw degrees of freedom, and remained significant ( $p < 0.05$ ) after accounting for spatial autocorrelation (Table 1). In contrast, values of the three phylogenetic metrics derived from the null model (assemblages drawn from species randomly selected across the phylogeny) were not correlated with species richness, MINT, nor MAP ( $r$  ranging from  $-0.009$  to  $0.008$ ,  $p = 1.000$  in all cases). Importantly, we find that MRD is negatively correlated with species richness, a pattern which supports the time hypothesis but not the diversification rates hypothesis.

At the continental scale, the SEM with MRD and PSV (Fig. 2A) explained 72.1% of the variance in species richness ( $p < 0.001$  based on gedf). Further, the total direct effect size of phylogenetic structure on species richness (i.e. sum of absolute values of coefficients of paths leading from MRD and PSV to species richness) was slightly greater than the total direct effect size of climate on species richness (i.e. sum of absolute values of coefficients of paths leading MINT and MAP to species richness) (Fig. 2A, Fig. 4A). The SEM including NRI (calculated based on null model 2) and PSV (Fig. 3A) explained more of the variance in species richness (82.9%), with  $p < 0.001$  based on gedf. The total direct effect size of phylogenetic structure on species richness for this second SEM was greater than the total direct effect size of climate on species richness by a factor of 3.7 (Fig. 3A, Fig. 4B). Using NRI values calculated based on the other three null models (null models 0, 1, and 3) in the SEM, the total direct effect sizes of phylogenetic structure on species richness was greater than the total direct effect sizes of climate on species richness by a factor of  $>2$  in all cases (Supplementary material Appendix 1, Fig. A2).

When data were analyzed for each major region in North America using the same SEM (with MRD and PSV), 90.9, 78.5, and 54.2% of the variances in species richness were explained by the two climatic variables and the two metrics of phylogenetic structure in eastern, central, and western North America, respectively (all three models significant at  $\alpha = 0.01$  using gedf). The total direct effect size (i.e. sum of absolute values of path coefficients for direct effects) of phylogenetic structure on species richness was much larger than that of climate in one of the three bands and slightly smaller than that of climate in two of the three bands (Fig. 2B–D, Fig. 4A). When MRD was replaced by NRI in the three regional models, the models explained 97.1, 92.2, and 83.9% of the variance in species richness in the three respective regions (all three significant at  $\alpha = 0.01$  using gedf). Using NRI, the total absolute effect size of phylogenetic structure on species richness was much larger than that of climate in all three regions (Fig. 3B–D, Fig. 4B). Specifically, the former was larger than the latter by a factor of 2.3, 2.6, and 11.5, respectively, for eastern, central, and North America (Fig. 4B).

The results of the SEM analyses were consistent with those of the regression analyses (Table 2). For example, the variation in angiosperm tree species richness that was explained by NRI and PSV was greater than that explained either by MINT and MAP or by MRD and PSV (Table 2), indicating that the conclusions drawn from the SEM analyses were robust.

