ORIGINAL ARTICLE

Geographical variation in the importance of water and energy for oak diversity

Xiaoting Xu[1,2], Zhiheng Wang[1,2]*, Carsten Rahbek[2,3], Nathan J. Sanders[2] and Jingyun Fang[1]

[1]*Department 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,* [2]*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen Ø DK-2100, Denmark,* [3]*Imperial College London, Grand Challenges in Ecosystems & the Environment Initiative, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*

ABSTRACT

Aim The water–energy dynamics hypothesis posits that species diversity is correlated with water availability and temperatures; diversity is lowest when water availability is reduced at low temperatures because few species can persist under such conditions. However, the relationship between water and energy availability and diversity likely varies geographically along environmental gradients. Here, we examined the drivers of such variability, using a global-scale data set on oaks.

Location Global.

Method To quantify spatial variation in both species diversity–water relationships and species diversity–energy relationships, we performed geographically weighted regressions (GWR) of (1) species diversity against energy availability, measured as potential evapotranspiration and temperature, and (2) species diversity against water availability, measured by precipitation and an aridity index. We then regressed the local slopes of these GWR models against water and energy separately, and water × energy combined to assess whether the regional-scale relationships among oak diversity, water and energy depended on climatic conditions at larger spatial extents.

Results We found that the effects of low water availability and cold temperatures on oak diversity varied geographically. In particular, the effects of water and energy availability on oak diversity increased as water and energy availability decreased. Furthermore, the interaction between water and energy availability influenced regional-scale oak diversity–energy relationships but not oak diversity–water relationships.

Main conclusion Our results suggest that the relationship between climate (and potentially climatic change) and oak diversity varies geographically, and that the effects of limiting water and temperature are likely to be most severe in arid environments.

*Correspondence: Zhiheng Wang, Department 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. E-mail: zhiheng.wang@pku.edu.cn

INTRODUCTION

Water and energy are essential for plant growth and reproduction. Water, as a solvent and source of oxygen and hydrogen for photosynthesis, is essential for nutrient transportation and metabolism (Nobel, 2009). Low temperatures lead to ice formation in plants and cause cellular dehydration and freeze-thaw cycles (Woodward, 1987, 1990; Nobel, 2009). Excessively high temperatures can alter a variety of plant structures and functions at the cellular level, inhibit photosynthetic activity and limit growth (Jenks & Hasegawa, 2008). Such effects of water and energy limitation on individuals might scale up to influence broad-scale patterns of plant diversity (O'Brien, 1998, 2006; O'Brien *et al.*, 2000; Currie *et al.*, 2004; Field *et al.*, 2005). For example, drought and extreme temperatures could cause tissue damage in trees,

and reduce tree growth and seedling recruitment, which in turn could ultimately limit the distribution of species (Terradas & Savé, 1992; Cavender-Bares *et al.*, 1999; Du *et al.*, 2007).

Previous studies focusing on the physiological basis of plant diversity gradients have examined the evidence not only for the effects of water and energy availability but also the interaction between water and energy availability (O'Brien, 1998; O'Brien *et al.*, 1998; Francis & Currie, 2003; Field *et al.*, 2005; Kreft & Jetz, 2007; Whittaker *et al.*, 2007). For example, in a series of now classic studies, O'Brien and co-workers showed that the relationship between species diversity and energy availability depends on water availability, due to higher evapotranspiration rates in warmer regions. Such observations formed the basis for a water–energy theory of global plant species richness (O'Brien, 1998, 2006; O'Brien *et al.*, 2000). Although the details of the physiological processes underlying the influence of water–energy interactions on individual growth, survival, and reproduction are still largely unresolved, several studies have indicated that water and energy availability could either strengthen or weaken the effects of low water availability (i.e. drought) and temperature extremes on plant distributions at broad spatial scales. For instance, high temperatures can hasten a decrease in photosynthesis and water-use efficiency (Rushton, 1993; Shah & Paulsen, 2003). In contrast, winter snow can weaken the effects of soil freezing stress, water loss through plant transpiration, and temperature fluctuations, thereby reducing the effects of freezing on plants (Groffman *et al.*, 2001; Oberhuber, 2004).

