



ORIGINAL
ARTICLE



Evolutionary history influences the effects of water–energy dynamics on oak diversity in Asia

Xiaoting Xu^{1,2}, Zhiheng Wang^{2*}, Carsten Rahbek², Jean-Philippe Lessard^{2,3} and Jingyun Fang^{1*}

¹Department of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing, 100871, China, ²Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, DK-2100, Copenhagen Ø, Denmark, ³Quebec Centre for Biodiversity Science, Department of Biology, McGill University, Montreal, QC, H3A-1B1, Canada

ABSTRACT

Aim Water–energy dynamics are often correlated with geographical patterns of terrestrial plant richness. However, the relative importance of water and energy on species richness is still being debated. Some studies suggest a transition in the relative importance of water and energy along a latitudinal gradient, i.e. that water is the most important factor at low latitudes, whereas energy is the leading factor at high latitudes. The generality of this transition is yet to be established and is the focus of the current study. In particular, we examine whether differences in the evolutionary histories of two subgenera of Asian oaks influence the derived models of water–energy dynamics.

Location Asia (70–140° E; 10–60° N).

Methods We performed geographically weighted regressions to quantify geographical variation in the relative importance of water and energy on the species richness of Asian oaks (*Quercus* L.). We also evaluated how evolutionary history influences the relative importance of water and energy in determining species richness, by comparing patterns in the two oak subgenera: *Quercus* subg. *Quercus* and *Quercus* subg. *Cyclobalanopsis*. In particular, we assessed how the ancestral climatic niche of these two subgenera (i.e. subgenus *Quercus* of temperate origin versus subgenus *Cyclobalanopsis* of tropical origin) relates to the relative importance of water and energy on contemporary diversity patterns.

Results We found no geographical transition line in the relative importance of water and energy along the latitudinal gradient studied. Instead, we found that the importance of energy relative to water on the species richness of subgenus *Quercus* increased from mid-latitudes (warm temperate regions) towards both tropical and boreal regions: this pattern might reflect that this subgenus originated in the temperate region. In contrast, the importance of both water and energy on the species richness of the tropical subgenus *Cyclobalanopsis* increased from tropical to boreal regions, probably due to a lack of adaptation to winter coldness.

Main conclusions Our results suggest that differences in the evolutionary history – specifically the ancestral climatic niche – of the two subgenera of oaks influence the effects of water–energy dynamics on species richness along a latitudinal gradient through niche conservatism.

Keywords

Cyclobalanopsis, evolutionary history, Fagaceae, geographically weighted regression, niche conservatism, *Quercus*, species diversity, water–energy dynamics.

*Correspondence: Jingyun Fang, Department of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Yiheyuan Road 5, Beijing 100871, China; Zhiheng Wang, Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.
E-mail: jyfang@urban.pku.edu.cn; zwang@bio.ku.dk

INTRODUCTION

An understanding of the latitudinal gradient of species richness is regarded as the ‘holy grail’ of ecology (Huston, 1994), and the mechanisms underlying this pattern have fascinated biogeographers and ecologists for more than two centuries (Lomolino *et al.*, 2005). Despite the large number of studies devoted to this issue, the underlying mechanisms remain elusive (Brown *et al.*, 2004; Currie *et al.*, 2004; Ricklefs, 2004; Wang *et al.*, 2009). Several studies have documented strong species richness–climate relationships across taxonomic groups and spatial scales (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Whittaker *et al.*, 2007; Wang *et al.*, 2011a). In particular, water–energy dynamics often appear to drive spatial patterns of species richness in plants (O’Brien, 1998; Francis & Currie, 2003; Field *et al.*, 2005). Nevertheless, the generality of the water–energy effects on spatial patterns of plant species richness is still open to question.

The relative importance of water and energy can differ among regions (Hawkins *et al.*, 2003). For example, a global meta-analysis on species richness patterns showed that the relative importance of water and energy on terrestrial plant species richness changed from the predominance of energy in cold temperate regions to the predominance of water in tropical regions (Hawkins *et al.*, 2003; coined as Hawkins’ conjecture by Whittaker *et al.*, 2007). However, the existence of such a latitudinal transition from strong effects of water limitation to that of energy limitation is still controversial, and remains poorly tested outside Europe and America (Whittaker *et al.*, 2007; Eiserhardt *et al.*, 2011). Hawkins *et al.* (2003) postulated the existence of a transition in the relative importance of water and energy limitations along the latitudinal gradient, arising from physiological limitations of terrestrial organisms: water is likely to be the limiting factor in warm regions where energy inputs are ample, while energy is likely to be more important in cold regions where energy inputs are low. However, previous studies did not consider the potential influence of differing evolutionary histories among taxonomic groups. To our knowledge, how evolutionary history might influence the effects of water–energy dynamics on the latitudinal gradient in species richness remains unexplored.

Researchers are increasingly aware of the influence of evolutionary processes on patterns of species richness (Latham & Ricklefs, 1993; Ricklefs *et al.*, 1999; Ricklefs, 2006; Donoghue, 2008). In particular, there is a growing appreciation for the role that niche conservatism might play in shaping species richness–climate relationships along latitudinal gradients (Wiens & Donoghue, 2004; Wiens *et al.*, 2010). More specifically, the tropical niche conservatism hypothesis (Wiens & Donoghue, 2004) posits that ancestral climatic niches (which are often tropical) are retained over long periods of time because evolutionary constraints prevent adaptation to newly available climatic niches following major episodes of climate change (e.g. the spread of temperate climates). As a result, the species richness of a given clade in a

given region might be low if ambient climatic conditions deviate from those conditions characterizing the clade’s ancestral niche, because of difficulties in evolving new adaptations (Wiens *et al.*, 2010). A more specific prediction might be that, along a contemporary climatic gradient, species richness should decrease with increasing differences between ambient climatic conditions and conditions characterizing the ancestral climatic niche. That is, the climatic conditions characterizing the ancestral niche of a clade should impose a strong limit on the distributions of its constituent species, and hence have a strong influence on patterns of species richness. Support for the importance of niche conservatism in shaping patterns of species richness was documented in South American trees (Giehl & Jarenkowiak, 2012), mammals world-wide (Buckley *et al.*, 2010) and Appalachian salamanders (Kozak & Wiens, 2010). Despite the growing evidence for the role of niche conservatism in shaping diversity gradients, the potential influence of niche conservatism on water–energy dynamics is largely unexplored.