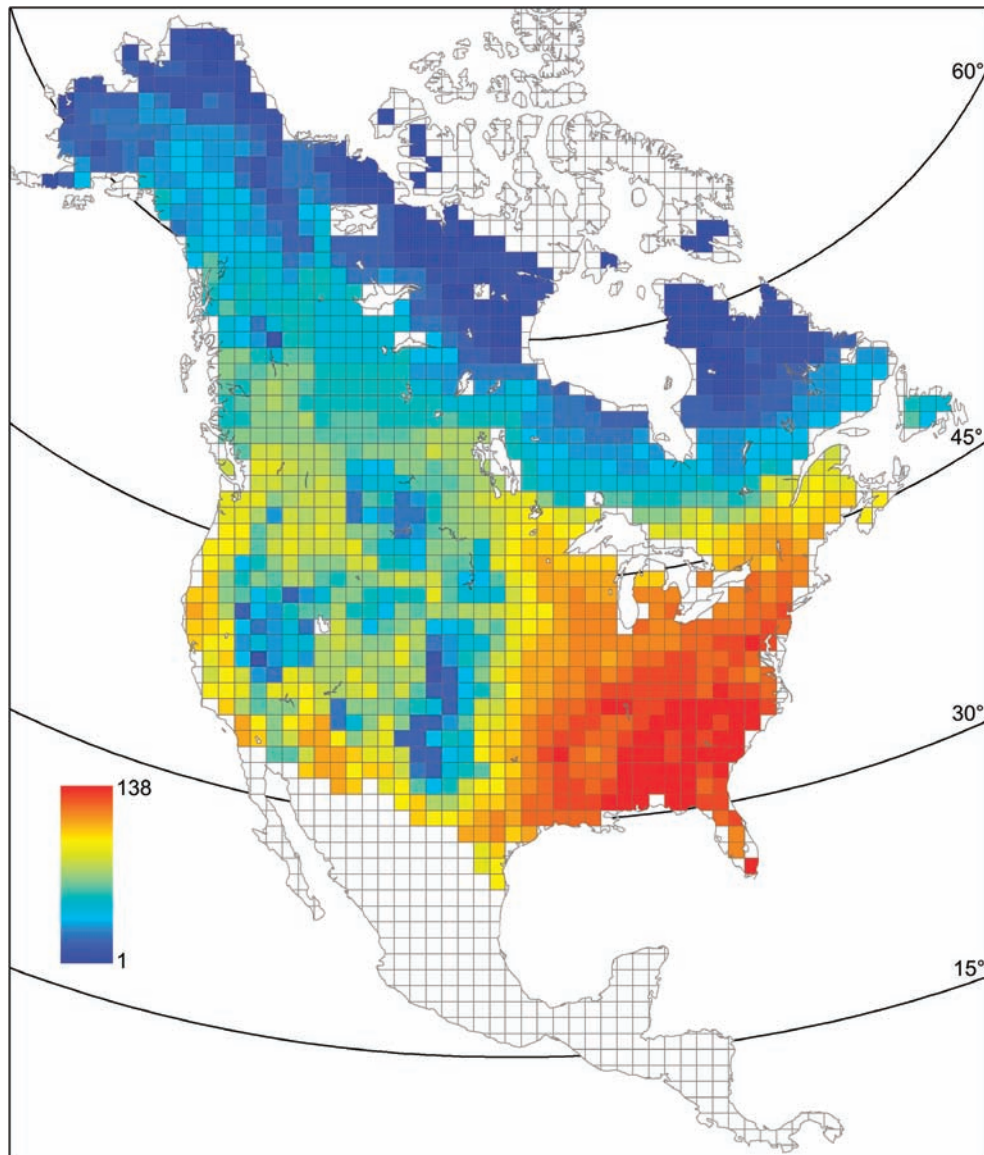


Figure 1. Spatial variation in angiosperm tree species richness in North America north of Mexico. Species richness in quadrats with land area less than 75% of a full quadrat is not shown.

## Discussion

In this study, we explore the causes of species richness patterns in North American angiosperm trees, integrating both phylogeny and climate and utilizing structural equation modeling (SEM). Our results are consistent with those of a recent study of South American trees (Giehl and Jarenkow 2012), which used SEM to show that richness is more strongly related to

patterns of phylogenetic structure (measured as phylogenetic species variability and phylogenetic species clustering) than to climatic (temperature and precipitation) variation, regardless of whether all tree species or only angiosperm tree species are considered. Our results support the idea that the combination of niche conservatism and the time-for-speciation effect explain much of the variation in tree richness in North America. As found by Qian et al. (2013) and reinforced in

Table 1. Pearson's correlation coefficients among minimum temperature (MINT), mean annual precipitation (MAP), mean root distance (MRD), phylogenetic species variability (PSV), net relatedness index (NRI), and angiosperm tree species richness (SR). Values in parentheses are p values according to the geographically effective degree of freedom (i.e. corrected for spatial autocorrelation).