Despite an ever-increasing awareness of the potential independent roles of energy and water availability on broad-scale patterns of diversity, our understanding of how and when water and energy availability interact to influence species diversity patterns across large scales is lacking, in part because the effects of water and energy availability need not be the same everywhere. That is, the effects of water and energy availability on individuals and on patterns of diversity could vary geographically due to the interactions between water and energy (O'Brien, 1993, 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003; Kreft & Jetz, 2007; Whittaker *et al.*, 2007; Sommer *et al.*, 2010). For example, the effects of water on species diversity likely increase as water becomes more limiting and as energy availability decreases (Janzen, 1967; Rangel & Diniz-Filho, 2005). Here, we use a species-rich genus of woody plants, *Quercus* L., to test the effects of water and energy availability, and more interestingly the effects of their interactions on species diversity patterns at global scales.

Species in the genus *Quercus* have broad climatic niches and are widely distributed in the Northern Hemisphere, occupying habitats ranging from the tropics and subtropics to cool temperate regions and drylands (Nixon, 1997; Wu *et al.*, 1999; Menitsky, 2005). Because of their high economic value, the distribution of *Quercus* species is well documented in most regions (see Appendix S1 in Supporting Informa-

tion). Moreover, physiological responses of many *Quercus* species to temperature, drought or flooding stress have been widely documented (Abrams, 1990; Cavender-Bares *et al.*, 1999, 2005; Cavender-Bares, 2007; Mahall *et al.*, 2009; Li *et al.*, 2013; Vitasse *et al.*, 2014). These features make *Quercus* a good model taxon for examining the effects of water and energy availability across climatic gradients. Specifically, we examined the interplay between water and energy availability on oak diversity in two ways. First, we evaluated whether the statistical effects of water and energy on oak diversity decrease as water and energy availability increase at broad geographical extents. Second, we examined how the interaction between water and energy is associated with diversity–water and diversity–energy relationships.

MATERIALS AND METHODS

Species distribution data

Quercus L. (i.e. oak species), including subgenus *Cyclobalanopsis* and subgenus *Quercus*, has more than 400 species. *Quercus* occurs in tropical and temperate forests and ranges from northern Colombia to Canada in the New World and from the Indo-Chinese Peninsula to Norway in Eurasia (Nixon, 1997; Wu *et al.*, 1999). Fossil and molecular evidence suggests that subgenus *Cyclobalanopsis* originated in the tropics while the subgenus *Quercus* originated in temperate regions (Zhou, 1992; Manos *et al.*, 1999; Denk & Grimm, 2010).

We compiled occurrence data for all oak species from published floras, checklists, databases and peer-reviewed journal articles (see Appendix S2 for a complete list of references). In addition to this exhaustive search, we used herbarium specimen data from the National Commission for Knowledge and Use of Biodiversity Data of Mexico (CONABIO, http://www.conabio.gob.mx/) to compile county-level data from Mexico. To reduce the uncertainty of specimen identification, only the specimens identified by trained taxonomists or organizations were used in our study. Infraspecific taxa were merged to species level. Island species and hybrids [(hybridization status according to *World Checklist of Fagaceae* (WCSP, 2011)] were excluded from our study. For detailed distributions of each species, see Appendix S1.

Because most occurrence data were recorded based on administrative divisions, we compiled our database based on these divisions. The map of global administrative divisions comes from the database of Global Administrative Areas (1.0, http://www.gadm.org/home). We compiled and updated the geographical names of species occurrences in the published literature following the GeoNames geographical database (http://www.geonames.org/, 21 January 2010). We estimated the size of each division by means of ARCGIS 10 using the Goode homolosine projection. To reduce the effects of area on the estimates of species diversity, we followed Xu *et al.* (2013) by aggregating connected divisions that were $< 100,000$ km^2 into larger divisions. After we

merged the small divisions, 70% of the divisions had areas between 180,000 and 250,000 km^2 (see Fig. S1 in Appendix S3). We excluded Cambodia from our analyses because it has not been adequately sampled; to date, only two oak species have been recorded there, which seems relatively low. In total, we compiled occurrence data for 370 of 400 oak species from 164 divisions. Finally, we tallied the number of oak species in each division.