In this study, we assessed the relative importance of water and energy on a latitudinal gradient of species richness, and evaluated whether niche conservatism might influence the effects of water–energy dynamics on species richness using geographically weighted regression (GWR) and species distribution data of the two Asian subgenera of oaks (*Quercus* L, Fagaceae): the temperate subgenus *Quercus* and tropical subgenus *Cyclobalanopsis* (Axelrod, 1983; Zhou, 1992; Manos *et al.*, 1999; Denk & Grimm, 2010). Hawkins *et al.* (2003) argued that the relative importance of water and energy in shaping spatial patterns of species richness shifted from low to high latitudes. Therefore, if patterns of species richness in Asian oaks follow Hawkins’ conjecture, we would expect that local r^2 values of the relationship between species richness and water availability would decrease with latitude, whereas local r^2 values of the relationship between species richness and energy would increase (Fig. 1a). Moreover, this pattern should be consistent across both subgenera of oaks studied here. In contrast, if niche conservatism influences the effect of water–energy dynamics on patterns of species richness, we would expect water–energy dynamics to vary between subgenera as a result of differences in their ancestral climatic niches (i.e. temperate versus tropical; see Materials and Methods for details of the evolutionary history of these two subgenera). In particular, for the tropical subgenus *Cyclobalanopsis*, we expect that the importance of both water and energy limitations on species richness should increase from the equator towards the North Pole (i.e. along the tropical–boreal gradient). However, for the temperate subgenus *Quercus*, the importance of water and energy limitations should increase when moving from mid-latitude regions towards both the equator and the North Pole (i.e. temperate–tropical and temperate–boreal gradients). Specifically, we predict: (1) a lack of clear water–energy transition line (as proposed by Hawkins *et al.*, 2003); and (2) an increase in local r^2 values (with high r^2 values indicating the importance of the envi-

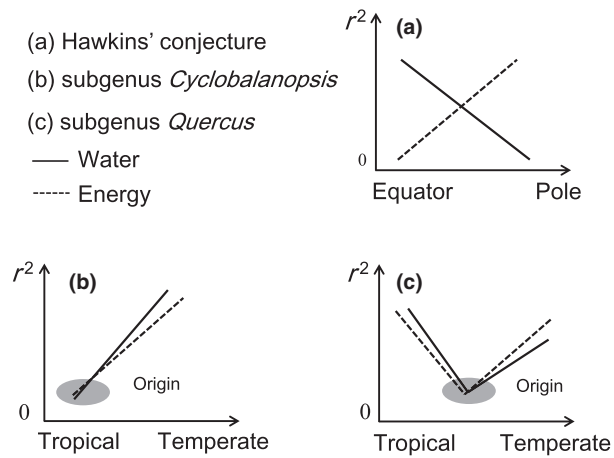


Figure 1 (a) Predicted variation in the strength (r^2) of the relationship between species richness and water or energy along the latitudinal gradient following the water–energy conjecture of Hawkins *et al.* (2003), wherein water limitation is the predominant factor at low latitudes and energy limitation predominates at high latitudes. (b) Assuming that adaptation ability to ambient climate decreases with increasing deviations from the ancestral climatic niche, local r^2 values of water or energy models for the Asian oak *Quercus* subg. *Cyclobalanopsis* increase with increasing latitude due to its tropical origin, but (c) a U-shaped pattern characterizes this relationship for the Asian oak *Quercus* subg. *Quercus* due to its temperate origin. Grey circles indicate the hypothesized area of origin.

ronmental variable in shaping the patterns of species richness) for the effect of water and energy availability from the equator to the North Pole for the tropical subgenus *Cyclobalanopsis* (Fig. 1b), but a U-shaped pattern for the temperate subgenus *Quercus* (Fig. 1c).

MATERIALS AND METHODS

Species distribution data

In this study, we compiled data on species distributions across an area bounded by Pakistan in the west, the Indochinese peninsula in the south, Siberia in the north and the Asian continental coastline in the east (about 70–140° E in longitude and about 10–60° N in latitude). Species distribution data were compiled from published floras, checklists, databases and peer-reviewed journal articles (see Appendix S1 in Supporting Information for a complete list of references).

Based on evidence from molecular phylogeny (Manos *et al.*, 1999; Denk & Grimm, 2010), fossil records (Jones, 1986; Zhou, 1992) and morphological studies (Deng *et al.*, 2008; Denk & Grimm, 2009), two subgenera of *Quercus* were identified. These studies suggested that subg. *Cyclobalanopsis* is a basal, tropical lineage that might be more closely related to other genera of the family Fagaceae than the rest of the genus *Quercus*, while subg. *Quercus* is a derived group that might have originated in temperate regions. It is uncertain as to when the two lineages separated, but some fossil evidence

from the Eocene suggests that subg. *Cyclobalanopsis* originated in a warmer and wetter environment than subg. *Quercus*, and may have undergone radiation soon after the divergence between American and Asian oaks (Manos & Stanford, 2001; Denk & Grimm, 2010). On the other hand, the crown group of *Quercus* may have diversified in mid-palaeolatitudes during the Oligocene, and evolved key innovations of functional traits adapted to cold, dry and fluctuating climate, including a deciduous life form and sclerophyllous/xeric leaves (Axelrod, 1983; Zhou, 1992). Therefore, we followed Menitsky (2005), Wu *et al.* (1999) and the *Oak Name Checklist* of the International Oak Society (<http://www.oaknames.org/>) to separate all Asian oak species into two subgenera. In total, we compiled 91 species of subg. *Cyclobalanopsis* and 35 species of subg. *Quercus*. Scientific names and synonyms followed that of Species 2000 (<http://www.sp2000.org/index.php>, accessed in October 2011) with minor modifications according to *Flora of China* (Wu *et al.*, 1999). Intraspecific taxa were merged to species level. Island species and hybrids were excluded from our study with the hybridization status according to *World Checklist of Fagaceae* (Govaerts *et al.*, 2011). In general, the distribution of subg. *Quercus* extends to Siberia in the North, and overlaps with that of subg. *Cyclobalanopsis* in subtropical regions (i.e. from the Indochinese peninsula to central China; Fig. S2 in Appendix S2). Appendix S3 shows the species list and distributions for each subgenus.

