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Phylogenetic support for the Tropical Niche Conservatism Hypothesis despite the absence of a clear latitudinal species richness gradient in Yunnan's woody flora

G. Tang[1], M. G. Zhang[2], C. Liu[3], Z. Zhou[1,4], W. Chen[4], and J. W. F. Slik[5]

[1]Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan, China
[2]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China
[3]Arthur Rylah Institute for Environmental Research, Department of Environment and Primary Industries, Heidelberg, Victoria 3084, Australia
[4]Key Laboratory of Biogeography and Biodiversity, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China
[5]Faculty of Science, Universiti Brunei Darussalam, Gadong, BE1410, Brunei Darussalam

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Abstract

The Tropical Niche Conservatism Hypothesis (TCH) tries to explain the generally observed latitudinal gradient of increasing species diversity towards the tropics. To date, few studies have used phylogenetic approaches to assess its validity, even though such methods are especially suited to detect changes in niche structure. We test the TCH using modeled distributions of 1898 woody species in Yunnan Province (southwest China) in combination with a family level phylogeny. Unlike predicted, species richness and phylogenetic diversity did not show a latitudinal gradient, but identified two high diversity zones, one in Northwest and one in South Yunnan. Despite this, the underlying residual phylogenetic diversity showed a clear decline away from the tropics, while the species composition became progressingly more phylogenetically clustered towards the North. These latitudinal changes were strongly associated with more extreme temperature variability and declining precipitation and soil water availability, especially during the dry season. Our results suggests that the climatically more extreme conditions outside the tropics require adaptations for successful colonization, most likely related to the plant hydraulic system, that have been acquired by only a limited number of phylogenetically closely related plant lineages. We emphasize the importance of phylogenetic approaches for testing the TCH.

1 Introduction

The Tropical Niche Conservatism Hypothesis tries to explain the generally observed latitudinal gradient of increasing species diversity towards the tropics and is based on three premises (Wiens and Donoghue, 2004): (1) historically, the tropical biome has occupied a large proportion of the world's land surface, which together with its relatively stable humid and warm climate, means that it was able to generate and maintain large numbers of co-existing species (Chow and Gaston, 2000; Fine and Ree, 2006); (2) angiosperms originated and initially diversified in tropical climates, result-

ing in most extant angiosperm lineages having a tropical origin (Ligard and Crane, 1988; Field et al., 2003; Biffin et al., 2012; Romdal et al., 2013); and (3) colonization of non-tropical biomes is difficult due to niche conservatism (Wiens and Donoghue, 2004; Wiens et al., 2010; Romdal et al., 2013). Although several studies have found support

5 for the TCH (Kooyman et al., 2011; Giehl and Jarenkow, 2012; Hawkins et al., 2014), not many have used methods that quantify community phylogenetic diversity and structure to assess its validity, even though such methods are especially suited to detect changes in trait diversity and niche structure (Webb et al., 2002; Wiens and Donghue, 2004; Swenson, 2011).

10 Traditionally, studies on biodiversity gradients have focused on species diversity which incorporates both species richness and the evenness of species' abundance. However, with the increasing availability of phylogenies for many organisms, such as the APG-phylogeny for plants (APG, 2009), phylogenetic diversity has become an important additional biodiversity indicator (Faith, 1992; Webb et al., 2002; Faith and Baker,

15 2006). Phylogenetic diversity is useful because it reflects the amount of evolutionary history encompassed within communities and, due the phylogenetic conserved nature of many species traits, forms a proxy for community trait and niche diversity (Webb et al., 2002; Swenson, 2011). High phylogenetic diversity will therefore generally indicate high trait diversity and the co-existence of taxa with a wide range of habitat

20 adaptations.

