

Global angiosperm family richness revisited: linking ecology and evolution to climate

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ABSTRACT

Aim The global richness gradient of angiosperm families is correlated with current climate, and it has been claimed that historical processes are not necessary to understand patterns of plant family richness. This claim has drawn criticism, and there have been doubts about the quality of the data used to quantify the pattern. We revisit this issue using the Angiosperm Phylogeny Group (APG) III classification and revised range maps, and we incorporate an evolutionary variable, family age, to explore covariation between evolution and ecology and their links to climate via the tropical conservatism hypothesis (TCH).

Location Global.

Methods The richness pattern for 408 families was derived from range maps, and family ages were derived from a dated angiosperm phylogeny. Patterns were generated for all families, 143 families composed of trees, and 149 families composed of herbs. We also examined family range size patterns to test the extent to which extratropical floras are nested subsets of tropical floras. Ordinary least squares (OLS) multiple and partial regressions were used to generate climate models for richness, mean range size and mean age for each plant dataset and to evaluate the covariation between contemporary climate and clade age as correlates of family richness.

Results We confirmed the strong association between contemporary climate and family richness. Age patterns predicted by TCH were also found for families comprising trees. The richness of herbaceous families, in contrast, was correlated with climate but the age pattern was not as predicted by TCH. Floras in cold and dry areas are strongly nested within richer tropical floras.

Main conclusions Phylogenetic niche conservatism at the family level offers a likely explanation for the global diversity gradient of trees, but not for non-desert herbs, probably because of the faster evolutionary rates for herbs and less constrained evolutionary responses to climate change. Thus, it appears that multiple processes account for the overall angiosperm family gradient. Our analysis also demonstrates that even very strong associations of taxon richness and climate do not preclude evolutionary processes, as has been widely argued, and that climatic and evolutionary hypotheses for richness gradients are not mutually exclusive.

Keywords

Angiosperms, climate–richness relationships, diversity gradients, family richness, global diversity, niche conservatism, plant richness, range size, tropical conservatism hypothesis.

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INTRODUCTION

Broad-scale richness gradients are closely associated with contemporary climate (Wright *et al.*, 1993; Hawkins *et al.*, 2003; Field *et al.*, 2009). As part of the evidence for climatic control of taxonomic richness, Francis & Currie (2003) generated models of angiosperm family richness including energy and water variables that accounted for more than 80% of the global spatial variation, from which they concluded that processes related to the evolutionary history were not necessary to understand current plant richness patterns.

Qian & Ricklefs (2004) then responded to Francis & Currie (2003), criticizing them on numerous grounds including the quality of the data and the interpretation of the statistical models. First, they argued that family concepts in plants are fluid and arbitrary, and the classification used by Francis & Currie (2003) was out of date as well as missing many families [e.g. the analysis included 306 families, whereas APG II (Angiosperm Phylogeny Group, 2003) listed 397 families]. Further, they claimed that the maps used by Francis & Currie (2003), taken from Heywood (1993), contained enough errors that the richness patterns and environmental associations were subject to doubt. They also argued that controlling for climate before examining residual geographically based variation minimized the observed differences between biogeographical regions, which in the opinion of Qian & Ricklefs (2004) obscured substantial historical effects. Finally, and most importantly, Qian & Ricklefs (2004) argued that ecological and evolutionary processes leading to correlations between climate and richness are strongly collinear, since angiosperms probably have a tropical origin (Crane & Lidgard, 1989) and have had to evolve freezing tolerance to colonize areas with low temperatures, which only a subset of clades has managed to do (Ricklefs, 2005). This evolutionary legacy of low family richness in northern latitudes thus explains why richness is correlated with contemporary climate.

In a reply Currie & Francis (2004) defended their conclusions, arguing that it was unlikely that errors in the data invalidated the patterns or the statistical models generated to explain them, and they admitted that their analysis did not preclude the existence of historical effects. They closed the debate by agreeing that historical processes could be collinear with contemporary climate, but that predictions from historically based hypotheses are difficult to generate and test, and the evidence for historical processes is contradictory.

The proposition by Qian & Ricklefs (2004) that climate influences plant taxonomic richness through the tropical origin of angiosperms and the evolution of freezing tolerance [see also Latham & Ricklefs (1993a) for an earlier presentation of this explanation] is now referred to as the tropical conservatism hypothesis (TCH; Wiens & Donoghue, 2004), which is receiving attention because it generates testable predictions about the phylogenetic structure of diversity gradients. A number of predictions are possible, depending on underlying assumptions, but generally, any clade will be richer in the climates most similar to those in which the group

initially evolved, due to phylogenetic niche conservatism limiting the number of subclades that are able to break into novel environments as well as to longer residence times in ancestral climates (Ricklefs, 2006). If the clade (such as angiosperms) arose in tropical climates, not only will it be more species rich in the tropics, but tropical biotas will generally contain more older, ancestral subclades constrained by niche conservatism, whereas non-tropical biotas will comprise members of more recent and evolutionarily derived subclades that have undergone niche evolution (which has then led to new radiations outside the tropics). Phylogenetic patterns consistent with this prediction have recently been documented for a number of animal groups (Hawkins *et al.*, 2005, 2006, 2007a; Wiens *et al.*, 2006, 2009; Hawkins & DeVries, 2009; Hawkins, 2010). For plants, Donoghue (2008) explicitly argued that the explanation offered by Latham & Ricklefs (1993a) and Qian & Ricklefs (2004) can account for the spatial distribution of plant richness, driven by tropical niche conservatism and the difficulty of evolving cold tolerance.

In this paper we revisit the debate concerning ecological versus evolutionary explanations for angiosperm richness gradients, updating the family classification and range maps and using phylogenetically based information on the evolutionary history of plant families to examine how climate might drive plant diversity. We address four specific questions. First, are the results of Francis & Currie (2003) robust to recent taxonomic changes in angiosperm families and the inclusion of all currently recognized families? Second, does climate operate on the angiosperm diversity gradient as a selective agent generating a replacement of plant families moving from the tropics to the extra-tropics, or as a filter selectively excluding families moving from warm and wet climates to cold or dry ones, as expected when tropical niche conservatism is operating? Third, do the floras of warm, wet tropical climates contain older families than those of regions that have undergone cooling or drying since the early Tertiary, as expected under TCH? Fourth, are influences of ecological and evolutionary processes on the richness gradient strongly collinear? We evaluate each of these questions for all angiosperm families and for a subset of arborescent and herbaceous families considered separately. The life-history traits of trees and herbs differ substantially, and they have very different rates of molecular and phenotypic evolution (Smith & Donoghue, 2008; Smith & Beaulieu, 2010). It is likely that the processes influencing their diversification rates also differ, and comparisons of patterns for the two groups may shed light on explanations for the diversity of angiosperms as a whole.