Environmental data

To estimate the effects of water and energy on oak species diversity, we selected a suite of frequently used water and ambient energy variables. Water variables included mean annual precipitation (MAP, mm), rainfall (RF, mm), aridity index (AI) and precipitation of the wettest quarter (PWQ, mm) and driest quarter (PDQ, mm). Rainfall was calculated as the sum of monthly precipitation when mean monthly temperature was above 0 °C (Francis & Currie, 2003). Ambient energy variables included mean annual temperature (MAT, °C), annual potential evapotranspiration (PET, mm), minimum monthly potential evapotranspiration (PETmin, mm), and mean temperature of the warmest quarter (MTWQ, °C) and the coldest quarter (MTCQ, °C). MAT, MTWQ, MTCQ, MAP, PWQ, PDQ and monthly precipitation/mean temperature with a spatial resolution of 2.5 × 2.5 arc minutes were from the WorldClim database (http://www.worldclim.org). PET, PETmin and AI with spatial resolutions of 30 arc seconds were from the CGIAR consortium for spatial information (http://www.cgiar-csi.org/). PET was calculated using the Hargreaves method, which required less parameterization and has reduced sensitivity to climatic inputs error (Trabucco et al., 2008; Fisher et al., 2011), and AI was calculated as MAP/PET (see http://www.cgiar-csi.org/). To match the size of species distribution regions, we calculated average values of each climatic variable within each geographical division using zonal statistics in ARCGIS 10 (ESRI, Redlands, CA, USA).

We then used principal components analysis (PCA) to account for collinearity among water and ambient energy variables (Pearson correlation coefficients > 0.7, see Tables S1 and S2 in Appendix S3). We extracted the first axis (PC 1) for both water (WPC1) and energy variables (EPC1) according to a broken-stick stopping rule (Jackson, 1993).

Statistical analyses

We used ordinary least square (OLS) regression and geographically weighted regression (GWR) to examine the relationships between oak species diversity and climate. The OLS regression assumed stationary (i.e. constant) relationships between oak diversity and climate across space and generated global slopes of diversity–water and diversity–energy relationships (Weisberg, 2005). In contrast, the GWR evaluated the spatial variation in diversity–water and diversity–energy relationships (Fotheringham et al., 2002). In particular, the

GWR estimated diversity–water and diversity–energy slopes for each focal administrative division (local slopes hereafter, in contrast to the 'global slopes' of the OLS regression) by assuming the decay of weight in local regressions with increasing distance between observations and the focal division (Fotheringham et al., 2002; Charlton et al., 2009; Svenning et al., 2009; Eiserhardt et al., 2011; Hortal et al., 2011). To account for the irregular spatial distribution of the administrative divisions, we used the adaptive bandwidth method, which allows the same number of divisions in each local regression (Svenning et al., 2009; Eiserhardt et al., 2011). Using the optimization algorithm based on the corrected Akaike information criterion (AIC$_c$), we selected the geographically closest 14 data points as the fixed bandwidth in the GWR.

To evaluate whether the sizes of administrative divisions may have potentially biased the geographical patterns of oak diversity and its relationships with climate due to species–area relationships (He & Legendre, 1996), we examined whether division area influenced on oak species diversity. We found that (1) the area of administrative divisions did not significantly change with latitude ($P = 0.188$), WPC1 ($P = 0.117$) and EPC1 ($P = 0.784$), and (2) division area was not a significant predictor of oak species diversity patterns according to OLS regression ($P = 0.165$) (see Table S3 and Fig. S2 in Appendix S3). These results suggest that areas of division do not systematically bias the patterns of oak diversity and their relationships with climate. Therefore, division area was not included as a predictor of species diversity in our analysis.