Phylogenetic data is now also commonly incorporated in studies of community assembly and structure, because it provides a new approach to reveal the evolutionary, ecological and biogeographic processes that underlie the distributions and assemblage of species (Cavender-Bares and Wilczek, 2003; Swenson et al., 2007; Cavender-Bares

25 et al., 2009). Webb (2000) introduced a simple, general method for quantifying the phylogenetic structure of local communities, the net relatedness index (NRI), that uses the phylogenetic distance between taxa on a phylogenetic tree to identify whether a community structure is phylogenetically clustered, random or overdispersed. The former is indicated by closely related species co-occurring more often than expected by a ran-

dom null model, the latter by distantly related species co-occurring more than expected (Webb, 2000; Webb et al., 2002). So far, these methods have mostly been used at small scale community ecological studies where they can reveal the respective roles of environmental filtering and competition on community assembly but rarely for studying re-
5 gional biogeographical patterns even though they are suitable for detecting basic, large scale patterns in the evolutionary organization of regional floras (Kooyman et al., 2011; Giehl and Jarenkow, 2012).

Here we explore the distribution patterns of phylogenetic diversity and community phylogenetic structure of Yunnan's flora to see how these correspond with TCH predic-
10 tions. Based on the TCH we predict that (1) the tropical regions of Yunnan should have the highest species and phylogenetic diversity due to the tropical origin of most plant lineages and the historically large area occupied by the tropical biome; (2) plant communities in the tropics will have either over-dispersed or random phylogenetic structure because they are more likely to contain species from all major plant lineages under con-
15 ditions of relatively low levels of environmental filtering (stable climate) but high levels of species interactions (competition) which can result in patterns of limiting similarity; (3) phylogenetic clustering should increase, while phylogenetic diversity should decline away from the tropics due to increasing influence of environmental filtering (increasingly variable and extreme climates) which due to niche conservatism should lead to
20 fewer and fewer tropical plant lineages being able to persist, while the species that have managed to adapt should form phylogenetically closely related sets of species; and (4) the observed phylogenetic patterns should be closely associated with environmental variables related to the transition from tropical to non-tropical biomes.

2   Methods

2.1   Species data

Our data included all woody species (except Fagaceae, for which we could not obtain permission) collected in Yunnan Province that were present in the herbaria of the Kun-
⁵ ming Institute of Botany (KIB), Chinese Academy of Sciences. Because most of these specimens had no latitude and longitude data, all collections were georeferenced using the location descriptions as provided on the labels. Of the 85 289 collections we were able to georeference 60 552 specimens at a grid resolution of 5 arc-minute (ca. 10 km × 10 km), avoiding duplicate species records in each grid cell. The 5 arc-minute
¹⁰ spatial resolution was chosen because higher location precision was difficult to achieve for most collections. Species that were present in fewer than 5 grid cells, the minimum number that could be statistically tested for significantly non-random habitat associations, were removed from the analysis. Of the 60 552 georeferenced specimens, 42 114 records belonging to 118 plant families representing 2319 species possessed adequate
¹⁵ data for further modeling.

2.2   Environmental data

Our environmental data included 19 bioclimatic variables plus elevation from the WORLDCLIM dataset (http://www.worldclim.org) and 15 soil variables from the FAO database (FAO, 2002) at the same 5 arc minute resolution as the georeferenced plant
²⁰ specimens. For the bioclimatic variables we selected the least correlated ones (Pearson's $r < 0.75$), to reduce problems with multi-colinearity of variables on the analysis (Appendix A, Supplement) (Graham, 2003). The final list of variables consisted of: (1) elevation; (2) BIO2: mean diurnal temperature range; (3) BIO4: temperature seasonality; (4) BIO7: temperature annual range; (5) BIO12: annual precipitation; (6) BIO14;
²⁵ precipitation of driest month; (7) BIO15: precipitation seasonality. Principal component analysis (PCA) was used to summarize soil variables in three independent axes that

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together explained 86.8 % of soil data variance (Table 1), bringing the total number of variables used in the analyses to ten (Fig. 1).

2.3 Species distribution modeling

Since detailed species distribution data for all grid cells in Yunnan Province were lacking, we used species distribution modeling to generate such data. In order to model species distributions we used the modeling application Maxent (ver. 3.3.1; www.cs.princeton.edu/~schapire/maxent/, Phillips et al., 2006). Maxent was specifically developed to model species distributions with presence-only data. Of available species distribution modeling algorithms, Maxent has been shown to perform best, especially when few presence records are available, while it is also the least affected by location errors in occurrences (Graham et al., 2007). Maxent was run with the following modeling rules: (1) for species with 5–10 collection records linear features were applied, (2) for species with 10–14 records quadratic features were applied, while (3) for species with > 15 records hinge features were applied (Raes and ter Steege, 2007).