MATERIALS AND METHODS

Plant richness data

The global family richness pattern was derived from the 413 families recognized by the APG III (Angiosperm Phylogeny Group, 2009) classification matched to the 506 family distri-

bution maps from Heywood *et al.* (2007). When family designations in Heywood *et al.* differed from those recognized by APG III, maps were combined according to the taxonomic information provided by APG III (Angiosperm Phylogeny Group, 2009) and the Angiosperm Phylogeny Website (APweb; Stevens, 2001 onwards). APweb was also used as the map source for 13 of the 16 families that were not mapped in Heywood *et al.* (2007); the remaining three families with no maps (Guamatelaceae, Lophiocarpaceae and Talinaceae) and marine families (Cymodoceaceae, Posidoniaceae and Zosteraceae) were excluded. Finally, although APG III includes Taccaceae within Dioscoreaceae, it acknowledged its distinct morphological characteristics and recent phylogenetic analyses suggesting that Taccaceae is a separate clade. Our database included this separation and comprises 408 families (see Table S1 in Supporting Information).

Patterns for trees and herbs were generated by classifying the range of growth forms of species in each family using information taken from APweb. Families that are exclusively or primarily trees and with no herbaceous species were classified as 'arborescent' ($n = 143$), and families that are exclusively or primarily herbaceous and contain no tree or liana species were classified as 'herbaceous' ($n = 149$). The remaining 116 families are either entirely shrubs or lianas or contain both tree and herbaceous species and were not analysed separately.

To compare our family richness gradient to that of Francis & Currie (2003), we converted their gridded data (provided by D. J. Currie, University of Ottawa) to centroids and intersected them with our grid (see 'Analytical protocols'). Cells in our grid that contained a centroid from their grid were extracted, and the two sets of richness values were correlated against each other.

The range maps were also used to calculate range sizes for each family. Mean range sizes were calculated in our global grid to evaluate relationships between family richness patterns and range size distributions and partially address the question of the extent to which climate operates on richness as a filter.

Plant age data

Most family ages were obtained from a dated version of the megatree of Davies *et al.* (2004) (available at http://www.phylodiversity.net/phyloomatic/davies_dated.new; accessed April 2010) which includes estimates for 377 families in our database and 24 additional families that were absent but regarded by APG III (Angiosperm Phylogeny Group, 2009) as being sister or polytomous to families that were in Davies *et al.* (2004). For the remaining seven families, Ripogonaceae was assigned the age of Smilacaceae, the family from which it was segregated by APG II (Angiosperm Phylogeny Group, 2003), Limeaceae and Petermanniaceae were assigned the averages of the ages of their closest ancestral and daughter families in the APG III megatree (available at <http://www.phylodiversity.net/phyloomatic/>; accessed April 2010) [Stegnospermataceae and Molluginaceae for Limeaceae, and Melanthiaceae and Colchicaceae for Petermannia-

ceae], and Misodendraceae and its sister family Schoepfiaceae were assigned the age provided by APweb for the former. No age estimates were available for Cynomoriaceae or Apodanthaceae, and they were assigned the average age across all families.

Environmental data

Our environmental models used the same data sources as Francis & Currie (2003) and included: mean annual temperature and annual precipitation (Legates & Willmott, 1992; data available at http://gcmd.nasa.gov/records/GCMD_gov.noaa.ngdc.G01976.html); Priestley–Taylor's annual potential evapotranspiration (PET) and Thornthwaite's annual actual evapotranspiration (AET) (Ahn & Tateishi, 1994; data available at <http://www.grid.unep.ch/data/data.php>); and annual water deficit (WD), computed as the difference between PET and AET.

Analytical protocols

All variables were binned in a 9300 km² global grid in a Behrman projection from which cells comprising Antarctica and small islands were excluded. This generated a maximum of 17,281 cells, although cells with < 50% of landmass and cells with no angiosperms were excluded from the analysis. Sample sizes varied slightly among analyses of the various plant groups due to the exclusion of empty cells for the group.

Following the analytical approach of Francis & Currie (2003), we used simple and multiple ordinary least squares (OLS) regression to explore relationships between plant family richness, mean range sizes and mean ages with respect to climate. In general we found that the models including various combinations of climatic predictors explained similar amounts of variance (all R^2 values were within 0.10 of each other), as long as they included measures of both energy and water inputs. We also found that the best model in Francis & Currie (2003), which included a linear term of WD and linear and quadratic terms of PET, also performed as well in our richness and mean age data as any other model combining the other climatic variables, and we focused on these variables to reduce redundancy and facilitate comparison with their results. We also used partial regression (Legendre & Legendre, 1998) to explore patterns of covariation between current climate and evolutionary processes based on multiple regression models including both climatic variables and mean family age. Separate models were generated for all response variables with all families, arborescent families only and herbaceous families only.

To explore the extent to which regression models successfully accounted for the spatial patterns of total, tree and herb family richness, we generated spatial correlograms using Moran's I at 27 distance classes (see Diniz-Filho *et al.*, 2003) and compared the raw autocorrelation in the data against the residual autocorrelation in the models containing only climatic predictors, only age, or both. Non-stationarity in relationships between richness and environment/age precluded spatially explicit modeling.

Finally, we examined patterns of compositional nestedness to quantify the extent to which composition of extra-tropical cells represents a subsample of tropical cells using three transects five cells wide and of variable length (Fig. S1). The transects were long and thin to focus interpretation of patterns on the latitudinal axis. Because geographically extensive cold climates are mostly found in the Northern Hemisphere, and to make all cells comparable, the nestedness analysis used only cells in continental landmasses north of the equator. To examine possible variation among regions arising from historical contingencies, separate transects were generated in the New World, the western Old World, and eastern Asia.

Three nestedness metrics were calculated: (1) NODF (nestedness metric based on overlap and decreasing fill; Almeida-Neto *et al.*, 2008); (2) matrix temperature, T (Atmar & Patterson, 1993), reported as $100 - T$, and (3) a novel metric, subsample nestedness (SSN), calculated as the proportion of families found in a less rich cell also found in a paired richer cell. As our focus was on the latitudinal pattern of family replacement, cells within each transect were assigned identical longitudes. We used a spatially explicit approach, generating metrics for all possible pairs of cells and then averaging values within 10 distance classes. This allowed us to quantify levels of nestedness with respect to the distance between pairs of cells on a north–south axis. The first two indexes were computed with ANINHADO (Guimarães & Guimarães, 2006; available at <http://www.guimaraes.bio.br>), and the third with a BASIC program written by us (available upon request). For statistical evaluation the observed values for the first two indices were compared against values obtained when the observed family occurrences in cells within each transect were distributed randomly; it was not possible to generate null models for SSN, so we generated 95% confidence intervals. In this paper we explore patterns of compositional nestedness, but phylogenetic nestedness of extra-tropical floras within tropical floras is also predicted under some scenarios of tropical niche conservatism. We will examine this elsewhere.

RESULTS

The angiosperm family richness gradient

The pattern of family richness we obtained is as would be expected based on the map of Francis & Currie (2003) (Fig. 1), and the spatial richness patterns are virtually identical (paired-cell correlation = 0.977). Because our data comprise 102 more families than Francis & Currie (2003), our absolute per-cell estimates are slightly higher (e.g. a maximum of 219 vs. 201), despite our smaller grain (c. 9300 km² vs. 35,000 km²). But despite differences in the data sets, the shape of the global gradient documented by Francis & Currie (2003) has remained extremely robust.