The local slope for a specific administrative division estimated by the GWR represents the statistical effects of local climatic conditions on diversity and indicates how many species will be gained or lost by changing a unit of water or energy availability. To identify variation in local statistical effects of climate on diversity at large geographical extents, we first built GWR models for diversity–water relationships (GWR water model) and diversity–energy relationships (GWR energy model), and then regressed the local slopes of the GWR water model (Wslopes) against WPC1 (the 1st access of the Water PCA) and the local slopes of GWR energy model (Eslopes) against EPC1 (the first axis of the Energy PCA) using linear models. To detect the interaction of water and energy on diversity–water (or diversity–energy) relationships at local scales, we built two additional linear models using Wslopes (or Eslopes) as dependent variables, and WPC1, EPC1 and their interactions as the independent variables in the model. We used a contour plot to view the statistical effects of the WPC1 and EPC1 interaction on oak diversity. A contour plot is the three-dimensional graph in which the Eslopes/Wslopes were interpolated to the climatic space of EPC1 and WPC1 (Davis, 2002).

Eleven regions with absolute value of standard residuals > 2.5 of GWR models were deemed to be unreliable, and were subsequently excluded from analysis (see Fig. S1 in Appendix S1). To account for inherent spatial autocorrelation in the patterns of GWR local slopes, we used Dutilleul's mod-

ified *t*-test (Dutilleul *et al.*, 1993) to examine the significance of the relationships between GWR slopes and predictors.

We conducted the GWR in ARCGIS 10 (ESRI) and the PCA and OLS in MATLAB 2013b with function 'princomp' and 'fitlm' respectively (MathWorks, Natick, MA, USA). We conducted Dutilleul's modified *t*-test in PASSaGE2 (Dutilleul *et al.*, 1993; Rosenberg & Anderson, 2011) and generated the contour plot with JMP 11.2.0 (SAS, Cary, NC, USA).

RESULTS

Principal components analysis showed that PDQ and MTCQ had the largest positive loadings on the first principal components for water (WPC1) and energy (EPC1) respectively (Table 1). This suggests that water and energy increased with increasing WPC1 and EPC1 respectively. Geographical patterns of WPC1 and EPC1 showed that energy availability increases with increasing latitude. Water availability is highest in low latitude and lowest in middle-east region and central United States (Fig. 1).

Oak species diversity was highest in Central America and Southwest China, and decreased towards the north and south (Fig. 2a). OLS models indicated that energy (*adj. r²* = 0.53, *N* = 153, *P* < 0.001) and water (*adj. r²* = 0.23, *N* = 153, *P* < 0.001) were related to oak species diversity, with global slopes of 0.46 and 0.36 respectively. Both the patterns in the residuals of OLS models (Fig. 2b,c) and the difference of AIC$_c$ values between GWR and OLS regressions suggest that the diversity–water and diversity–energy relationships varied geographically (AIC$_c$ of water model: GWR 276.27 vs. OLS 530.15; energy model: GWR 271.04 vs. OLS 462.95). Therefore, we used the results of the GWR models in all subsequent analyses.

Table 1 The loadings and cumulative sum of variance of the first two principal components (PC) for the principal components analysis (PCA) of water and energy predictors. Using the broken-stick stopping rule (Jackson, 1993), only the first axes for water (WPC1) and energy variables (EPC1) respectively were selected for the oak diversity–climate relationship. See Materials and Methods for the meaning of each climatic variable.

Climatic variables	PC 1	PC 2
Water		
MAP	0.5087	0.4982
RF	−0.1061	−0.1717
AI	−0.1844	−0.3342
PWQ	−0.3154	−0.4707
PDQ	0.7723	−0.6237
Cumulative sum of variance	75.5%	94.1%
Energy		
MAT	0.4704	0.4556
PET	0.0018	0.0816
PETmin	−0.3862	0.6271
MTWQ	−0.0056	−0.6258
MTCQ	0.7934	0.0305
Cumulative sum of variance	88.3%	95.9%