Most distributional data were recorded by administration units, and so we standardized our distribution data by these units. The administration boundaries maps were from the GADM database of Global Administrative Areas (version 1, <http://www.gadm.org/home>). The recorded geographical names in different literature were updated following the GeoNames of the global geographical database (<http://www.geonames.org/>), and were then linked to the global administration units. The sizes of the administration units ranged from 5285 to 320,000 km². In order to reduce any area effects on the estimation of species richness, we aggregated adjacent units that were less than 100,000 km² into larger units according to data availability and the areas of the majority of units. The areas of units in the final data set ranged from 90,000 to 320,000 km². For each unit, species number was counted, and the area was calculated in ArcGIS 10 (ESRI, Redlands, CA, USA) using the Albers equal-area conic projection. The latitude of each geographical unit was the latitude of its geometric centroid.

Climatic data

In order to test the effects of water and energy availability on species richness, we selected the most frequently used water and energy variables. The energy variables included mean annual temperature (MAT, °C), annual potential evapotranspiration (PET, mm), minimum monthly potential evapotranspiration (PET_{min}, mm), and mean temperature of the warmest (MTWQ, °C) and coldest quarters (MTCQ, °C).

The water variables were mean annual precipitation (MAP, mm), rainfall (RF, mm), aridity index (AI), and the mean precipitation of the wettest (MPWQ, mm) and driest quarters (MPDQ, mm). Rainfall was defined as the sum of monthly precipitation in months with a mean temperature above 0 °C (Francis & Currie, 2003). To avoid collinearity among variables, principal components analysis (PCA) was conducted for water and energy variables respectively to get the major water (PCw) and energy gradients (PCe). The broken-stick stopping rule was used to select how many components should be extracted from PCA analysis (Jackson, 1993).

MAT, MTWQ, MTCQ, MAP, MPWQ, MPDQ and monthly mean precipitation and temperature were obtained from the WorldClim database (<http://www.worldclim.org/>) with spatial resolutions of 2.5 × 2.5 arc-minutes. PET and AI data with a resolution of 30 arc-seconds were downloaded from the CGIAR Consortium for Spatial Information (<http://www.cgiar-csi.org/>). We used zonal statistics in ARCGIS 10 to calculate the mean values of each variable within each geographical unit.

Statistical analyses

We first evaluated the relationship between species richness and water or energy variables using ordinary least squares (OLS) regression models. This model assumes a global relationship between the response variable and predictors over geographical space (Jetz *et al.*, 2005). However, because the relationship between ecological variables and climate varies geographically (Svenning *et al.*, 2009), we used geographically weighted regression (GWR) models to detect whether either the richness–water relationship or the richness–energy relationship varies spatially.

Geographically weighted regression performs a regression for each data point (regression point) and estimates regression parameters. For each regression point, GWR assumes that observations which are nearer the regression point should have a greater weight than those that are further away (Charlton *et al.*, 2009). To account for the irregular spacing of our data points, the weight was computed by using an adaptive Gaussian kernel, which allows the same proportion of all data points (bandwidth) to be used for each regression. The corrected Akaike information criterion (AIC_c)-based optimization algorithm was used to select bandwidth. A fixed bandwidth with 14 data points, which can minimize AIC_c values for both the richness–energy model and the richness–water model simultaneously, was used to allow comparability of the results from different regression points of richness–energy model and richness–water model.

Geographically weighted regression was used to explore the relationships between species richness and water/energy for the two subgenera separately. The local r^2 values represented local explanatory power of water (r^2_{W}) and energy (r^2_{E}) on species richness at specific localities. The difference between energy and water r^2 was calculated as

$r^2_{\text{diff}} = r^2_{\text{E}} - r^2_{\text{W}}$, and represented the relative importance of the two factors in shaping species richness in different localities. For a given locality, r^2_{diff} values between −0.05 and 0.05 suggest that water and energy contribute equally to species richness. In contrast, $r^2_{\text{diff}} > 0.05$ suggests that energy is the dominant factor, whereas $r^2_{\text{diff}} < -0.05$ suggests that water is the dominant factor. Localities where the standard deviations of GWR model residuals were > 2.5 were deemed to be unreliable, and were excluded from the subsequent analysis. Area was not a significant predictor of species richness in either OLS ($P > 0.05$) or GWR models (difference in AIC_c between the model including area as a variable and the model excluding area is < 3). Area was therefore excluded from the analysis. Figure S1 in Appendix S2 shows the relationship between species richness and area.

To examine how the amount of local variation explained by water and energy changed along the latitudinal gradient, we first regressed r^2_{E} and r^2_{W} against latitude, and then used Davies' test to test whether the slope is non-constant (Davies, 1987). A significant result from Davies' test suggests non-constant relationships between r^2_{E} (or r^2_{W}) and latitude, in which case we used piecewise linear regression (PWL) to explore the segmented relationships between r^2_{E} (or r^2_{W}) and latitude; otherwise, the OLS model was used. Because the inherent spatial autocorrelation of GWR results will inflate Type I error in model significance tests, we used modified t -tests (Dutilleul *et al.*, 1993; Rosenberg & Anderson, 2011) to test the significance of correlation between local r^2 and latitude. In piecewise linear regression analysis, modified t -tests were used to test the significance of each segment. To quantitatively compare the performance of the OLS and PWL models, we performed a likelihood ratio test (LLR test; Feder, 1975).