Although there are far fewer arborescent and herbaceous families in the polar and sub-polar zones than in the wet tropics, their gradients in the sub-tropical and temperate zones are substantially different (Fig. 1b,c). The latitudinal gradient

of arborescent families is almost twice as steep as the gradient for herbaceous families (0.853 vs. 0.488 families/degree), and tree family richness is highest in the tropics in all parts of the world (Fig. 1b). In contrast, the richness of herbaceous families remains high as far north as 45°, and parts of the northern temperate zone, particularly in the Nearctic, are richer than many areas in the tropics (Fig. 1c).

Francis & Currie's (2003) strongest regression model contained potential evapotranspiration ($PET - PET^2$) and water deficit (WD) and explained 83.7% of the variance in family richness. The same model based on our richness data has equally strong explanatory power (Table 1a). We also found that actual evapotranspiration by itself generated a strong model that did not require a polynomial term ($r^2 = 0.763$). Irrespective, the relationships between water, energy and richness identified by Francis & Currie (2003) are extremely robust to the differences in the plant data.

Climatic models for arborescent and herbaceous families differ from the overall angiosperm model, although not substantially (Table 1a1,2). The relatively high herb richness of the temperate zone generates a stronger negative PET^2 coefficient and a model with somewhat weaker explanatory power, but both groups have strong (for herbs) to very strong (for trees) statistical relationships with energy and water.

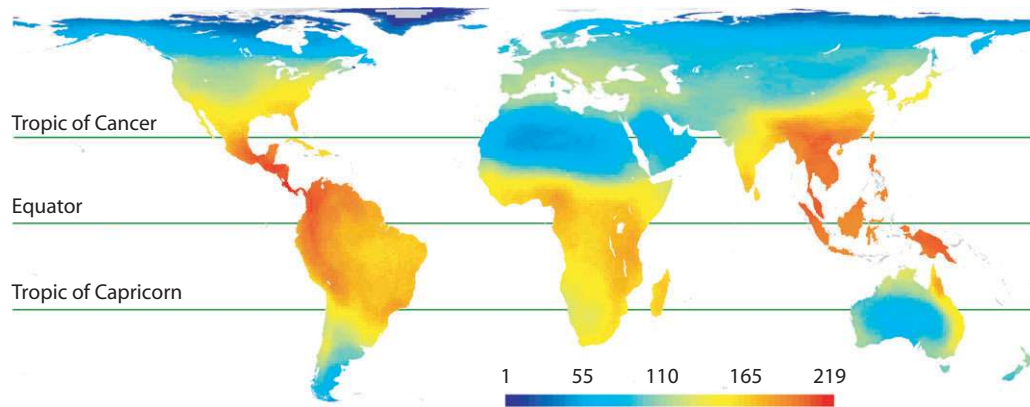
Residual spatial autocorrelation in the richness gradient after fitting the climatic models (Fig. S1) indicates that the models explain most of the spatial pattern in the data, but not all. Substantial unexplained pattern remains in the smallest distance class in all three data sets, which is typical of broad-scale analyses based on range maps due to a combination of using filled-in ranges and macroclimatic predictors. However, residual Moran's I values > 0.1 or < -0.1 are found in a number of distances classes in all three plant groups, indicating that the climate models do not explain all spatial structure across all scales, and that additional spatially structured variables are needed to account completely for the global richness gradient.

The global range size gradient

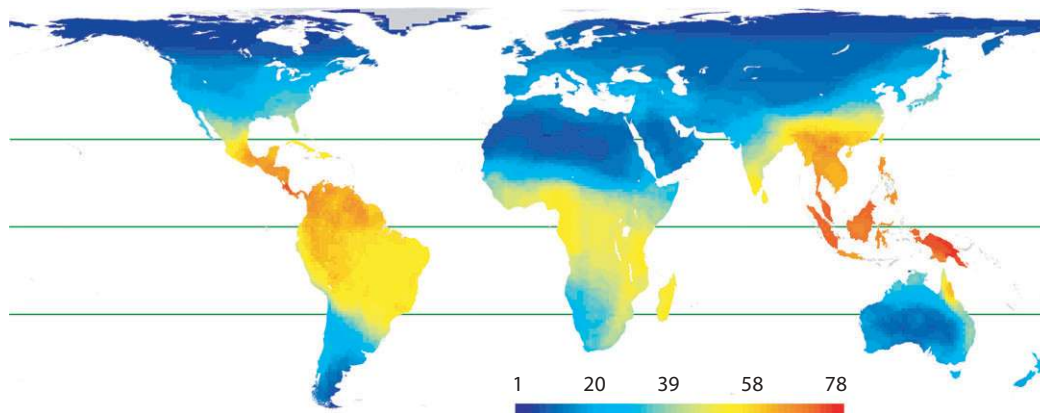
Average family range sizes are smallest in the tropics and largest in northern latitudes and in major deserts (Fig. 2a). Further, the range size pattern is strikingly similar to the richness gradient (cf. Fig. 1a), and they are tightly correlated ($r = -0.978$). Thus, family richness can be considered a linear transformation of range size patterns, and the climate–richness relationship can be interpreted directly via the range dynamics of angiosperm families. Because mean range size is so strongly correlated with richness, a climate-based regression model for range size also has very strong explanatory power (Table 1b). Separate models for trees and herbs are also strong (Table 1b1,2).

Extra-tropical floras are largely nested subsets of tropical floras in all three regions of the world, and the three nestedness metrics generated equivalent results (Fig. 3). In all cases nestedness is much higher than expected under a random

(a) All families



(b) Arborescent families



(c) Herbaceous families

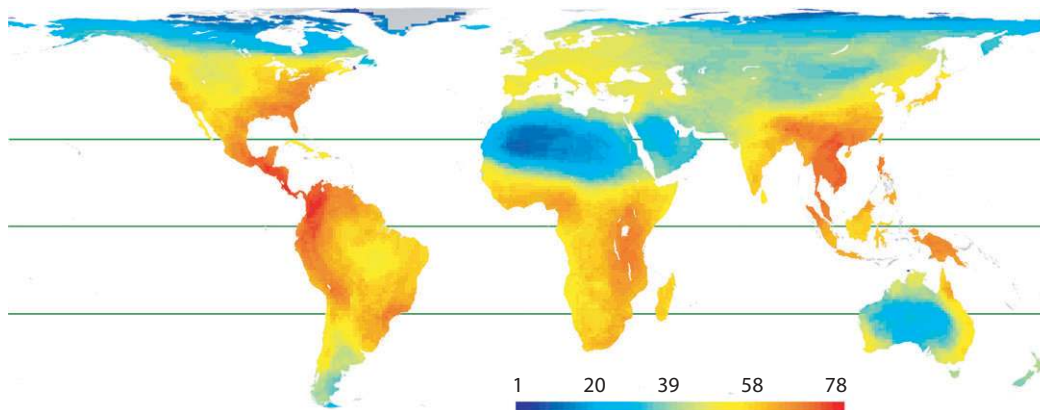


Figure 1 Global pattern of angiosperm family richness in a 9300 km² grid. (a) All 408 families, excluding marine and small-island endemics, (b) 143 arborescent families comprising exclusively or primarily trees but no herbaceous species, and (c) 149 herbaceous families comprising exclusively or primarily herbs but no trees or lianas. Note difference in scales of (a) and (b, c).