Variable	MINT	MAP	MRD	PSV	NRI
MAP	0.410 (0.150)				
MRD	-0.649 (0.004)	-0.479 (0.037)			
PSV	0.850 (0.001)	0.520 (0.061)	-0.709 (0.001)		
NRI	-0.661 (0.003)	-0.360 (0.118)	0.697 (0.001)	-0.779 (0.001)	
SR	0.642 (0.025)	0.707 (0.008)	-0.731 (0.001)	0.742 (0.005)	-0.488 (0.042)

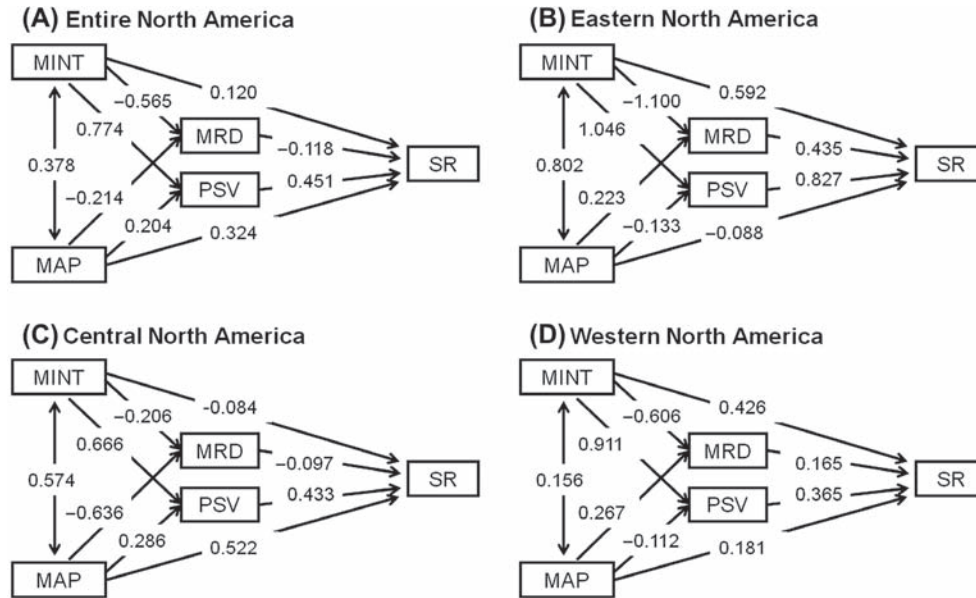


Figure 2. Structural equation models examining the influence of minimum temperature (MINT), mean annual precipitation (MAP), mean root distance (MRD), and phylogenetic species variability (PSV) on angiosperm tree species richness (SR) in entire (A), eastern (B), central (C), and western (D) North America. Values are standardized partial regression coefficients.

the present study using the SEM approach, regional assemblages in which species richness is highest tend to have species that are (on average) more distantly related to each other, as predicted by this time-based model. Conversely, species in more species-poor environments tend to be more closely related, suggesting that few clades were able to invade these environments. Furthermore, given the strongly negative relationship between MRD and richness, we do not support the hypothesis that these richness patterns are explained by higher diversification rates in clades in more species-rich environments. Our results show that climate

strongly influences these measures of phylogenetic structure (Table 1). However, we find that the seemingly direct effects of climate on richness are relatively weak after accounting for phylogenetic structure, when using PSV and NRI. We also find that phylogenetic information explains considerably less variation when using MRD. Our results also suggest that phylogenetic patterns in regional assemblages need not be completely obscured by recent dispersal.