As a measure of the accuracy of the SDMs, we used the threshold independent and prevalence insensitive area under the curve (AUC) of the receiver operating characteristic (ROC) plot produced by Maxent. All measures of SDM accuracy require absences. When these are lacking, as is the case here, they are replaced by pseudo-absences or sites randomly selected at localities where no species presence was recorded (Phillips et al., 2006). However, when SDM accuracy measures are based on presence-only data and pseudo-absences, the standard measures of accuracy (e.g. the often used measure AUC > 0.7) do not apply (Raes and ter Steege, 2007). Therefore, we applied the bias corrected null-model developed by Raes and ter Steege (2007) to test the AUC value of an SDM developed with all presence records against the AUC values expected by chance for the same number of collecting locallities. However, this assumes that collection localities represent a random subset of the study areas environmental space. In many cases this is not a valid assumption due to collecting biases (Kleidon and Mooney, 2000; Tsoar et al., 2007).

To check for collecting bias in our dataset we tested whether our 1406 collection localities formed a random subsample of the environmental predictor space. To do this we divided each of the environmental predictors into 10 equal-interval bins based on the ranges observed for Yunnan (Loiselle et al., 2008). We then tested whether the
5 observed frequency distributions represented by the 1406 collection localities differed from those observed for whole Yunnan using a Chi-square test. This showed that for most environmental predictors the collection locations represented non random subsamples of Yunnan's environmental predictor space. To correct for this bias we developed a bias corrected null model by testing each species models AUC value against
10 1000 AUC values that were generated randomly by only subsampling from the 1406 collection localities using the same number of locations (grid cells) as were used to model the species. When the observed AUC value fell in the top 95 % of randomly generated AUC values, it was considered to have a significant non-random distribution and was used in our further analyses. For the 2319 species available for modeling in Yun-
15 nan, 1996 species showed a significantly non random distribution (AUC value $\geq$ 95 % C.I.).

In order to determine the patterns of botanical richness of Yunnan, a threshold is needed that defines at what level of Maxent prediction values a species is considered present or absent in a grid cell. For SDMs represented by $\geq$ 10 records we used
20 the fixed "10 percentile presence" threshold for this purpose (Raes and ter Steege, 2007). For species represented by 5–9 records we used either the "sensitivity specificity equality" or the "sum maximization" threshold, whereby the sensitivity specificity equality threshold means that the absolute value of the difference between sensitivity and specificity is minimized and the sum maximization means that the sum of sensitivity
25 and specificity is maximized. Once the threshold is set, a series of presence/absence layers of all the species becomes available. Using these layers we created a presence/absence matrix in which the rows represent the 4936 grid cells covering Yunnan and the columns represent the presence of the 1996 modeled species (Appendix B,

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Supplement). Species richness was then defined as the summed number of species in each grid cell.

2.4   Constructing the phylogenetic tree

All the gymnosperms were excluded from the analysis and the remaining 1898 angiosperm species were used as input for the plant phylogeny reconstruction program PHYLOMATIC (www.phylodiversity.net/phylomatic/) to get a phylogenetic supertree containing all our species, although this tree is currently mostly resolved up to family level, with most species forming polytomies within their respective families. Branch lengths of the tree were determined by using the BLADJ algorithm in PHYLOCOM 4.1 (http://phylodiversity.net/phylocom/) with known molecular and fossil dates (Wikstrom et al., 2001; Webb et al., 2008). At the time of extraction, this phylogeny was based on APGII (APG, 2003).