model or has narrow errors (Table S2). In the New World and eastern Asia, cells > 6000 km apart remain nested at > 79.5% and reflect smooth reductions in richness moving north. In Africa, Asia Minor and Europe the richness gradient is more complex and slightly less nested at intermediate distances due to the presence of Mediterranean families not occurring farther

south, but SSN at the longest distance class is similar to the other regions (Fig. 3). The nestedness analysis indicates that low-richness areas contain large-ranged families also found in high-richness areas, whereas smaller-ranged families drop out as richness decreases (also visually apparent when cells are ranked from highest to lowest richness, Fig. 3g–i). That is, the

	Predictor (standardized coefficients)				Model R^2
	PET	PET ²	WD	Age	
(a) Family richness (climate)	1.85	-0.77	-0.71	-	0.844
(1) Tree families	1.28	-0.15	-0.71	-	0.873
(2) Herb families	1.87	-0.93	-0.75	-	0.696
(b) Mean range size (climate)	-1.74	0.64	0.70	-	0.850
(1) Tree families	-1.53	0.46	0.58	-	0.804
(2) Herb families	-1.50	0.47	0.67	-	0.741
(c) Mean age (climate)	0.93	-0.22	-0.90	-	0.596
(1) Tree families	1.76	-0.81	-0.23	-	0.778
(2) Herb families	0.16	-0.09	-0.67	-	0.389
(d) Family richness (climate + age)	1.46	-0.68	-0.34	0.41	0.913
(1) Tree families	0.89	0.02	-0.66	0.23	0.885
(2) Herb families	1.82	-0.91	-0.45	0.47	0.829

Table 1 Global ordinary least squares (OLS) regression models of (a, d) family richness, (b) mean range size and (c) mean family age for all 408 angiosperm families studied. Note that age is modelled as a response variable in (c) and as a predictor in (d). Models for herb ($n = 149$) and tree ($n = 143$) families are also provided for comparison. Predictor variables are PET = potential evapotranspiration, WD [water deficit] = PET - AET [actual evapotranspiration], and Age = mean age of families.

tropics contain families varying from being narrowly distributed endemics to cosmopolitan, but only the most widely distributed families occur in the far north and major deserts.

The ranges of arborescent and herbaceous families largely follow those of all families, with some differences (Fig. 2b,c). Tree family ranges are smaller than herb family ranges (mean = 22,063,915 km², SE = 2,400,333 vs. mean = 39,605,515 km², SE = 3,367,965), and the geographic pattern of mean tree range size is very similar to that found for all families, except in Australia (Fig. 2b) due to 13 Australasian endemic tree families. The nestedness of tree family richness in the longest distance classes is also very strong as measured by SSN: 100 in the western Old World, 83.0 in the New World and 78.6 in eastern Asia (Fig. 3a-c). Mean range sizes of herbs also tend to be relatively small in the tropics, although the eastern USA and northern California also support relatively narrowly ranged families on average (Fig. 2c). Even so, nestedness levels are high in all regions, with SSNs in the longest distance classes ranging from 69.1 in the western Old World, 80.6 in eastern Asia and 83.5 in the New World (Fig. 3a-c). Thus, although herb families are more widely distributed than arborescent families, their richness pattern still reflects primarily a filtering out of smaller-ranged families moving from the tropics towards the pole, with a limited replacement by temperate-zone families.

The nested nature of the richness gradient in the Northern Hemisphere is further reflected by the fact that few families are strictly extra-tropical in the Holarctic: only 2% (3/149) of tree families occur exclusively north of the Tropic of Cancer, and only 7% (10/143) of herbaceous families do so. Among the 116 remaining families comprising shrubs, lianas or a mix of growth forms, only two (1.7%) are exclusively northern extra-tropical.

The strong link between family richness and ranges sizes together with the high levels of nestedness indicate that climate primarily drives angiosperm family richness as a filter; selectively excluding families moving into colder and drier climates to a much greater extent than it selects for the replacement of tropical families by non-tropical families in cold, dry regions.

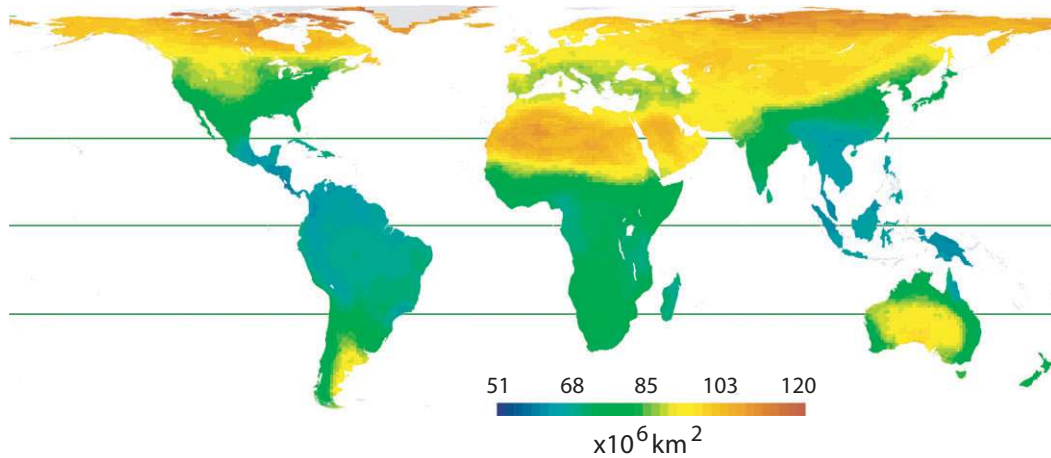
The ages of tropical and extra-tropical floras

The geographic distribution of mean family age is not entirely consistent with the version of the tropical conservatism hypothesis developed in the Introduction (Fig. 4a). Tropical floras are substantially older than those of deserts and northern tundra, as predicted, but mean family age is also older in parts of the extra-tropics, including the south-eastern USA, and across a broad band across the boreal zone of Eurasia. This complex pattern results in a climate model for mean age with moderate explanatory power (Table 1c). It also arises from mixing essentially opposite age patterns for trees and herbs; arborescent families are oldest in the tropics/sub-tropics and the Southern Hemisphere, and youngest on average in the northern temperate, boreal and sub-polar zones (Fig. 4b), whereas herbaceous families are oldest across much of North America and the forest belt of Eurasia (Fig. 4c). Herbaceous families are youngest on average in the Sahara and Australian deserts, Tierra del Fuego and the northern tundra zone, but are not especially old in the tropics. Fundamentally different relationships between climate and age for trees and herbs are also reflected by very different multiple regression models. Tree ages are strongly associated with climate, being oldest on average in warm climates (Table 1c1), whereas herb ages are somewhat weakly associated with climate but are youngest in dry regions (Table 1c2). Thus, a strong TCH signal is found among those families comprising only trees, but the prediction that tropical herb families are older than temperate-zone families is rejected.