Few studies have simultaneously investigated the relative effects of climate and evolutionary explanations (inferred from phylogenetic structure) on species richness across a

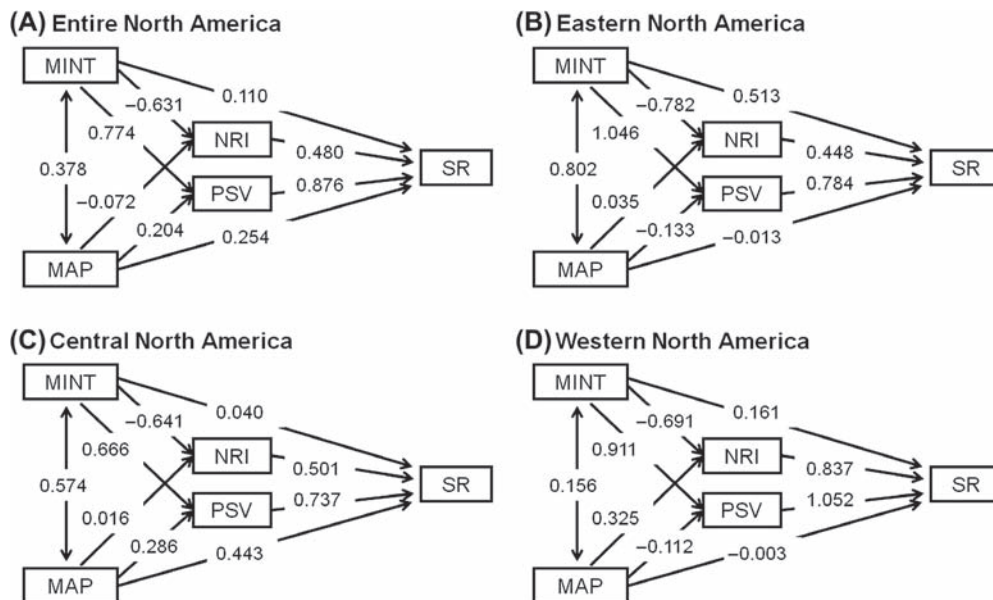


Figure 3. Structural equation models examining the influence of minimum temperature (MINT), mean annual precipitation (MAP), net relatedness index (NRI), and phylogenetic species variability (PSV) on angiosperm tree species richness (SR) in entire (A), eastern (B), central (C), and western (D) North America. Values are standardized partial regression coefficients.

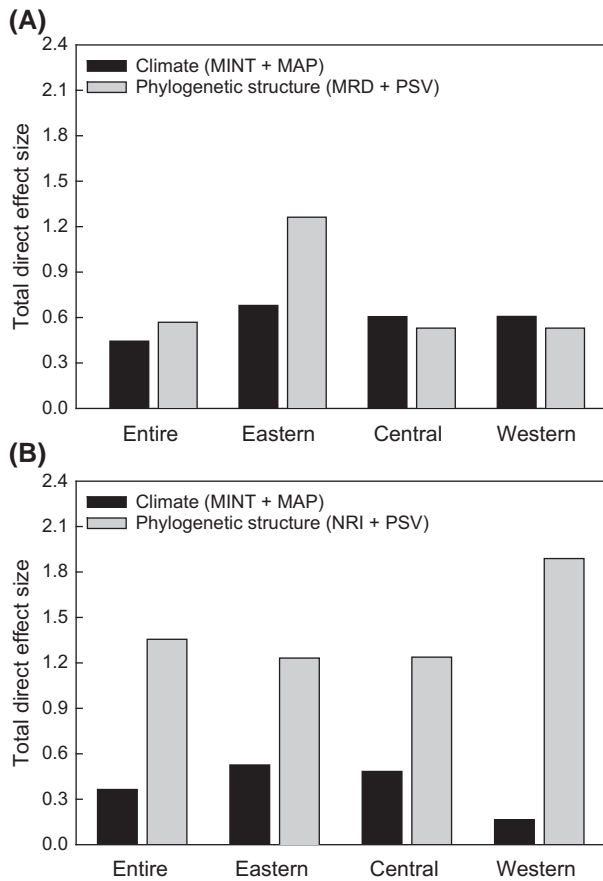


Figure 4. The total direct effects (i.e. absolute values of path coefficients of direct effects) of climate (minimum temperature and mean annual precipitation; black bars) and phylogenetic structure [(A) mean root distance (MRD) and phylogenetic species variability (PSV); (B) net relatedness index (NRI) and phylogenetic species variability (PSV); gray bars] on angiosperm tree species richness.