Species richness was log-transformed. GWR and OLS were conducted and mapped in ARCGIS 10. Davies' tests and PWL were completed and plotted in the R package SEGMENTED (Muggeo, 2003, 2008; R Development Core Team, 2011), and LLR tests were carried out using the R package LMTTEST (Zeileis & Hothorn, 2002). PCA analyses were conducted using the 'princomp' function in MATLAB 2012a (MathWorks, Natick, MA, USA).

RESULTS

Principal components analysis, using the broken-stick model as a stopping rule, extracted the first axis (PC 1) for both water and energy groups. The proportion of variance explained by the first axis was more than 80% (Table S1 in Appendix S2) for both water and energy groups. The mean temperature of the coldest quarter and the mean precipitation of the driest quarter had the largest positive loadings on the first energy and water principal components, respectively (Table S1), which means that energy and water availability increased with increasing value of PC 1.

The significantly smaller AIC_c values of GWR models than OLS models (Table 1) and clear geographical patterns of

Table 1 Corrected Akaike information criterion (AIC_c) values of the geographically weighted regressions (GWR) and ordinary least-squares (OLS) regressions for species richness–climate models of two Asian oak subgenera, subgenus *Quercus* and subgenus *Cyclobalanopsis*.

	Richness–water model		Richness–energy model	
	OLS	GWR	OLS	GWR
Subgenus <i>Quercus</i>	157.61	103.31	155.49	101.09
Subgenus <i>Cyclobalanopsis</i>	87.24	75.78	98.27	77.63

residuals in OLS models (Fig. S3 in Appendix S2) indicated a strong spatial heterogeneity of richness–climate relationship. Local r^2 values under GWR models showed no water–energy transition along latitude for either subgenus (Fig. 2). The LLR test shows that the PWL model fits the data significantly better than the OLS model (Table 2).

We found strong latitudinal gradients in the explanatory power of energy (r^2_E) for subg. *Quercus*, and in the explanatory power of water (r^2_W) for subg. *Cyclobalanopsis* (Table 3). For subg. *Quercus*, both r^2_E and r^2_W showed non-constant trends along latitudinal gradients (Davies' test: $P < 0.001$). Piecewise linear regression identified the break-point at 27.82° N for r^2_E and at 44.21° N for r^2_W . Local r^2_E decreased before the break-point, and increased thereafter. For subg. *Cyclobalanopsis*, both r^2_E and r^2_W increased along latitudinal gradients, but only r^2_W increased significantly. These results are more consistent with the expectations of the tropical niche conservatism hypothesis, which suggests an increase in the local r^2 of water and energy availability from southern to northern latitudes for species belonging to subg. *Cyclobalanopsis*, but a U-shaped pattern in the r^2 of energy availability for those of subg. *Quercus* (Fig. 3). Notably, comparison of the local r^2 values for the two clades suggested that, at low latitudes ($< c. 25^\circ$ N), water and energy had higher r^2 on the species richness of subg. *Quercus* spp. than subg. *Cyclobalanopsis* spp. (one tailed t -test: r^2_E , $t = 3.38$, $P < 0.01$; r^2_W , $t = 5.04$, $P < 0.01$). In contrast, at latitudes above $c. 25^\circ$ N, water and energy correlated more strongly (higher r^2) with the species richness of subg. *Cyclobalanopsis* than that of subg. *Quercus* (one tailed t -test: r^2_E , $t = -3.486$, $P < 0.01$; r^2_W , $t = -6.531$, $P < 0.01$) (Fig. 4).

The local r^2_{diff} , which is the difference between local r^2_E and local r^2_W (see Materials and Methods), was 0.10 on average for subg. *Quercus*, and showed a break point at 35.59° N. The relative importance of energy decreased with latitude below (south of) 35.59° N, but significantly increased at high latitudes (Table 3, Fig. 3). For subg. *Cyclobalanopsis*, the r^2_{diff} was -0.09 on average, and showed a break point at 23.53° N. To the south of 23.53° N, the r^2_E and r^2_W were very similar, while to the north, the relative importance of water significantly increased. Local r^2_{diff} for subg. *Quercus* was greater than zero in 41 of 54 localities (Fig. 3c), but only 9 of 35 localities for subg. *Cyclobalanopsis* (Fig. 3f), suggesting that

subg. *Quercus* spp. are more limited by energy while subg. *Cyclobalanopsis* spp. are more limited by water.

DISCUSSION

We assessed the relative importance of water and energy availability in determining the species richness of the two subgenera of Asian oaks along a latitudinal gradient encompassing tropical, temperate and boreal ecosystems. We did not find a clear latitudinal transition zone marking a shift from the predominance of water limitation to that of energy as proposed by Hawkins *et al.* (2003). For subg. *Quercus*, the strength of the relationship between energy and species richness showed a U-shaped pattern along the latitudinal gradient. In contrast, the r^2 of both water and energy on the species richness of subg. *Cyclobalanopsis* increased monotonically from low to mid-latitudes. In addition, we found stronger energy limitation for the temperate clade and stronger water limitation for the tropical clade. These patterns were consistent with predictions arising from niche conservatism (but not with tropical niche conservatism) and suggested that differences in water–energy dynamics between these two subgenera of oaks might result from differences in their ancestral climatic niches. We conclude that niche conservatism might influence water–energy dynamics, such that evolutionary history and contemporary climate interact to shape the latitudinal gradient in the species richness of oaks across Asia.