Considerable spatial variation existed in the slopes of both the diversity–water (Wslopes) and diversity–energy relationships (Eslopes) (Fig. 2e,f). As expected, energy availability (EPC1) significantly influenced the diversity–energy relationships. In particular, the Eslopes (the local slopes between oak diversity and EPC1) significantly declined with the increase in energy availability (Fig. 3a, modified *t*-test, *P* < 0.05). More interestingly, the water × energy interaction significantly influenced changes in the Eslopes (Table 2), suggesting that the decreasing rate of Eslopes along the gradient of EPC1 is influenced by WPC1. Specifically, in extremely dry and wet regions, Eslopes changed from positive to negative and decreased faster than in other regions (Fig. 4b). Likewise, water availability (WPC1) also significantly influenced the local slopes between oak diversity and WPC1 (Wslopes) (Fig. 3b, modified *t*-test, *P* < 0.05). However, the water × energy interaction did not influence the Wslopes, suggesting that the decreasing rate of Wslopes with water availability was not influenced by energy availability (Fig. 4a).

Taking both water availability and energy availability into consideration, we found that species diversity of oaks was highest in the areas where energy was high but water availability was intermediate (Fig. 4c), and where local slopes of both the GWR water model and GWR energy model were smallest (Fig. 4d).

DISCUSSION

The key findings from our global-scale analysis of oak diversity are that: (1) the effects of water and energy availability
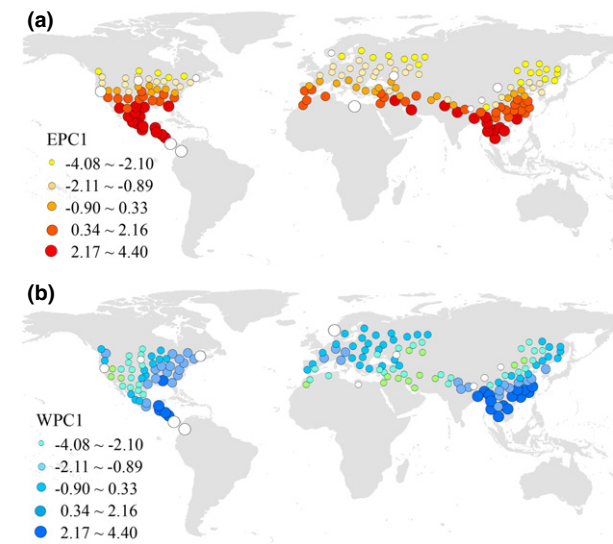