broad geographical extent. To our knowledge, the study of Algar et al. (2009) is the only one comparable to ours in terms of spatial scale. Our results offer several interesting contrasts to those of Algar et al. (2009). Those authors utilized a similar SEM approach, applied to New World treefrogs (Hylidae). However, they found little relationship between either PSV or MRD and species richness, at the spatial scale of  $100 \times 100$  km regions, and suggested that richness patterns were not explained by the tropical conservatism hypothesis (in contrast to the conclusions of a previous analysis of patterns of hylid frog richness at larger spatial scales; Wiens et al. 2006). Instead, they argued that rich-

Table 2. Coefficients of determination for the regression models of angiosperm tree species richness against climatic variables (MINT and MAP) and phylogenetic variables (MRD, NRI and PSV). Both linear and quadratic terms of each variable were included. See Table 1 for variable abbreviations.

Region	MINT + MAP	MRD + PSV	NRI + PSV
Entire North America	0.670	0.696	0.780
Eastern North America	0.897	0.904	0.945
Central North America	0.851	0.729	0.859
Western North America	0.618	0.474	0.847

ness patterns were explained by precipitation alone, without any influence of evolutionary factors.

We suggest that the differences in results may be explained by differences in methods. Algar et al. (2009) did not utilize a time-calibrated phylogeny, unlike our study and the previous regional-scale treefrog study (Wiens et al. 2006). Nevertheless, they interpreted their results as rejecting the time-based tropical conservatism hypothesis. The conclusions of Algar et al. (2009) on treefrog richness are also contradicted by a study of hylid frogs utilizing a time-calibrated phylogeny at a smaller spatial scale (local sites; Wiens et al. 2011). Given that Algar et al. (2009) did not include time directly, the fact that they failed to find time to be important in explaining richness patterns is perhaps unsurprising.

The results of some previous studies on trees are consistent with some of our results, but utilized different methodologies. For example, Qian et al. (2013) related species richness of angiosperm trees in regional assemblages in North America to climate, phylogenetic structure, and clade age and found that tree species tend to be more phylogenetically related (clustered) in regions with lower winter temperature; however, they did not examine the relative effects of climate and phylogenetic structure on tree species richness. Hawkins et al. (2011) addressed the causes of global angiosperm family richness (including trees), incorporating both climate and clade age. They supported a relationship between climate and richness for tree families (but not herbaceous families), with more tree families in warmer and wetter regions. They considered their results to be consistent with the tropical conservatism hypothesis, by showing that older families are associated with areas of higher family richness. In a highly complementary study, Hawkins et al. (2014) showed that older tree families in North America are associated with warmer climates, that younger families are associated with cold climates and a series of traits related to cold tolerance, and that these traits show a phylogenetic pattern consistent with niche conservatism. Thus, their results are also consistent with the tropical conservatism hypothesis (although they do not address species richness directly) and provide evidence that conservatism in cold tolerance in older lineages helps drive this pattern. Ricklefs (2005) used phylogenies to show that temperate tree lineages are nested within older tropical clades, a pattern also consistent with the tropical conservatism hypothesis. Kerkhoff et al. (2014) also supported the tropical conservatism hypothesis for angiosperms using a large-scale phylogeny (12 521 species), based on the inferred long-term occurrence of angiosperms at tropical latitudes, infrequent invasions of temperate regions, and high phylogenetic diversity in tropical regions.