In accordance with niche conservatism, species richness for each clade declined with increasing departure of ambient climatic conditions from that of the ancestral climatic niche (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004; Wiens *et al.*, 2010). In our study, the subgenus *Cyclobalanopsis* originated and diversified in a more humid and tropical-like climate than the subgenus *Quercus* (Zhou, 1992; Denk & Grimm, 2010). The subgenus *Quercus*, on the other hand, originated in more temperate climates and evolved tolerances to drought and cold (Axelrod, 1983; Zhou, 1992; Manos *et al.*, 1999). For example, previous studies on North American oaks found that species of subg. *Quercus* were well-adapted to dry environments, due to their deep-penetrating root system, thick leaves and small stomata (Hinckley *et al.*, 1979; Abrams, 1990). The significant differences in the physiological tolerance of the two subgenera are consistent with the differences in the relative importance of water and energy in shaping the patterns of species richness. Compared to species of subg. *Quercus*, species of subg. *Cyclobalanopsis*, which are pre-adapted to a warm and wet climate, are more limited by the cold and dry climate typical of mid-latitudes (25–40° N; see Fig. 4). In contrast species of subg. *Quercus*, which are highly tolerant of drought and cold, are more negatively affected by the warm and wet climatic conditions typical of low latitudes than subg. *Cyclobalanopsis* (Fig. 4). Our results are consistent with previous findings, and suggest that the interaction between evolutionary history and contemporary climate contributes to the effects of water–energy dynamics

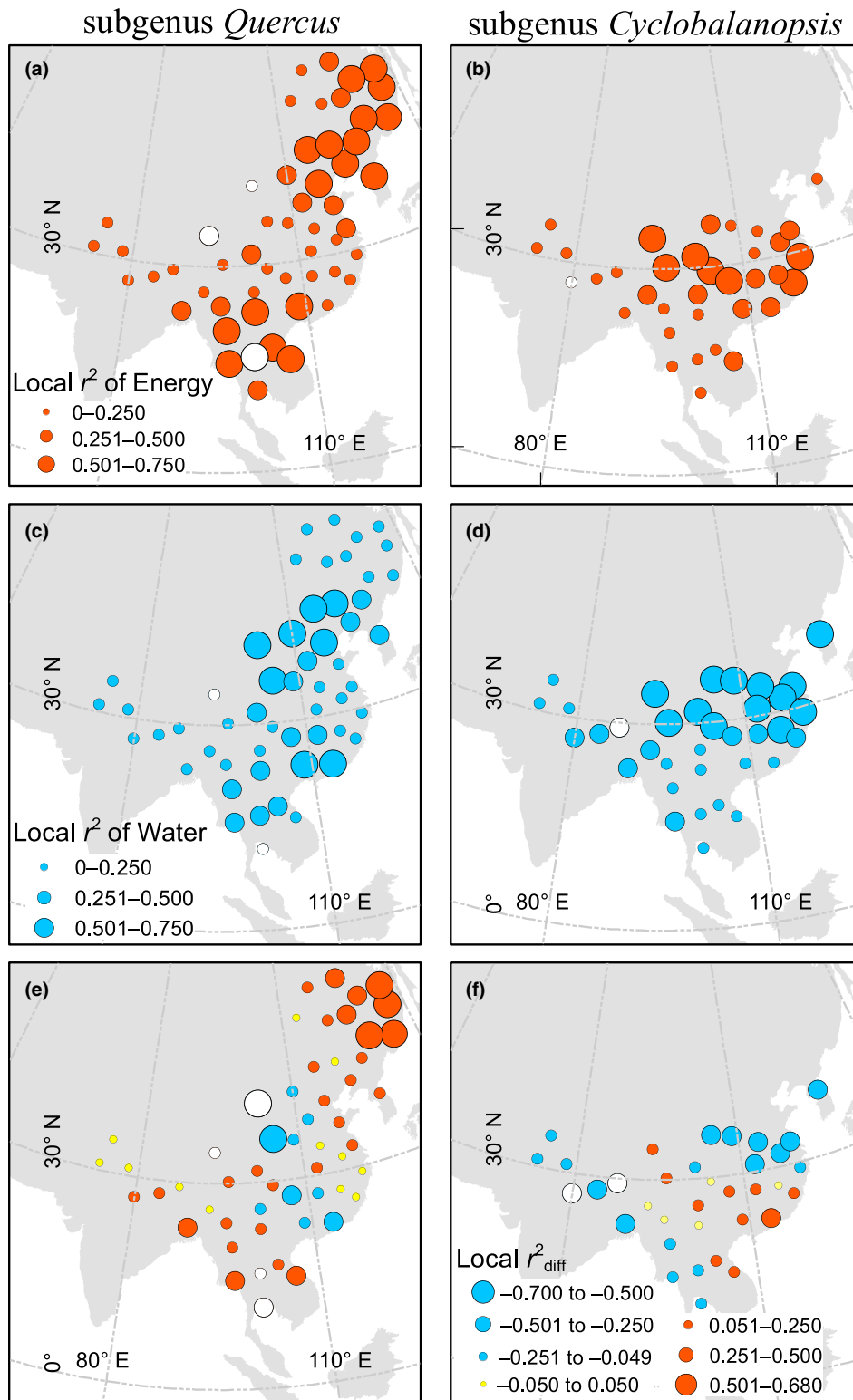


Figure 2 Geographical variation in local values of r^2 for (a,b) energy and (c,d) water models, and (e,f) differences (r^2_{diff}) between water and energy models for two subgenera of Asian oaks. Left column, *Quercus* subg. *Quercus*; right column, *Quercus* subg. *Cyclobalanopsis*. In panels a–d, the size of the dots indicates the strength of the regression models (i.e. local r^2 value) and colours indicate the explanatory variable in the model (blue, water; orange, energy) with species richness as response variable. In panels e–f, colours indicate whether the effect of water limitation (blue dots, negative values of local r^2_{diff}) or energy limitation (orange dots, positive values of r^2_{diff}) predominates. White dots represent localities with absolute standard deviation of residuals larger than 2.5, which were excluded from the regression analyses.

Table 2 Log likelihood values of ordinary least-squares (OLS) and piecewise linear (PWL) regression models and results of likelihood ratio tests for the relationship between species richness and water or energy variables along latitudinal gradients for Asian oak *Quercus* species of the subgenera *Quercus* and *Cyclobalanopsis*.