Figure 1 The first axes of the principal components analysis for (a) water variables (WPC1) and (b) energy variables (EPC1). White dots represent the localities with absolute standard residuals in GWR models larger than 2.5, which we excluded from the regression analysis.
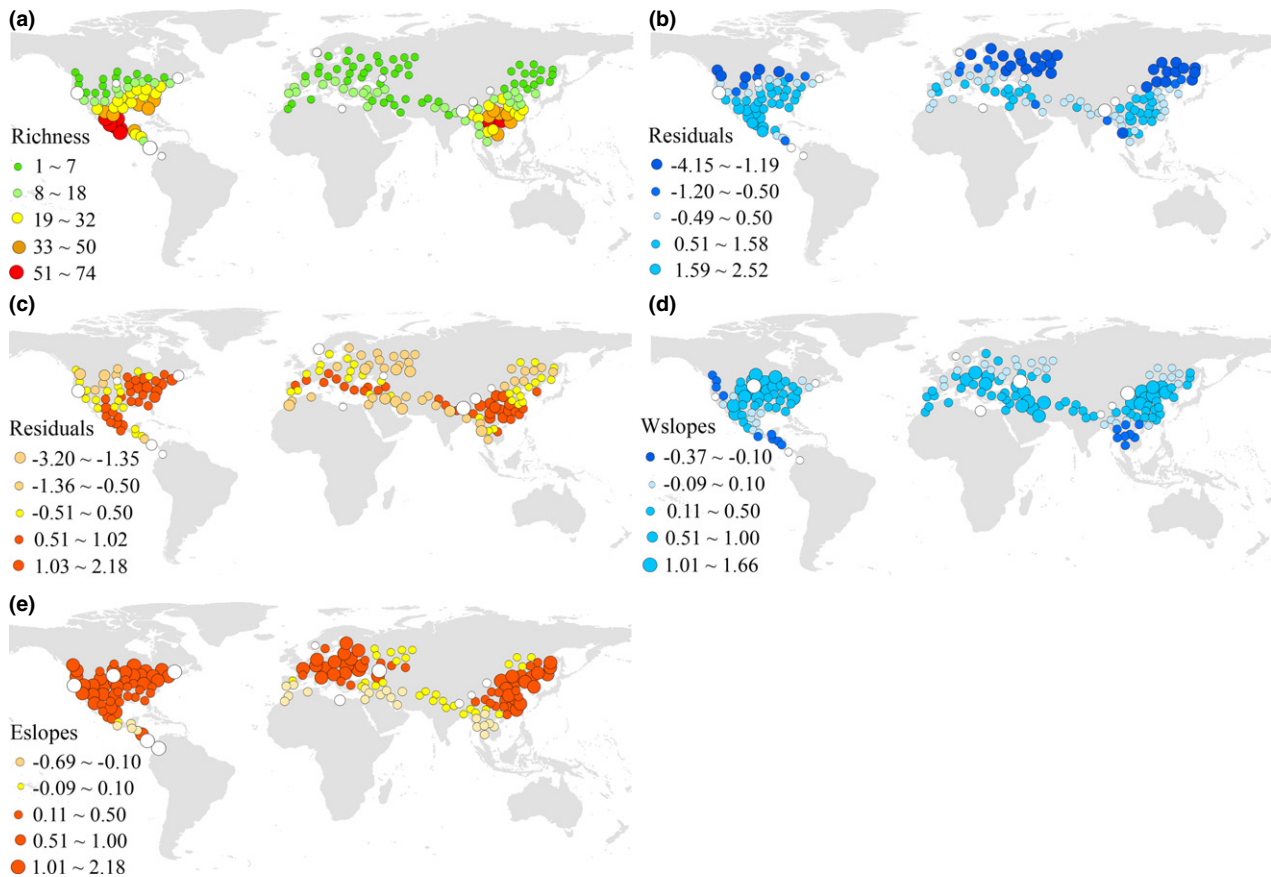
Figure 2 Global patterns in oak (*Quercus* L.) species diversity in relation to climate. (a) Species diversity. Species diversity was natural-log transformed in OLS regressions. The residuals of the OLS regression between oak species diversity and water and energy availability are shown in (b) and (c) respectively. (d and e) The local slopes of water models (i.e. Wslopes) and energy models (i.e. Eslopes) evaluated using geographically weighted regressions (GWR). 'Local slopes' (in contrast to 'global slopes' of OLS regression) are referred to the slopes of each administrative division estimated by the GWR. White dots represent the localities where the absolute standard residuals were larger than 2.5 and were excluded from the following analysis.
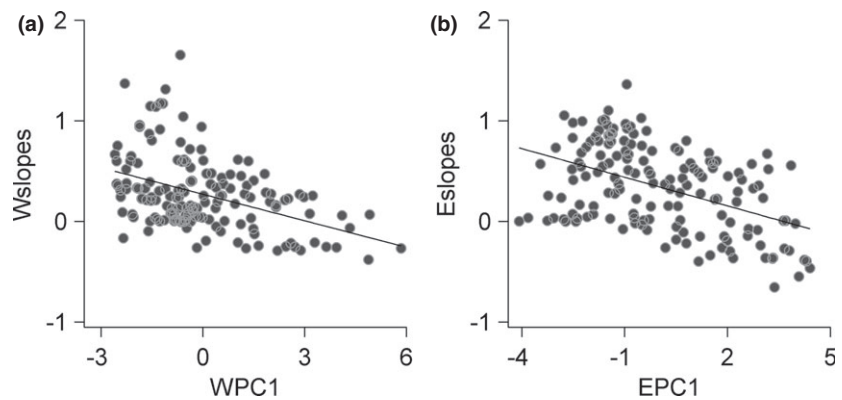

Figure 3 Local slopes of the GWR models decreased significantly ($P < 0.01$) along both water and energy gradients. (a) The local slopes of oak diversity–water relationship (Wslopes), and (b) The local slopes of oak diversity–energy relationship (Eslopes). WPC1 and EPC1, the first PC axes 1 of the PCA for water and energy variables respectively.