Fine and Ree (2006) examined the current species richness of trees in different biomes across the globe, as a function of present biome area and biome area in the past. They found that present-day patterns of tree richness are related to the estimated past area of biomes, and not to their present-day area. This analysis supported a key prediction of the tropical conservatism hypothesis that is especially difficult to test: that more clades arise in tropical regions because tropical regions had greater area until relatively recently. However, they did not address the potential role of time and niche conservatism in explaining richness



patterns (i.e. based on patterns of phylogeny and climate in regional assemblages).

Our approach also has some limitations for addressing the causes of richness patterns. Most importantly, it is a relatively indirect way of examining the processes of speciation, extinction, and dispersal and their contribution to diversity patterns. For example, there is no direct test of a time-for-speciation effect on regional diversity (based on how long different regions or climates have been inhabited; Wiens et al. 2006, 2011, Kozak and Wiens 2012). Nor is there a direct test of niche conservatism (e.g. based on model-fitting analyses using the phylogeny and climatic variables; Kozak and Wiens 2010, Hawkins et al. 2014, Kerkhoff et al. 2014). There is also no direct analysis of the relationship between climatic variables and rates of diversification. Although we could perform some of these analyses with our phylogenetic and climatic data, such analyses would be compromised by our inclusion of only North American species. Better tests should include species both in and outside of North America. In addition, analyses of North America alone cannot fully address hypotheses for global biodiversity patterns (such as high tropical richness). Analyses within continents do not necessarily generalize to global patterns, and North America does not contain mesic tropical forests, a biome containing many of earth's species (Kreft and Jetz 2007). Nevertheless, North America contains strong climatic gradients extending from tropical to polar areas, and much of the latitudinal diversity gradient is not simply between temperate and tropical areas. Finally, the relationships between NRI, PSV, and MRD and the processes that addressed here would also benefit from further study. Nevertheless, despite these many limitations, we do find that these phylogenetic variables show strong relationships with richness patterns.

We note that our results also show that, across North America, temperature has a stronger effect on measures of phylogenetic structure than precipitation (Fig. 2A, 3A). In contrast, precipitation has a stronger effect on species richness that is more independent of phylogenetic structure than temperature. These patterns may reflect phylogenetic conservatism in tolerance to cold temperatures in plants (now documented or suggested in many studies; Hawkins et al. 2014, Zanne et al. 2014), but much less phylogenetic conservatism in traits related to drought tolerance. This could be an interesting topic for future studies.

In conclusion, in this study, we analyze the relationships between phylogeny, climate, and species richness using structural equation modeling (SEM) and data on the angiosperm trees of North America. Our results show that climate seems to influence patterns of phylogenetic structure within regions, and these patterns of phylogenetic structure seem to reflect the ecological, evolutionary and biogeographic processes that directly influence patterns of species richness. The specific patterns of phylogenetic structure are consistent with the idea that high richness arises in certain climatic regimes due to greater time-for-speciation in these climates and limited dispersal between climatic regimes over macroevolutionary time scales. Our results reinforce the idea that the observed relationships between climate and richness must arise through a combination of evolutionary, biogeographic, and ecological processes, and that a strong relationship between climate and richness is not

inconsistent with the evolutionary drivers of richness patterns. The approach that we take here (see also Algar et al. 2009) should be relevant to many other taxa and geographic regions.

*Acknowledgements* – We thank Robert E. Ricklefs for useful discussion and helpful comments. We are grateful to Adam Algar, and Zhiheng Wang for constructive comments on the manuscript. We thank Matthew R. Helmus, Eliot Miller, and Yves Rosseel for advice on using R codes for computing PSV, MRD, and path coefficients.