Subgenus	Model r^2	Log-likelihood			χ^2	P-values
		OLS (d.f. = 3)	PWL (d.f. = 5)			
<i>Quercus</i>	r^2_E	1.717	11.757		20.080	< 0.001
<i>Quercus</i>	r^2_W	8.418	13.386		9.936	0.006
<i>Quercus</i>	r^2_{diff}	2.999	10.051		14.102	< 0.001
<i>Cyclobalanopsis</i>	r^2_E	3.590	—		—	—
<i>Cyclobalanopsis</i>	r^2_W	10.658	—		—	—
<i>Cyclobalanopsis</i>	r^2_{diff}	6.274	10.500		8.451	0.015

Table 3 Local r^2 values of the relationship between species richness and water or energy along latitudinal gradients for Asian oak *Quercus* species of the subgenera *Quercus* and *Cyclobalanopsis*. The significance of the break-points were tested using Davies' test (Davies, 1987), and the slopes before and after break-points were estimated using piecewise linear (PWL) regression models with one break-point. P-values are for the slopes of each segment. P-values of modified *t*-tests are shown in parentheses.

Subgenus	Model r^2	Break point (95%CI)	Slope (South)	P-values	Slope (North)	P-values
<i>Quercus</i>	r^2_E	27.82 (24.21–31.43)	−0.036	0.001 (0.076)	0.016	< 0.001 (0.264)
<i>Quercus</i>	r^2_W	44.21 (38.34–50.09)	0.007	0.106 (0.377)	−0.034	0.014 (0.079)
<i>Quercus</i>	r^2_{diff}	35.59 (29.85–41.33)	−0.013	0.019 (0.167)	0.027	0.017 (0.483)
<i>Cyclobalanopsis</i>	r^2_E	OLS	0.007	0.256 (0.568)	OLS	OLS
<i>Cyclobalanopsis</i>	r^2_W	OLS	0.027	< 0.001 (0.063)	OLS	OLS
<i>Cyclobalanopsis</i>	r^2_{diff}	23.53 (17.87–29.2)	0.038	0.148 (0.303)	−0.035	< 0.001 (0.026)

OLS: P-values of both Davies' tests and likelihood ratio test (LLR) tests are larger than 0.05, which implies a consistent linear relationship; therefore only the ordinary least-squares (OLS) model was used (see Table 2 for results of likelihood ratio tests).

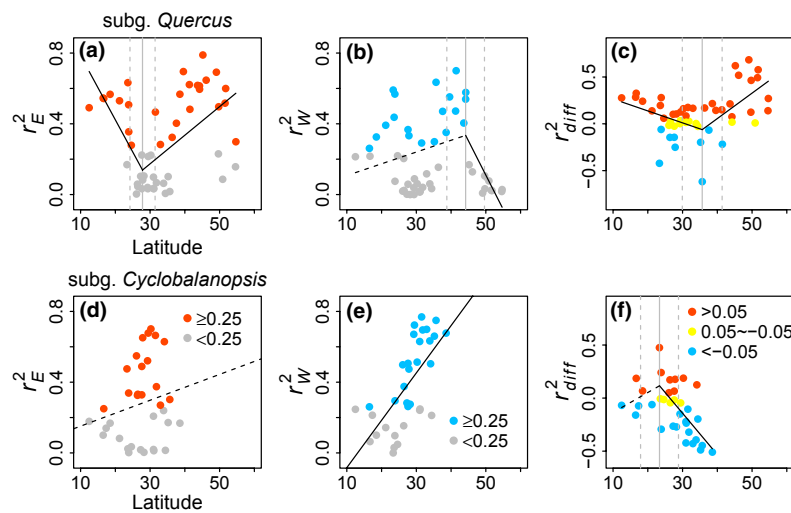


Figure 3 Latitudinal gradients of local r^2 for energy models (r^2_E), water models (r^2_W) and relative importance of water and energy ($r^2_{diff} = r^2_E - r^2_W$) for (a–c) *Quercus* subgenus *Quercus* and (d–f) *Quercus* subgenus *Cyclobalanopsis*. Black lines and grey lines in the figure were estimated by piecewise linear regression. Solid grey lines show the break and dashed grey lines show the 95% confidence interval for the break-points. Black solid lines, $P < 0.05$; black dashed lines, $P > 0.05$. (a,b,d & e) Orange dots, local $r^2_E \geq 0.25$; blue dots, local $r^2_W \geq 0.25$; grey dots, local r^2_W or $r^2_E < 0.25$. (c & f) Orange dots, local $r^2_{diff} > 0.05$; yellow dots, $0.05 \geq \text{local } r^2_{diff} \geq -0.05$; blue dots, local $r^2_{diff} < -0.05$.

on species richness (Ricklefs, 2006). For mammals, Buckley *et al.* (2010) also found that evolutionary history affects the species richness–climate relationship across terrestrial mammalian clades, with the relationship between species richness

and temperature being negative for young clades but positive for old tropical clades.

Niche conservatism alone cannot account for spatial patterns of species richness and several other factors could also

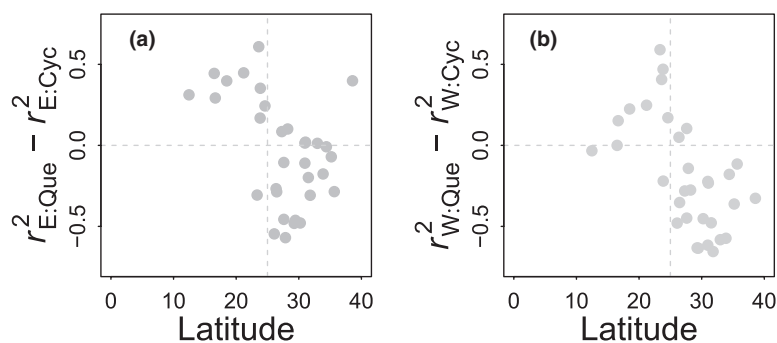


Figure 4 Comparison of local r^2 difference of (a) energy and (b) water models between two Asian oak *Quercus* subgenera (subgenus *Quercus*; subgenus *Cyclobalanopsis*) for locations in which both subgenera occurred. When latitude is lower than 25° N, water and energy are strongly limiting for subgenus *Quercus*, whereas when latitude is greater than 25° N, both water and energy are strongly limiting for subgenus *Cyclobalanopsis*. $r^2_{E:Que}$, local r^2 of energy models for subgenus *Quercus*; $r^2_{E:Cyc}$, local r^2 of energy models for subgenus *Cyclobalanopsis*; $r^2_{W:Que}$, local r^2 of water models for subgenus *Quercus*; $r^2_{W:Cyc}$, local r^2 of water models for subgenus *Cyclobalanopsis*.