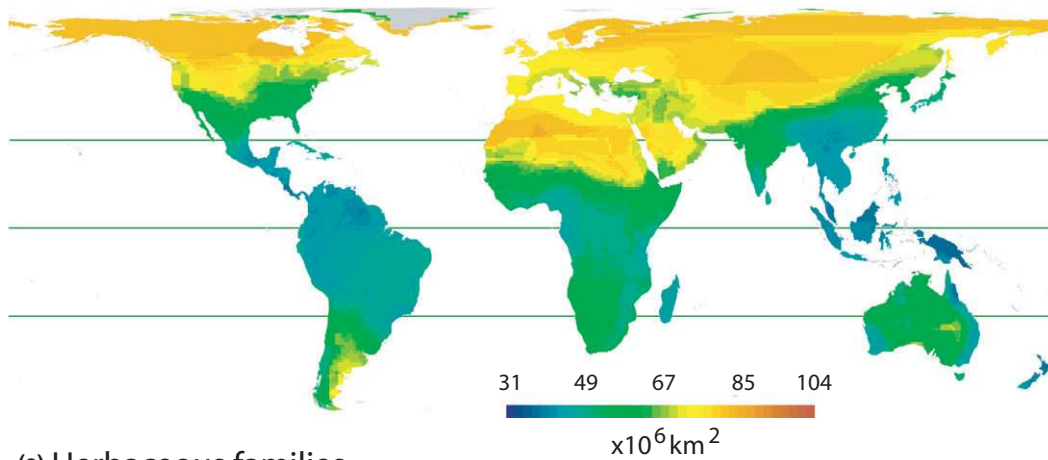
Covariance between current climate and family age

Mean family age and richness are moderately positively correlated across all families ($r = 0.740$) and tree families ($r = 0.770$) but more weakly for herb families ($r = 0.449$). Thus, for all groups richness is more strongly associated with current climate than with evolutionary history as measured by family ages. Age-based models also contain more unexplained spatial structure than the climate models, especially for all

(a) All families



(b) Arborescent families



(c) Herbaceous families

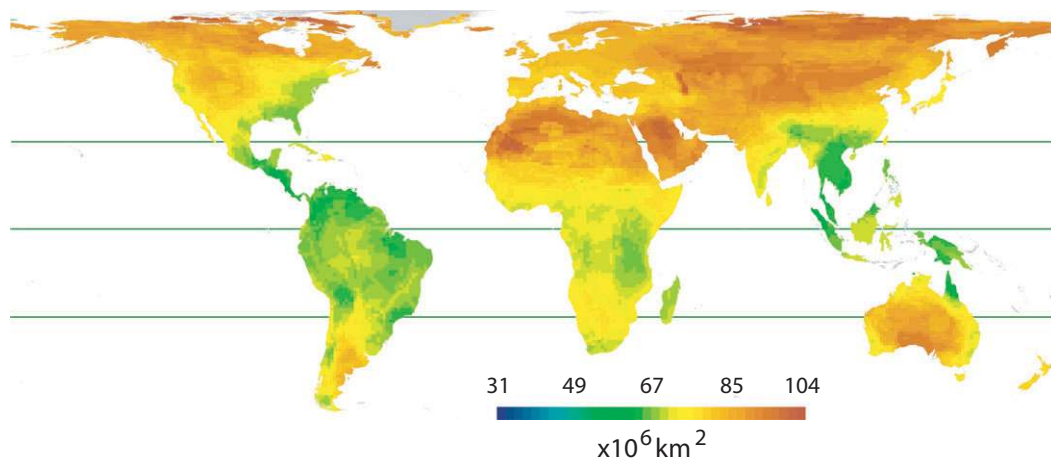


Figure 2 Global pattern of mean range size of angiosperm families. (a) All families ($n = 408$), (b) arborescent families only ($n = 143$), and (c) herbaceous families only ($n = 149$). Note difference in scales of (a) and (b, c).

families and herbaceous families (Fig. S2). Adding age to the climatic models increased their explanatory power for all families as well as herbs, but not for trees (Table 1d), and the models combining both age and climate successfully account

for almost all of the spatial structure in the global gradient except at the smallest distance class (Fig. S2).

Partitioning the independent and covarying associations of family richness with climate and age indicates substantial