## References

- Algar, A. C. et al. 2009. Evolutionary constraints on regional faunas: whom, but not how many. – *Ecol. Lett.* 12: 57–65.
- Angiosperm Phylogeny Group 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. – *Bot. J. Linn. Soc.* 161: 105–121.
- Barbour, M. G. and Billings, W. D. 1988. North American terrestrial vegetation. – Cambridge Univ. Press.
- Bell, C. D. et al. 2010. The age and diversification of the angiosperms re-visited. – *Am. J. Bot.* 97: 1296–1303.
- Brouillet, L. and Whetstone, R. D. 1993. Climate and physiography. – In: Flora of North America Editorial Committee (eds), Flora of North America north of Mexico, Vol. 2. Oxford Univ. Press, pp. 15–46.
- Cardillo, M. 2011. Phylogenetic structure of mammal assemblages at large geographical scales: linking phylogenetic community ecology with macroecology. – *Phil. Trans. R. Soc. B* 366: 2545–2553.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Condamine, F. L. et al. 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. – *Ecol. Lett.* 15: 267–277.
- Currie, D. J. and Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. – *Nature* 329: 326–327.
- Ding, Y. et al. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. – *Oikos* 121: 1263–1270.
- Donoghue, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. – *Proc. Natl Acad. Sci. USA* 105: 11549–11555.
- Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. – *Biometrics* 49: 305–314.
- Fine, P. V. A. and Ree, R. H. 2006. Evidence for a time-integrated species–area effect on the latitudinal gradient in tree diversity. – *Am. Nat.* 168: 796–804.
- Francis, A. P. and Currie, D. J. 2003. A globally consistent richness–climate relationship for angiosperms. – *Am. Nat.* 161: 523–536.
- Freckleton, R. P. et al. 2008. Relating traits to diversification: a simple test. – *Am. Nat.* 172: 102–115.
- Fritz, S. A. and Rahbek, C. 2012. Global patterns of amphibian phylogenetic diversity. – *J. Biogeogr.* 39: 1373–1382.
- Giehl, E. L. H. and Jarenkow, J. A. 2012. Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. – *Ecography* 35: 933–943.
- Graham, A. 1999. Late Cretaceous and Cenozoic history of North American vegetation north of Mexico. – Oxford Univ. Press.
- Hawkins, B. A. et al. 2011. Global angiosperm family richness revisited: linking ecology and evolution to climate. – *J. Biogeogr.* 38: 1253–1266.