2.5   Calculating phylogenetic diversity and community phylogenetic structure

We calculated phylogenetic diversity (PD) for each grid cell in Yunnan province. PD measures the minimum length of all the branches required to span a given set of taxa on the phylogenetic tree (Faith, 1992). PD turned out to be highly correlated with species richness in our data set, with a Pearson's correlation coefficient of 0.986. Because we were especially interested in identifying areas where phylogenetic diversity was lower or higher than expected for a given species richness, we also calculated a standardized PD (PDS) by randomly choosing 26 species (the lowest number of species found in the 4936 grid cells) from each grid without replacement and calculating PD (Slik et al., 2009). We repeated this a hundred times to get the mean value of PDS for each grid. We compared our PDS values with the residuals obtained from a linear regression between species richness and PD and found that they produced similar results (Appendix C, Supplement), confirming that PDS does indeed reflect a species richness controlled phylogenetic diversity value.

Mean pairwise distance (MPD) was used to measure the phylogenetic relatedness of species in each $\sim 10\,\text{km} \times 10\,\text{km}$ grid cell. MPD measures the mean pairwise phylogenetic distance between all species present in a grid cell. These values were then standardized to the net relatedness index (NRI) (Webb, 2000) as follows:

$$\text{NRI}_{\text{sample}} = -1 \times \frac{\text{MPD}_{\text{sample}} - \text{mean}(\text{MPD}_{\text{random}})}{\text{sd}(\text{MPD}_{\text{random}})} \tag{1}$$

where $\text{MPD}_{\text{sample}}$ represents the observed mean pairwise phylogenetic distance between species in a grid cell; $\text{MPD}_{\text{random}}$ represents the mean random phylogenetic distance between species which is based on randomly shuffling species labels across the tips of the phylogeny, using 1000 randomizations (Kembel, 2009); while sd represents standard deviation. Positive values indicate phylogenetic clustering, while negative values indicate phylogenetic over-dispersion.

2.6 The influence of the environment on phylogenetic patterns

Before we analysed the relationships between PD, SR, PDS, and NRI with the environmental variables we first tested for spatial autocorrelation in these four indices using Moran's I. This showed that they were all strongly spatially autocorrelated (Appendix D, Supplement). In order to control for this spatial autocorrelation, we calculated eigen-vector based spatial filters as applied in the software package "Spatial Analysis for Macroecology" (SAM) version 4.0 (Rangel et al., 2010). This method extracts spatial filters using the Principal Components of Neighbour Matrices: PCNM (Brocard and Legendre, 2002). These spatial filters were subsequently added as fixed (i.e. present in all multiple regressions) predictive variables in the model selection procedure. The model selection procedure calculated ordinary least square (OLS) linear multiple regression models based on each possible combination of predictor variables (in our case we had 10 environmental variables, i.e. 1023 possible models) and ranks these according to their Akaike Information Criterion with a correction for finite sample sizes (AICc) with the best model having the lowest AICc value. To determine the individual

and shared contributions of the environmental and spatial variables on explained model data variance we applied partial correlation analysis by contrasting the environmental variables with the spatial filter variables in SAM version 4.0.

Because these analyses were computationally intensive when using the whole data set of 4936 grid cells, we randomly selected 500 grid cells ($\sim 10\%$) from Yunnan for each analysis and repeated this 50 times. In this way we obtained mean values for the standardized regression coefficients and explained variances for each environmental variable, while also obtaining the number of times a variable was selected in the 50 models. The number of times that a variable was selected indicates the importance of the variable (importance value), which varies between zero (never selected in any model, i.e. low importance) to one (present in all 50 models, i.e. high importance). Significant deviation from zero for the mean standardized regression coefficient of each environmental variable was determined by ranking the 49 observed standardized regression coefficients and determining whether zero fell within the top or bottom 5% (depending on the direction of the considered regression coefficient). All analyses were performed in SAM version 4.0 (Rangel et al., 2010). The complete matrix of species vs. grid cells is provided in Appendix D (Supplement).

3 Results

PD and species richness were strongly correlated with a Pearson's correlation coefficient of 0.986. Due to this high correlation, PD identified the same two diversity hotspots as species richness did: the northwest and the southeast of Yunnan (Fig. 2). PDS, however, showed a markedly different diversity pattern, with a gradual lowering of diversity from south to north Yunnan (Fig. 2). The difference between PD and PDS was most apparent for Yunnan's northwest, southwest and central-east (Fig. 2). The NRI analysis also revealed a latitudinal gradient from phylogenetically over-dispersed communities in the south to phylogenetically clustered communities in the north of Yunnan (Fig. 2).