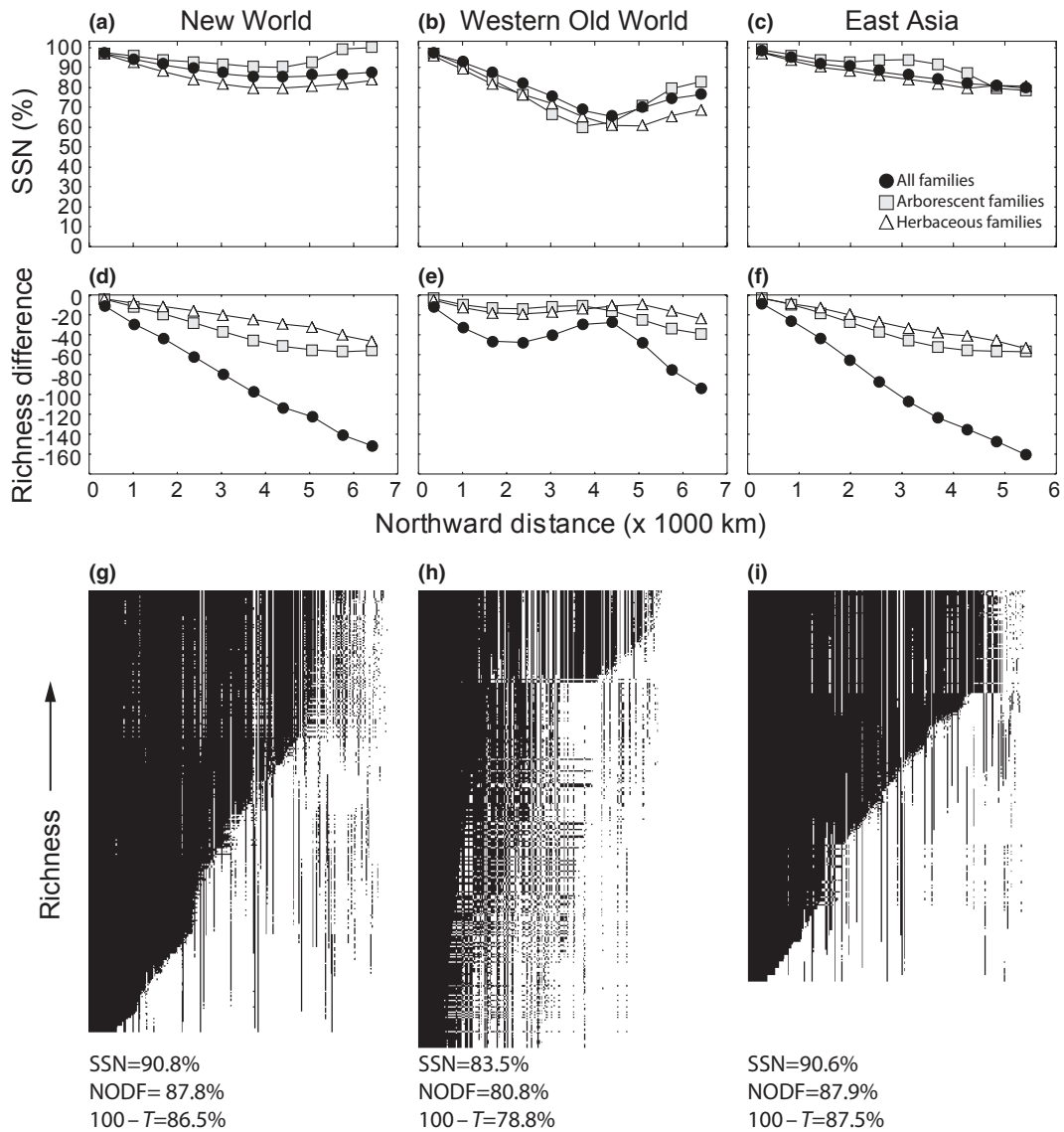


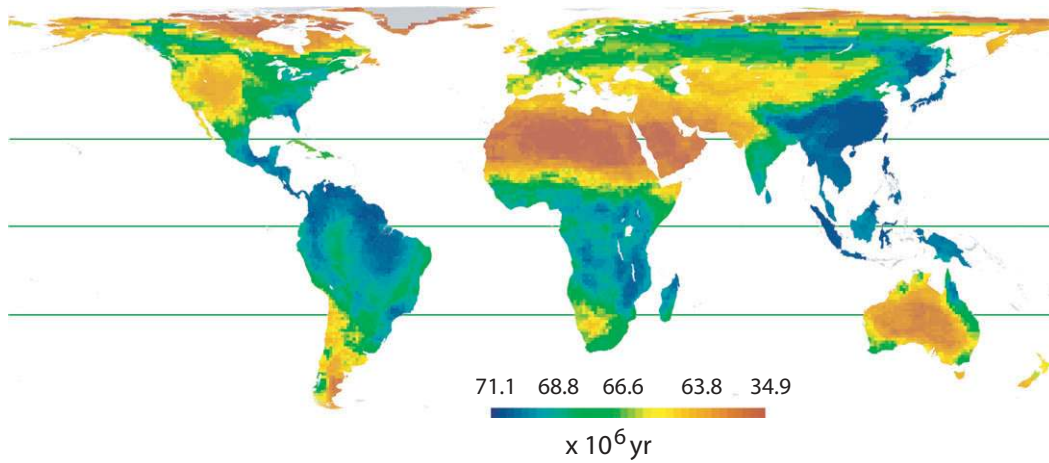
Figure 3 Nestedness patterns of total, arborescent and herbaceous family richness in three regions (see Fig. S1 for transect locations). (a–c) Spatial patterns of mean subsample nestedness (SSN) for cells grouped in 10 distance classes, (d–f) spatial patterns of changes of family richness moving from the equator northwards within each transect, and (g–i) maximally packed presence–absence matrices for all cells in each transect, with three nestedness metrics (SSN, NODF and $100 - T$, see text). Points in (a–c) also include 95% confidence intervals, which in all cases are narrower than the heights of the symbols.

covariance of current conditions and deep evolution (Fig. 5a), and that most of the age-related signal in the richness pattern covaries with the climatic gradient. But the relationships across all families conceal substantial differences between herbs and trees. High overlap between climate and age for tree families (Fig. 5b) is consistent with the proposition that covariation between tree richness and climate is a legacy of the evolutionary development of the flora. Indeed, virtually all of the evolutionary signal measured by family age can be explained by climate. In contrast, herb family richness is strongly associated with current climate, but there is also a moderate independent relationship with age (Fig. 5c). Surprisingly, there is minimal overlap between climate and age, suggesting that most of the climatic

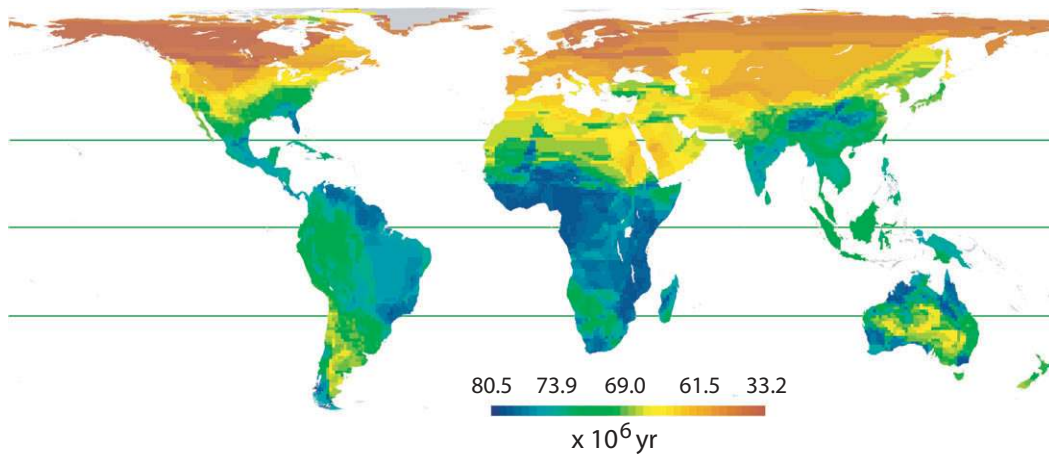
control of herb family richness is independent of how long the families have existed, and simultaneously that the evolutionary signal is largely independent of current climatic gradients.

Based on the evolutionary metric at our disposal, family age, the proposition that climate and family richness are correlated at least in part due to an evolutionary legacy of angiosperm evolution that is itself associated with climate is supported across all families and particularly strongly for arborescent families. Herbs, on the other hand, seem to be responding much more strongly to current climate *per se*, and although their gradient contains clear age structure (see Fig. 4c) most of this structure has arisen independently of the climatic gradient described by contemporary variables.