- Hawkins, B. A. et al. 2014. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. – *J. Biogeogr.* 41: 23–38.
- Helmus, M. R. et al. 2007. Phylogenetic measures of biodiversity. – *Am. Nat.* 169: E68–E83.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Clim.* 25: 1965–1978.
- Hortal, J. et al. 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. – *Ecol. Lett.* 14: 741–748.
- Kamilar, J. M. and Guidi, L. M. 2010. The phylogenetic structure of primate communities: variation within and across continents. – *J. Biogeogr.* 37: 801–813.
- Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. – *Bioinformatics* 26: 1463–1464.
- Kerckhoff, A. J. et al. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. – *Proc. Natl Acad. Sci. USA* 111: 8125–8130.
- Kerr, J. T. and Currie, D. J. 1999. The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. – *Ecoscience* 6: 329–337.
- Kozak, K. H. and Wiens, J. J. 2010. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. – *Am. Nat.* 176: 40–54.
- Kozak, K. H. and Wiens, J. J. 2012. Phylogeny, ecology, and the origins of climate–richness relationships. – *Ecology* 93: S167–S181.
- Krefl, H. and Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. – *Proc. Natl Acad. Sci. USA* 104: 5925–5930.
- Latham, R. E. and Ricklefs, R. E. 1993. Global patterns of tree species richness in moist forests: energy–diversity theory does not account for variation in species richness. – *Oikos* 67: 325–333.
- Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. – *Ecol. Lett.* 10: 315–331.
- Montoya, D. et al. 2007. Contemporary richness of Holarctic trees and the historical pattern of glacial retreat. – *Ecography* 30: 173–182.
- O’Brien, E. M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa’s woody flora. – *J. Biogeogr.* 20: 181–198.
- Pontarp, M. et al. 2012. Phylogenetic analysis suggests that habitat filtering is structuring marine bacterial communities across the globe. – *Microbial Ecol.* 64: 8–17.
- Pyron, R. A. and Wiens, J. J. 2013. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. – *Proc. R. Soc. B* 280: 20131622.
- Qian, H. 2008. Effects of historical and contemporary factors on global patterns in avian species richness. – *J. Biogeogr.* 35: 1362–1373.
- Qian, H. et al. 2013. Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. – *Global Ecol. Biogeogr.* 22: 1183–1191.
- Rabosky, D. L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. – *Ecol. Lett.* 12: 735–743.
- Rangel, T. F. L. V. B. et al. 2010. SAM: a comprehensive application for spatial analysis in macroecology. – *Ecography* 33: 46–50.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – *Science* 235: 167–171.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. – *Ecol. Lett.* 7: 1–15.
- Ricklefs, R. E. 2005. Phylogenetic perspectives on patterns of regional and local species richness. – In: Bermingham, E. et al. (eds), *Tropical rainforests: past, present, and future*. Univ. of Chicago Press, pp. 16–40.
- Ricklefs, R. E. 2006a. Evolutionary diversification and the origin of the diversity–environment relationship. – *Ecology* 87: S3–S13.
- Ricklefs, R. E. 2006b. Global variation in the diversification rate of passerine birds. – *Ecology* 87: 2468–2478.
- Ricklefs, R. E. and Schluter, D. 1993. Species diversity: regional and historical influences. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, pp. 350–363.
- Santos, B. A. et al. 2010. Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. – *PLoS One* 5: e12625.
- Savage, J. A. and Cavender-Bares, J. 2012. Habitat specialization and the role of trait lability in structuring diverse willow (genus *Salix*) communities. – *Ecology* 93: S138–S150.
- Smith, B. T. et al. 2012. An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. – *Ecol. Lett.* 15: 1318–1325.
- Smith, S. A. et al. 2011. Understanding angiosperm diversification using small and large phylogenetic trees. – *Am. J. Bot.* 98: 404–414.
- Stephens, P. R. and Wiens, J. J. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. – *Am. Nat.* 161: 112–128.
- Stevens, R. D. 2006. Historical processes enhance patterns of diversity along latitudinal gradients. – *Proc. R. Soc. B* 273: 2283–2289.
- Stevens, R. D. 2011. Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. – *Proc. R. Soc. B* 278: 2528–2536.
- Svenning, J.-C. et al. 2008. High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. – *J. Biogeogr.* 35: 394–406.
- Wang, Z. et al. 2011. Patterns, determinants and models of woody plant diversity in China. – *Proc. R. Soc. B* 278: 2122–2132.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – *Am. Nat.* 156: 145–155.
- Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. – *Am. Nat.* 170: S86–S106.
- Wiens, J. J. 2011. The causes of species richness patterns across space, time, and clades and the role of “ecological limits”. – *Q. Rev. Biol.* 86: 75–96.
- Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology, and species richness. – *Trends Ecol. Evol.* 19: 639–644.
- Wiens, J. J. et al. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. – *Am. Nat.* 168: 579–596.
- Wiens, J. J. et al. 2007. Phylogenetic history underlies elevational patterns of biodiversity in tropical salamanders. – *Proc. R. Soc. B* 274: 919–928.
- Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – *Ecol. Lett.* 13: 1310–1324.
- Wiens, J. J. et al. 2011. Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. – *Ecol. Lett.* 14: 643–652.
- Wiens, J. J. et al. 2013. Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). – *Evolution* 67: 1715–1728.
- Zanne, A. E. et al. 2014. Three keys to the radiation of angiosperms into freezing environments. – *Nature* 506: 89–92.

Supplementary material (Appendix ECOG-00952 at <[www.ecography.org/readers/appendix](http://www.ecography.org/readers/appendix)>). Appendix 1.