on oak species diversity decrease from dry and cold regions to wet and warm regions, and (2) the interaction between water and energy availability significantly influences the oak diversity–energy relationship but not the oak diversity–water relationship. Together, these results indicate that the effects of water and energy availability on oak diversity vary along

global gradients of water and energy availability, but the water × energy interaction has significant effects on only the species diversity–energy availability relationship. Because the genus *Quercus* has a broad distribution and ranges from tropical to temperate regions, our findings on the effects of water–energy interactions on diversity–climate relationships

Table 2 Analysis of variance (ANOVA) for the relationships between the local slopes of the geographically weighted regression (GWR) models for oak diversity–climate relationships and water availability (WPC1), energy availability (EPC1) and water–energy interaction (WPC1 × EPC1). Wslopes, local slopes of the GWR between oak diversity and WPC1; Eslopes, local slopes of the GWR oak diversity and EPC1. The results showed that water–energy interaction significantly influenced the changes in Eslopes.

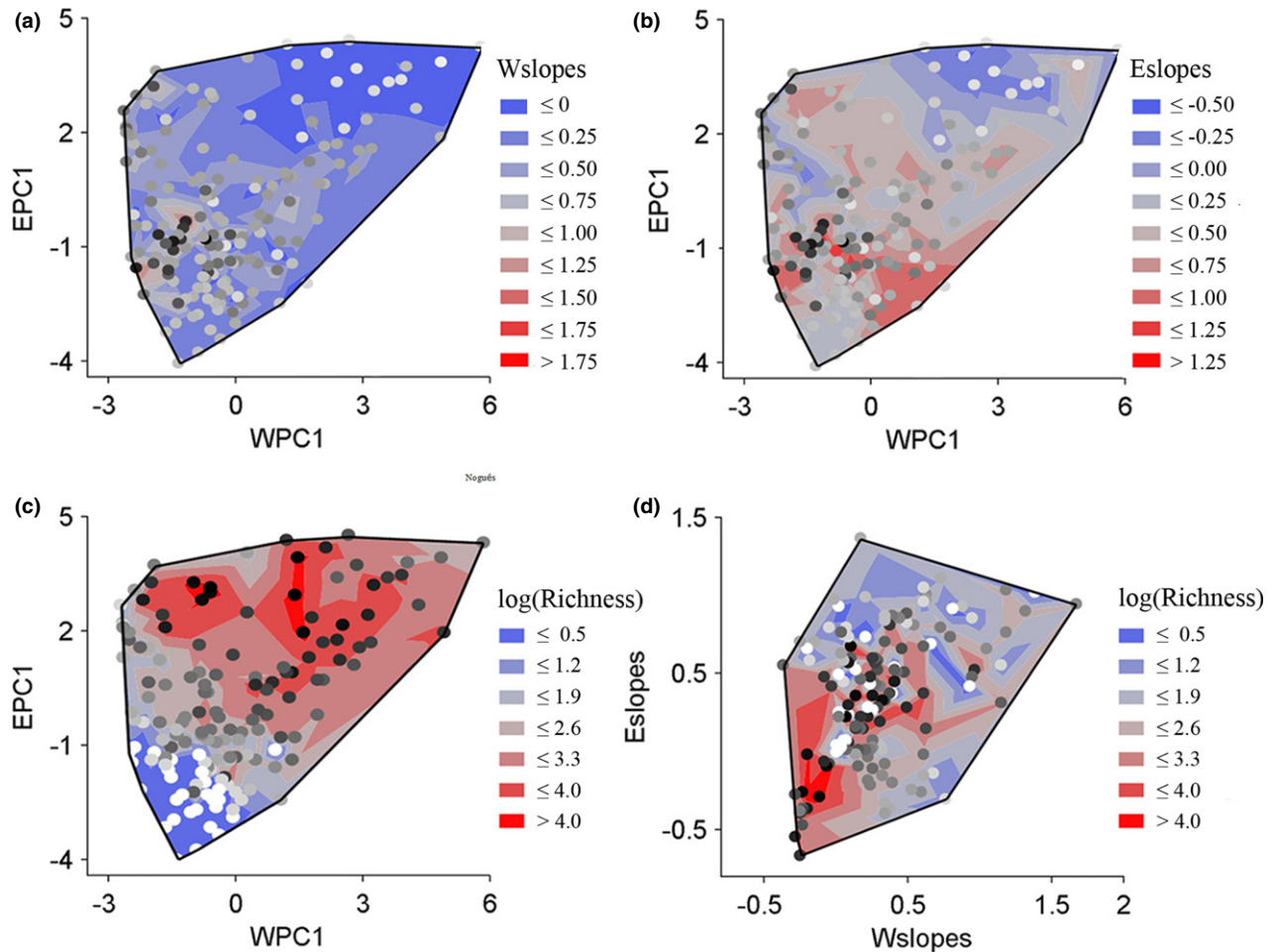| Wslopes ~ WPC1 × EPC1				Eslopes ~ EPC1 × WPC1			
Factors	d.f.	F	P	Factors	d.f.	F	P
WPC1	1	23.885	< 0.001	EPC1	1	39.262	< 0.001
EPC1	1	0.986	0.322	WPC1	1	0.056	0.813
WPC1 × EPC1	1	1.853	0.176	EPC1 × WPC1	1	1.809	< 0.001