(a) All families



(b) Arborescent families



(c) Herbaceous families

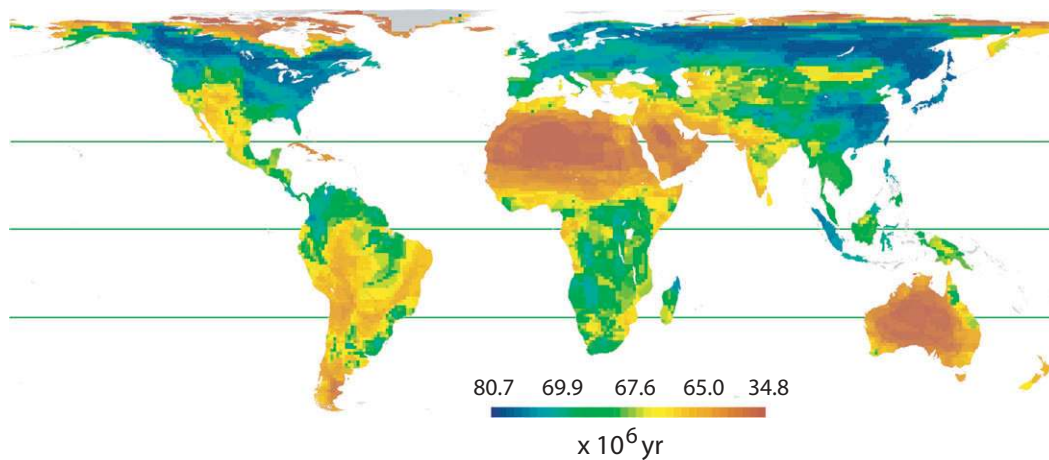


Figure 4 Global pattern of mean maximum age of angiosperm families. (a) All families ($n = 408$), (b) arborescent families only ($n = 143$), and (c) herbaceous families only ($n = 149$). Colour scales are based on 32 quantiles.

DISCUSSION

Most of our analyses generated clear answers to the four questions on which we focused, but they also identified some of the complexity that must underlie the angiosperm family

richness gradient. One unambiguous result is that the global pattern identified by Francis & Currie (2003) is reproducible despite being based on only 75% of the families currently recognized. As an emergent property, the pattern of taxon richness derived from range maps is relatively insensitive to the

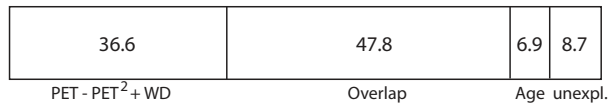
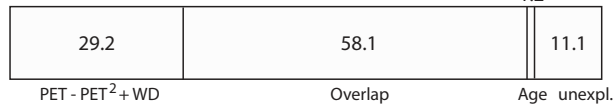
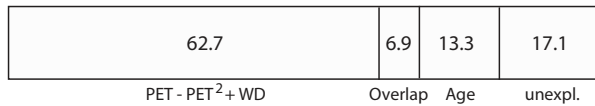
(a) All families**(b) Arborescent families****(c) Herbaceous families**

Figure 5 Partial regressions of family richness against climate and mean family age for (a) all angiosperm families ($n = 408$), (b) arborescent families only ($n = 143$), and (c) herbaceous families only ($n = 149$). Numbers within bars are percentages of variation in richness explained by each component. The overlap region represents variation in richness that cannot be unambiguously assigned to either climate or age due to collinearity between them. The variation not explained by the model is also provided.

details of how taxa are distinguished and mapped, and even to the taxonomic completeness of the data. It also follows that statistical evaluations of richness patterns with respect to environmental gradients are robust, and currently known links between plant family richness and climate are unlikely to change even if future phylogenetic work redefines the plant clades currently considered to be families. The stability of climatic models for woody plant richness across multiple taxonomic levels of resolution (Field *et al.*, 2005; O'Brien, 2006) further indicates that plant diversity and climate are so closely linked that associations between plants and water/energy cannot be decoupled by vagaries in how plants are classified or how detailed their distributions are mapped.

Analyses of taxon richness gradients focused on woody groups invariably find strong associations between richness and water/energy gradients (e.g. Currie & Paquin, 1987; Adams & Woodward, 1989; O'Brien, 1993; Field *et al.*, 2005; Hawkins *et al.*, 2007b; Montoya *et al.*, 2007), and disagreement about the link between tree diversity and climate is not about whether it exists but why (Latham & Ricklefs, 1993b; McGlone, 1996; Francis & Currie, 1998; Svenning & Skov, 2007). The association between climate and herb richness is more tenuous and in some situations cannot be found even when matching woody plant richness does correlate with climate (Bhattarai & Vetaas, 2003). And in cases when broad-scale herb taxon richness and climate are correlated, the associations are weaker than for woody plants (Oberle *et al.*, 2009; Wang *et al.*, 2009). We similarly found a statistically weaker association between climate and herb family richness than for woody families, but a model that explains 70% of the variance in global richness of

herbaceous families is not a poor fitting model. That is, we find associations indicative of climatic control of taxon richness for herbs at the global extent, even when using a simple model including only two of many potential climatic predictors.

How climate drives angiosperm family richness seems unambiguous, given both the very strong association between range sizes and richness and the high levels of compositional nestedness of floras moving from high-richness floras of the wet tropics to low richness floras of deserts and tundra. Our findings are consistent with the hypothesis for the diversity of northern temperate trees developed by Latham & Ricklefs (1993b), based on presumed difficulties for tree clades to adapt to the widespread cold climates that appeared in the Oligocene. It is further consistent with a version of the tropical conservatism hypothesis that proposes that niche conservatism at the family level has remained strong among plants relative to niche evolution. We also find very similar nestedness patterns for both herbs and trees, indicating that despite differences in their richness gradients, associations with climate, range size distributions and age patterns, the same underlying process applies to both. Climate primarily drives higher level angiosperm diversity via a filtering process irrespective of the families' growth form.

The range size pattern also suggests a simple interpretation for a widely studied ecogeographical rule, Rapoport's rule, as it applies to angiosperm families. Range sizes are larger in the north and in deserts than in the wet tropics, but not because the families that have colonized these regions differ from tropical groups by having broader climatic tolerances (Stevens, 1989). Most families in the extra-tropics are also tropical; they just differ from other tropical families by including species that have evolved traits that have permitted range expansions into cold or dry climates. This is a subtle but important difference in the usual explanation of this ecogeographical pattern that may arise from considering range sizes of higher level clades rather than species. Our focus on families may also explain the very strong correlation between mean range size and richness, not typical of analyses at the species level (e.g. Graves & Rahbek, 2005; Orme *et al.*, 2006; Kraft *et al.*, 2010). On the other hand, range size patterns analogous to those described by Rapoport's rule generated by nested range structures have been found at the species level over smaller spatial extents (Beketov, 2009, and references therein).

Although range size patterns represent one line of evidence that angiosperm family diversity may be influenced by tropical niche conservatism, patterns of family age generate a more complex picture. Overall, tropical angiosperm assemblages are older in the tropics than in most parts of the extra-tropics, but given the very different mean age patterns of tree and herbs (they are weakly negatively correlated, $r = -0.223$), interpretation of the general age gradient may not be informative. On the other hand, the pattern of mean ages of tree families is as predicted by tropical niche conservatism (see Fig. 4b), if we assume significant niche conservatism (i.e. intolerance to freezing) at the family level. The tropics contain the oldest tree families, and mean family age decreases with decreasing

temperature, resulting in a strong environmentally based regression model for mean age of tree families (see Table 1c1). The age gradient reflects that while the numbers of both young and old tree families drop out of the flora northward, older groups drop out more rapidly, leaving only the youngest families in northern Canada, Scandinavia and Siberia.