All the selected optimal models had high overall R^2 (ranging between 0.788 and 0.842) indicating that the regression models explained observed patterns in PD, species richness (SR), SPD and NRI well (Table 2). However, after accounting for data variance that was purely driven by geographic distance between grid cells the amount of data variance explained by the environment was slightly reduced (ranging between 0.517–0.658). Data variance explained exclusively by distance between grid cells was low (ranging between 0.074 and 0.206).

PD and SR showed very similar model results (Table 2), both being driven mostly by elevation (positive), temperature diurnal range (negative), annual rainfall (positive), rainfall in driest month (negative) and soil PCA-axes 1 and 3 (both negative). PDS differed from PD and SR in the strongly negative impact of temperature seasonality (which did not significantly impact PD and SR), the weak impact of soil PCA axis 1, and the reversal in direction of correlation for rainfall in driest month and soil PCA-axis 3. NRI was mostly affected by rainfall and soil variables and, unlike PS, SR and PDS, not by temperature variables (Table 2).

4   Discussion

As predicted by the TCH, PDS identified a clear latitudinal decline in evolutionary information content of plant communities from south to north, corresponding to the transition from the warm tropical to cooler sub-tropical, temperate, boreal and alpine biomes. This pattern corresponded to a similar latitudinal trend that we detected in the net relatedness index (NRI), which, as hypothesized, showed a change from phylogenetically over-dispersed towards clustered plant communities from south to north Yunnan. Our observations mirror the results obtained by the few other studies that have applied phylogenetic methods to study the transition from tropical to sub-tropical and temperate floras (Australia, Kooyman et al., 2011, South America Giehl and Jarenkow, 2012) which also detected phylogenetic over-dispersion in the tropical regions and in regions of known historic environmental stability (refugia), while phylogenetic clustering domi-

nated outside the tropical biome and in regions with historically unstable environmental conditions. Indeed, PDS and NRI were both significantly affected by climate instability and harshness in our analyses, with declining PDS with increasing temperature seasonality, increasing temperature diurnal range and declining rainfall in driest month, while phylogenetic clustering increased with declining annual and driest month rainfall and declining soil water availability.

The TCH is generally based on the assumption that tropical plant lineages have difficulty adapting to low temperatures, and especially frost, leading to the observed decline in species richness and PDS towards colder and more extreme climates (Wiens and Donoghue, 2004; Giehl and Jarenkow, 2012; Romdal et al., 2013). Our results only partly confirm this as they do show declining species richness and PDS in climates with larger temperature diurnal ranges and seasonality, but, on the other hand, also show an overall increase in species richness and PDS with increasing elevation, which is correlated with declining temperatures. Additionally, NRI was not affected by temperature at all in our analyses, indicating that the processes relating to the phylogenetic structuring of the plant community, i.e. clustering vs. over-dispersion seem not to be driven by temperature.

In Yunnan, the most consistent environmental drivers of species richness, PDS and NRI were actually related to rainfall patterns and how much of this rainfall is stored in the soil and thus available for plants. Both species richness and PDS declined in drier habitats and/or soils that were unable to store the water sufficiently, while plant communities also became phylogenetically more clustered under such circumstances, indicating non-random loss of species compared to areas with wetter climates and/or soils such as found in the tropical region of Yunnan. Drought is known to strongly affect growth and mortality patterns in woody plants (Kleidon and Mooney, 2000; Slik, 2004; Phillips et al., 2010; Tan et al., 2013) because it can lead to strong negative pressures between roots and leaves which may eventually lead to vessel cavitation and thus partial or complete disruption of the water flow within the plant (Hacke et al., 2001). The hydrological system of woody plants is strongly phylogenetically conserved, i.e.

hydraulic failure related mortality due to drought is likely to be phylogenetically non-random (Zhang et al., 2011) and thus capable to affect both PDS and NRI simultaneously. Interestingly, the impact of freezing temperatures also leads to increased cavitation risk in vascular plants (Jansen et al., 2003; Biffin et al., 2012; Choat, 2013). Overall,

5   our study indicates that in Yunnan drought, rather than temperature, seems to be the major factor controlling the phylogenetically non-random pattern in species richness and PDS combined with increasing phylogenetic clustering towards higher latitudes, and that the hydraulic system of woody plants may be a main causal candidate driving these patterns.