contribute to these patterns. Previous studies have suggested that the heterogeneous topography of the south-eastern Tibetan Plateau has contributed significantly to species richness in Asia by promoting allopatric speciation and interspecific diploid hybridization in this region (Wang, 1992; Latham & Ricklefs, 1993; Liu *et al.*, 2006). The possible rapid speciation events of oaks in the south-eastern Tibetan Plateau (Zhou, 1992) might also have contributed to the lower r^2 of water and energy for oak species richness in this region than for other regions at lower or higher latitudes.

Our findings of the lack of water–energy transition differed from previous tests of Hawkins' conjecture (Whittaker *et al.*, 2007; Eiserhardt *et al.*, 2011), which is probably due to the historical differences between Asia and other continents (Ricklefs *et al.*, 2004). Hawkins *et al.* (2003) studied 22 plant data sets, most of which were from America and only two of which were global (but with few localities from Asia). Other tests of Hawkins' conjecture were based on data from Europe (Whittaker *et al.*, 2007) and tropical to subtropical regions of America (Eiserhardt *et al.*, 2011). In contrast, our study focused on Asia, which has a different geological and evolutionary history from Europe and America. In particular, Asia was connected to tropical regions even during the global cooling periods in the late Tertiary and in the Quaternary glacial–interglacial cycles. Therefore, many clades retracted into glacial refugia in southern and south-western China and the Indochinese peninsula and survived the severe climate changes since the late Tertiary there (Latham & Ricklefs, 1993). In contrast, Western Europe and eastern North America are separated from the tropics and subtropics by the Mediterranean Sea and the Gulf of Mexico, respectively, and many clades became extinct because their southward contraction during glacial periods was stopped by the geographical barriers (Huntley, 1993; Latham *et al.*, 1993). These large differences in regional histories among these three continents might have significantly altered the relationship between species richness and water–energy dynamics, and hence the water–energy transition. As such, a discrepancy exists in the

relative importance of various climatic factors for shaping patterns of tree species richness in North America and Asia. For example, Ricklefs *et al.* (2004) compared the determinants of flowering plant diversity in Eastern Asia and eastern North America, and found that January temperature was the only significant climatic variable affecting species richness in Eastern Asia, whereas both January temperature and summer precipitation were significant in eastern North America.

To conclude, we tested the water–energy transition conjecture of Hawkins *et al.* (2003) and evaluated the role of evolutionary history in mediating the effect of water–energy dynamics on the latitudinal species richness gradient in oaks. Our analysis did not find a single water–energy transition zone as predicted by Hawkins *et al.* (2003). Instead, our results suggest that evolutionary history determines the relative importance of water and energy on spatial patterns of species richness through niche conservatism. In particular, we showed that – in most localities – species richness in subg. *Quercus* is more limited by energy, whereas species richness in subg. *Cyclobalanopsis* is more limited by water (Fig. 3). These results are consistent with a growing body of evidence supporting the view that evolutionary and historical processes, and in particular niche conservatism, interact with contemporary climate to shape spatial patterns of diversity in vascular plants (Ricklefs, 2006; Wang *et al.*, 2011b). Ultimately, experimental studies are needed to directly detect the changes in physiological adaptations (e.g. adaptation to drought, freezing and heat) for coping with 'extreme' climatic conditions as one moves away from the more 'benign' climatic conditions characterizing the ancestral niche.

ACKNOWLEDGEMENTS

We thank W.H. Du of the Institute of Botany, Chinese Academy of Science, for his help in constructing the species distribution database and S.H. Yek of the University of Copenhagen for improving an earlier draft. Financial

support was provided by: the National Natural Science Foundation of China (31021001) to J.F. and X.X.; Peking University and the Chinese Scholarship Council to X.X.; the Marie Curie Actions under the Seventh Framework Programme (PIEF-GA-2010-275666) to Z.W.; and the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate to C.R., Z.W., J.-P.L. and X.X.