In contrast to trees, the age gradient of herbaceous families (see Fig. 4c) appears to be inconsistent with the version of the tropical niche conservatism outlined in the Introduction. There are a number of possible reasons, but four factors could easily cause a breakdown in the predicted pattern. First, all taxonomic levels are to some extent arbitrary, and the age of a higher level clade depends on how it is defined; that is, the age of the node beyond which all subsequent radiations are considered to be members of the same family. If not all herb 'families' are equivalent phylogenetically and there is spatial structure in how families are defined, this could generate an age gradient that contains artefactual components. This explanation begs the questions of why trees show a substantially different pattern that is consistent with TCH.

A second possibility is that the family level of classification, even if applied consistently across all clades, may not be the level at which niche conservatism constrains the distribution of traits across herbaceous groups. Trait evolution among herbs may be so rapid that there is no phylogenetic association of key traits (e.g. the evolution of freezing tolerance) at the family level. Thus, although many old herbaceous families currently occur in northern Siberia, there may have been so much niche evolution since their origin that family ages are not relevant to understanding their current distributions.

Thirdly, there may be a functional difference between trees and herbs due to their morphologies that influence how the latter respond to climatic cooling. As Latham & Ricklefs (1993b) and Donoghue (2008) have pointed out, adaptation to cold tolerance may be difficult for tropical trees, requiring complex modifications of biochemistry, physiology and morphology to protect stems and buds from cold damage. In contrast, herbaceous species can be protected from frost by being annual, or by the production of underground buds and stems, which could have decoupled evolutionary trajectories from the spread of cold climates in the temperate zones.

Fourthly, tropical niche conservatism may not explain the family richness gradient of herbaceous groups. If evolutionary rates of herbs are faster in the tropics (e.g. Wright *et al.*, 2006; Gillman *et al.*, 2010), and a more rapid tempo of diversification has resulted in many recent radiations of groups divergent enough to be considered separate families, average clade ages will be younger in the tropics, as we find. Again recalling the highly nested structure of the herb family richness gradient, the underlying pattern is that some older families are widespread in both the tropics and extra-tropics (although not in deserts), but younger families are concentrated in the tropics and deserts, dropping out of floras at a faster rate than older families moving into more mesic and colder parts of the Northern Hemisphere. Climate filters out herb families in the north, but not the older ones.

A core tenet of tropical niche conservatism that climate–richness relationships include an evolutionary signal because of spatial correlation between past and present climates is generally met for angiosperm families, but the very different patterns of mean age of trees and herbs again require a more nuanced interpretation. Overall, adding age to the climatic model of family richness improved the explanatory power of the model to over 90% and explained almost all spatial structure, a very strong model by any standard. And as argued by Qian & Ricklefs (2004), there appears to be strong overlap between contemporary and historical processes (see Fig. 5a). The covariation between climate and age is particularly strong for trees (see Fig. 5b), and virtually all of the variance in richness associated with age can also be explained by climate. Integrating all lines of evidence generated by our correlational approach leads to the conclusion that tree family diversity contains a strong niche conservatism signal, and a significant part the explanation for tree richness gradients reflects their tropical origin and evolutionary response to global climatic cooling beginning in the late Tertiary (Latham & Ricklefs, 1993b; Donoghue, 2008).

As with most patterns related to herbs, the relationships among climate, age and richness are unexpected and subject to multiple possible interpretations. Adding age to the climate model substantially improved the explanatory power of the model (see Table 1), but most of the age signal is independent of climate. Consequently, a conclusion that ecological processes related to climate are more important to herb diversity than history (Francis & Currie, 2003; Currie & Francis, 2004) is tenable, although how those processes work remains unclear (Currie *et al.*, 2004). We also cannot eliminate the possibility that other historical processes not described by family age are important, including regional variation in extinction rates, Pleistocene glaciations or barriers to dispersal. The relatively strong independent contribution of family age indeed suggests that historical processes do have explanatory power, but we have no evidence as to what the processes might be. Irrespective, the substantial statistical independence of climate and age for herbs is not what we expect from an explanation for diversity in which tropical niche conservatism at deeper nodes in the phylogeny is the dominant process.

Although herb families in cold climates are not necessarily young, those in the major deserts are (see Fig. 4c). The growth form and habitat preferences of early angiosperms are uncertain (Soltis *et al.*, 2005), but the oldest fossils suggest a fast-growing, weedy life history in either aquatic or riparian habitats (Royer *et al.*, 2010). It is a curious coincidence that the youngest families of herbs are found in the most arid habitats, given that we find no indication of family level niche conservatism with respect to cold. On the other hand, it is more consistent with the relatively young age of current deserts, none probably being older than Miocene (25–12 Ma) and most being substantially younger (Axelrod, 1979; Behrensmeyer *et al.*, 1992).

Although a correlative approach to studying diversity gradients cannot unambiguously resolve the problem of the

extent to which ecological or evolutionary forces shape patterns of taxonomic richness, our analysis implicates a specific macroevolutionary process, phylogenetic niche conservatism, as having a major role in explaining why most trees occur in the tropics, and illustrates one way that even strong correlations between current climate and taxon richness can reflect the effects of evolutionary processes. For herbs the answer is less clear. Niche conservatism could still be operating at lower taxonomic levels, or perhaps differential speciation rates are more important for rapidly evolving herbaceous clades. Analysis of rates of molecular evolution in clades with both trees and herbs has demonstrated significantly higher and more variable rates of molecular evolution for herbs (Smith & Donoghue, 2008), and rates of climate niche evolution have been found to be substantially slower for trees than herbs (Smith & Beaulieu, 2010). The faster rates of herb evolution may reflect an accelerated rate of adaptation to changing climatic conditions, with multiple acquisitions of key traits that may have led to evolutionary diversification in nested herbaceous clades. The complexity of this process is illustrated by the rise of ecological dominance of C_4 grasses in the lower latitudes (Edwards *et al.*, 2010). Multiple evolutionary transitions to C_4 photosynthesis are reflected in diverse C_4 photosynthetic pathways, and in combination with other adaptations associated with ecological dominance, suggest that no one factor underlies the dominance of these grasses in the tropics. The dominance at higher latitudes of grasses with the ancestral C_3 photosynthetic pathway suggests a very different pattern from woody species, where older, basal clades are more likely to occur at lower latitudes. Similarly complex patterns are likely to be associated with other species-rich, herbaceous clades. Whatever combination of processes account for herbal diversity at the global scale, it seems likely that there is no single answer for all taxonomic groups, even within a well defined, but very large clade such as the angiosperms.

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SUPPORTING INFORMATION

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

Table S1 List of angiosperm families included in the analysis, with maximum ages, range sizes and growth forms.

Table S2 Nestedness metrics in three latitudinal based transects.

Figure S1 Transects used for the nestedness analysis.

Figure S2 Correlograms of raw and residual spatial autocorrelation after generating climate and age regression models.

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