10   Interestingly the decline in PDS along the latitudinal gradient was slower than the decline in species richness. Species richness showed a sharp drop at the transition from tropical to sub-tropical climates, while the decline in PDS corresponded more with the transition from sub-tropical to temperate climates located further north. Apparently, even though species richness is strongly lowered directly outside the tropical biome,

15 phylogenetic diversity remains high along a broad transition zone, more or less corresponding to the sub-tropical biome. The sub-tropics therefore seem to represent a transition zone where species are filtered out of the species pool in such a way that plant communities become increasingly phylogenetically clustered towards higher latitudes. The reason of the lag between species richness and phylogenetic diversity remains un-

20 clear, but may be related to past North–South migrations of plants under the influence of Pleistocene ice ages. While species diversity may be directly controlled by current climate (Slik et al., 2009), phylogenetic diversity may respond slower because it does not depend on species richness per se, but on species composition, which depends, at least partly, on past migration patterns and biogeography.

25   Northwest Yunnan defied the general pattern of declining species richness with increasing latitude. This region was instead characterized by high levels of species richness, but low levels of PDS. The northwest of Yunnan is a topographically diverse region with elevations varying between 1000 and 5000 m, often with large parts of this elevation range being present within short distance intervals, such as in the three par-

allel rivers region (Wu, 1987; Sun et al., 2011; Zhang et al., 2012). This means that almost all vegetation types, from sub-tropical to alpine can be found within this region, leading to the observed high species richness. Northwest Yunnan is also character-ized by high endemic species richness because of fast speciation caused by extensive
5   geological movement and climate change in the last few million years (Wu, 1987; Sun et al., 2011). The combination of high species richness with low PDS supports the hypothesis of the relatively young age of most speciation events in this region as it indicates clustering of species within a limited number of highly diverse plant lineages.

    Our results generally support the predictions made by the TCH. First of all it shows
10 that PDS is highest in the tropics and declines towards more variable, drier and cooler climates, indicating that the tropics are characterized by a phylogenetically diverse flora while more northern floras become increasingly depauperate in phylogenetic informa-tion content and, due to phylogenetic conservatism in many traits, possibly also in niche structure. Second, it shows that phylogenetic clustering increases away from
15 the tropics, indicating that the observed decline in PDS towards more variable, cooler and drier climates is accompanied by a phylogenetically non-random filtering process which eventually results in more northern floras being characterized by a limited set of closely related plant species. Thirdly, it shows that the shifts in phylogenetic diver-sity and community structure in Yunnan are mostly linked to rainfall regime and soil
20 moisture availability, rather than by temperature patterns, although both drought and freezing may act via the same mechanism, hydraulic failure, to produce the observed phylogenetic patterns.

The Supplement related to this article is available online at doi:10.5194/bgd-11-7055-2014-supplement.

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Table 1. PCA factor loadings for the three soil axes (within brackets the amount of explained data variance) used in the study. Highest factor loading in each row indicated in bold. Cation-exchange-capacity (CEC); carbon (C); nitrogen (N).