REFERENCES

- Abrams, M.D. (1990) Adaptations and responses to drought in *Quercus* species of North-America. *Tree Physiology*, **7**, 227–238.
- Axelrod, D.I. (1983) Biogeography of oaks in the Arcto-Tertiary Province. *Annals of the Missouri Botanical Garden*, **70**, 629–657.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2131–2138.
- Charlton, M., Fotheringham, S. & Brunson, C. (2009) *Geographically weighted regression white paper*. National Centre for Geocomputation, National University of Ireland Maynooth, Co, Kildare.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Davies, R.B. (1987) Hypothesis-testing when a nuisance parameter is present only under the alternative. *Biometrika*, **74**, 33–43.
- Deng, M., Zhou, Z., Chen, Y.Q. & Sun, W.B. (2008) Systematic significance of the development and anatomy of flowers and fruit of *Quercus schottkyana* (subgenus *Cyclobalanopsis*: Fagaceae). *International Journal of Plant Sciences*, **169**, 1261–1277.
- Denk, T. & Grimm, G.W. (2009) Significance of pollen characteristics for Infrageneric classification and phylogeny in *Quercus* (Fagaceae). *International Journal of Plant Sciences*, **170**, 926–940.
- Denk, T. & Grimm, G.W. (2010) The oaks of western Eurasia: traditional classifications and evidence from two nuclear markers. *Taxon*, **59**, 351–366.
- Donoghue, M.J. (2008) A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences USA*, **105**, 11549–11555.
- Dutilleul, P., Clifford, P., Richardson, S. & Hemon, D. (1993) Modifying the *t*-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.
- Eiserhardt, W.L., BJORHOLM, S., Svenning, J.C., Rangel, T.F. & Balslev, H. (2011) Testing the water–energy theory on American palms (Arecaceae) using geographically weighted regression. *PLoS ONE*, **6**, e27027.
- Feder, P.I. (1975) The log likelihood ratio in segmented regression. *The Annals of Statistics*, **3**, 84–97.
- Field, R., O'Brien, E.M. & Whittaker, R.J. (2005) Global models for predicting woody plant richness from climate: development and evaluation. *Ecology*, **86**, 2263–2277.
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.
- Giehl, E.L.H. & 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**, 1–11.
- Govaerts, R., Andrews, S., Coombes, A., Gilbert, M., Hunt, D., Nixon, K. & Thomas, M. (2011) *World checklist of Fagaceae*. Royal Botanic Gardens, Kew, Richmond. Available at: <http://apps.kew.org/wcsp/home.do> (accessed October 2011).
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hinckley, T.M., Dougherty, P.M., Lassoie, J.P., Roberts, J.E. & Teskey, R.O. (1979) Severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. *American Midland Naturalist*, **102**, 307–316.
- Huntley, B. (1993) Species-richness in north-temperate zone forests. *Journal of Biogeography*, **20**, 163–180.
- Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Jackson, D.A. (1993) Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology*, **74**, 2204–2214.
- Jetz, W., Rahbek, C. & Lichstein, J.W. (2005) Local and global approaches to spatial data analysis in ecology. *Global Ecology and Biogeography*, **14**, 97–98.
- Jones, J.H. (1986) Evolution of the Fagaceae: the implications of foliar features. *Annals of the Missouri Botanical Garden*, **73**, 228–275.
- Kozak, K.H. & Wiens, J.J. (2010) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist*, **176**, 40–54.
- Latham, R.E. & 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.
- Latham, R.E., Ricklefs, R.E. & Schluter, D. (1993) Continental comparisons of temperate-zone tree species diversity. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 294–314. University of Chicago Press, Chicago, IL.

- Liu, J.-Q., Wang, Y.-J., Wang, A.-L., Hideaki, O. & Abbott, R.J. (2006) Radiation and diversification within the *Ligularia–Cremathodium–Parasenecio* complex (Asteraceae) triggered by uplift of the Qinghai-Tibetan Plateau. *Molecular Phylogenetics and Evolution*, **38**, 31–49.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2005) *Biogeography*, 3rd edn. Sinauer Associates, Sunderland, MA.
- Manos, P.S. & Stanford, A.M. (2001) The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Sciences*, **162**, S77–S93.
- Manos, P.S., Doyle, J.J. & Nixon, K.C. (1999) Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution*, **12**, 333–349.
- Menitsky, Y.L. (2005) *Oaks of Asia*. Science Publishers, New Hampshire.
- Muggeo, V.M.R. (2003) Estimating regression models with unknown break-points. *Statistics in Medicine*, **22**, 3055–3071.
- Muggeo, V.M.R. (2008) segmented: an R package to fit regression models with broken-line relationships. *R News*, **8**, 20–25.
- O'Brien, E.M. (1998) Water–energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography*, **25**, 379–398.
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org>.
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, **87**, S3–S13.
- Ricklefs, R.E., Latham, R.E. & Qian, H. (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos*, **86**, 369–373.
- Ricklefs, R.E., Qian, H. & White, P.S. (2004) The region effect on mesoscale plant species richness between eastern Asia and eastern North America. *Ecography*, **27**, 129–136.
- Rosenberg, M.S. & Anderson, C.D. (2011) PASSaGE: pattern analysis, spatial statistics and geographic exegesis, version 2. *Methods in Ecology and Evolution*, **2**, 229–232.
- Svenning, J.C., Normand, S. & Skov, F. (2009) Plio-Pleistocene climate change and geographic heterogeneity in plant diversity–environment relationships. *Ecography*, **32**, 13–21.
- Wang, W.T. (1992) On some distribution patterns and some migration routes found in the eastern Asiatic region. *Acta Phytotaxonomica Sinica*, **30**, 97–117.
- Wang, Z., Brown, J.H., Tang, Z. & Fang, J. (2009) Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America. *Proceedings of the National Academy of Sciences USA*, **106**, 13388–13392.
- Wang, Z., Fang, J., Tang, Z. & Lin, X. (2011a) Patterns, determinants and models of woody plant diversity in China. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2122–2132.
- Wang, Z., Fang, J., Tang, Z. & Lin, X. (2011b) Relative role of contemporary environment versus history in shaping diversity patterns of China's woody plants. *Ecography*, **34**, 1124–1133.
- Whittaker, R.J., Nogués-Bravo, D. & Araújo, M.B. (2007) Geographical gradients of species richness: a test of the water–energy conjecture of Hawkins *et al.* (2003) using European data for five taxa. *Global Ecology and Biogeography*, **16**, 76–89.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19**, 639–644.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.
- Wu, Z., Raven, P.H. & Hong, D. (eds) (1999) *Flora of China (Cycadaceae through Fagaceae)*, Vol. 4. Science Press, Beijing, and Missouri Botanical Garden, St. Louis, MO.
- Zeileis, A. & Hothorn, T. (2002) Diagnostic checking in regression relationships. *R News*, **2**, 7–10.
- Zhou, Z. (1992) Origin, phylogeny and dispersal of *Quercus* from China. *Acta Botanica Yunnanica*, **14**, 227–236.

SUPPORTING INFORMATION

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

Appendix S1 Literature used to construct the oak distribution database.

Appendix S2 Supplementary results and analyses.

Appendix S3 List of Asian oak species and their distributions.

BIOSKETCH

Xiaoting Xu is a PhD student and her research interests are the global pattern of oak species diversity and the underlying evolutionary and climatic mechanisms.

Author contributions: X.X., Z.W., C.R., J.-P.L. and J.F. conceived the ideas; X.X. and Z.W. collected the data; X.X. and Z.W. analysed the data; all authors led the writing.

Editor: K. C. Burns