Factor	Axis 1 (61.9 %)	Axis 2 (14.9 %)	Axis 3 (10.0 %)
Base saturation topsoil	−0.108	0.372	**−0.421**
CEC soil topsoil	−0.016	**0.342**	−0.142
CEC clay topsoil	−0.094	**0.348**	−0.294
C : N ratio topsoil	−0.005	**0.290**	0.075
Organic carbon pool	0.083	0.148	**0.386**
Effective soil depth	−0.281	**0.395**	0.213
Soil drainage	0.161	−0.250	**−0.417**
Easy available water	**−0.644**	−0.154	0.069
Nitrogen topsoil	0.019	**0.115**	0.011
Organic carbon topsoil	0.131	0.150	**0.299**
pH topsoil	−0.105	0.249	**−0.365**
Soil moisture storage	**−0.644**	−0.154	0.069
Soil production index	−0.035	**0.194**	0.007
Mineral grain size subsoil	−0.058	**−0.264**	−0.162
Mineral grain size topsoil	−0.077	−0.216	**−0.289**

Table 2. Average of 49 models, with each model calculated based on a random selection of 500 grid cells ($\sim 10\,\%$ of total) from Yunnan and selected based on lowest Akaike Information Criterion (AICc) for Phylogenetic diversity (PD), Species richness (SR), Standardized PD (PDS) and Nearest Relative Index (NRI) vs. environmental variables, using spatial filters to compensate for spatial autocorrelation. Variables within each column show mean standardized regression coefficients followed by importance values. Variables in bold represent regression coefficients significantly ($p < 0.05$) different from zero. R^2 indicates adjusted variance explained by the model (total), by environment (E) only, by spatial distance between sites (S) only, and that shared by the environment and space. RA = Annual rainfall; RDM = Rainfall in driest month; RS = Annual rainfall seasonality; TDR = Temperature diurnal range; TR = Annual temperature range; TS = Annual temperature seasonality; S1 = Soil PCA-axis 1; S2 = Soil PCA-axis 2; S3 = Soil PCA-axis 3.

	PD	SR	PDS	NRI
Elevation	**0.165/0.94**	**0.181/0.98**	**0.112/0.67**	**0.085/0.39**
TDR	**−0.402/0.92**	**−0.366/0.96**	**−0.488/0.98**	0.140/0.39
TS	−0.318/0.76	−0.328/0.61	**−0.641/0.98**	0.189/0.51
TR	−0.240/0.35	−0.188/0.55	0.360/0.69	0.043/0.47
RA	**0.464/1.00**	**0.437/1.00**	**0.238/1.00**	**−0.343/0.98**
RDM	**−0.277/0.96**	**−0.288/0.98**	**0.214/0.92**	**−0.224/0.98**
RS	−0.151/0.76	**−0.164/0.76**	−0.08/0.47	**−0.120/0.65**
S1	**−0.164/1.00**	**−0.160/0.98**	−0.05/0.65	**−0.115/0.98**
S2	−0.059/0.41	**−0.100/0.47**	0.04/0.41	−0.045/0.47
S3	**−0.123/1.00**	**−0.148/1.00**	**0.126/1.00**	**−0.200/1.00**
Spatial filters (n)	29.0	27.5	24.1	25.8
R^2-total	0.833	0.823	0.788	0.842
R^2-E	0.105	0.098	0.106	0.107
R^2-S	0.187	0.206	0.074	0.075
R^2-(E + S)	0.540	0.517	0.609	0.658
AICc	9980.1	5758.5	6014.7	1404.4
F	66.3	62.5	56.0	78.5
P	< 0.001	< 0.001	< 0.001	< 0.001
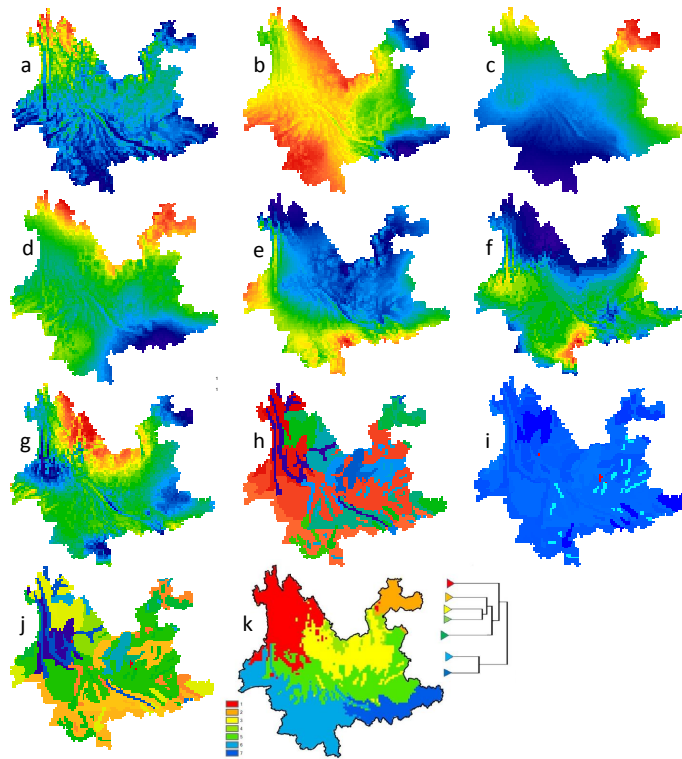
Figure 1. Spatial patterns of the ten included environmental data layers for the SDMs and floristic patterns for Yunnan Province: **(a)** elevation; **(b)** mean diurnal temperature range; **(c)** temperature seasonality; **(d)** temperature annual range; **(e)** annual rainfall; **(f)** rainfall in driest month; **(g)** rainfall seasonality; **(h)** soil PCA axis 1; **(i)** soil PCA axis 2; **(j)** soil PCA axis 3; **(k)** seven main floristic regions of Yunnan, with the two blue regions representing the (sub-)tropical biome and the relationships between the regions indicated by the dendrogram on the right side of the map. All values increase from blue to red following a rainbow spectrum, except for the floristic regions map.
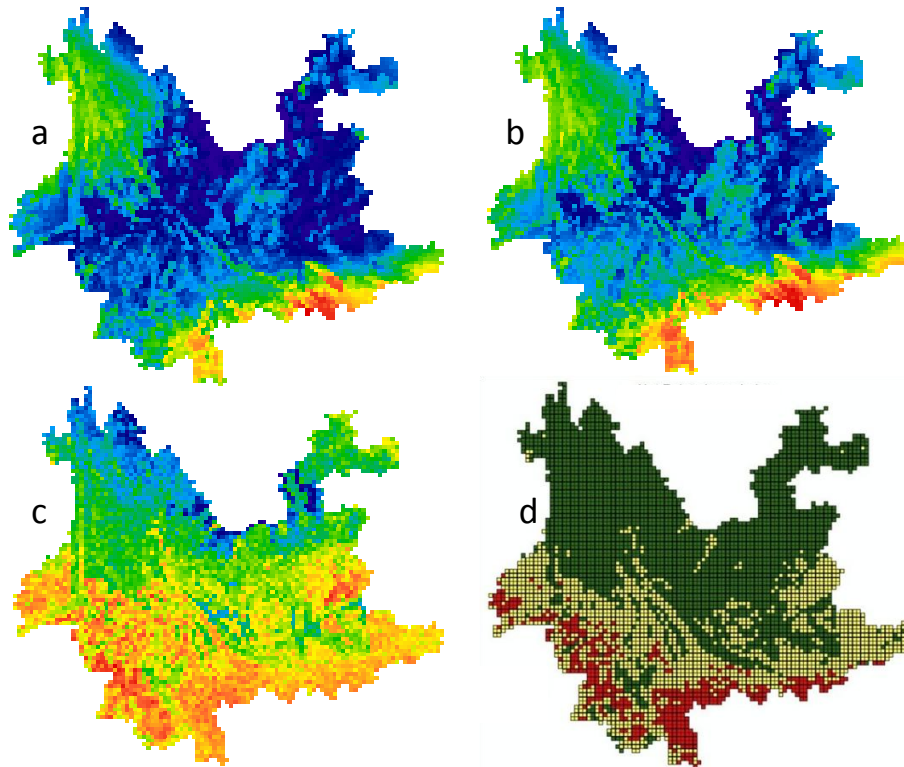
Figure 2. Spatial patterns of **(a)** species richness; **(b)** phylogenetic diversity; **(c)** standardized phylogenetic diversity; and **(d)** net relatedness index. For **(a–c)** values increase from blue to red following the rainbow spectrum. For **(d)** the colours indicate: red (over-dispersed), yellow (random), and green (clustered).

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