Figure 4 Variation in local slopes of geographically weighted regression (GWR) models for oak diversity–climate relationship along water (WPC1) and energy (EPC1) gradients as shown by contour plots. (a) The local slopes for diversity–water relationship (Wslopes); (b) The local slopes for diversity–energy relationship (Eslopes). (c and d) Variation in log-transformed oak species diversity along EPC1 and WPC1 respectively.

in oaks potentially apply to similar woody taxa. However, caution is needed before extending these findings to many other plant taxa because plant lineages can of course have dramatically different evolutionary histories and physiological tolerances (Wang *et al.*, 2011; Topel *et al.*, 2012; Romdal *et al.*, 2013; Xu *et al.*, 2013).

Our results indicate that with colder temperatures (i.e. the decrease in EPC1) and increasing drought (the decrease in WPC1), the influence of water and energy availability on oak species diversity became stronger, suggesting that low temperatures and drought are critical limitations of oak species diversity. This finding is consistent with previous studies on the physiological mechanisms of species diversity patterns of both oaks and other groups (Terradas & Savé, 1992; O'Brien, 1998; Fang & Lechowicz, 2006). Physiological studies have shown that low temperature or drought can limit leaf net

photosynthesis, lead to loss of hydraulic conductivity, reduce root and radial growth, and prevent seedling recruitment (Epron & Dreyer, 1993; Cavender-Bares *et al.*, 1999, 2005; Apostol *et al.*, 2007; Cavender-Bares, 2007; Mahall *et al.*, 2009). For example, alpine trees will cease shoot and root growth when ambient temperatures are lower than 5 °C (Körner, 2012). Root growth and respiration of red oak (*Quercus rubra*) also decline with decreasing temperature (Apostol *et al.*, 2007). On the other hand, drought stress could reduce leaf size, stem extension and water-use efficiency, and cause cell damage (Farooq *et al.*, 2009). The influence of low temperatures and drought on plant physiology might have arisen from phylogenetically conservative niche evolution within this group and scaled up to shape the responses of species distributions and diversity to climate (Woodward, 1987; Terradas & Savé, 1992; Xu *et al.*, 2013). Indeed, recent studies on *Quercus* evolution have detected significant phylogenetic conservatism in both drought and cold tolerance of oak species (Niinemets & Valladares, 2006; Koehler *et al.*, 2012).

The negative diversity–water and diversity–energy relationships in regions with high levels environmental energy and water (Figs 1 & 2) might have underlying physiological mechanisms. On the one hand, warmer temperatures damage tree growth and survival in several ways. For example, warm temperatures inhibit the net assimilation rate of photosynthetic CO_2 for *Quercus pubescens* L. (Haldimann & Feller, 2004), and may then break the dormancy and lead to a phenological disorder for temperate deciduous tree species like oaks (Vitasse *et al.*, 2014). On the other hand, environmental water (e.g. floods) could deprive oxygen to plant roots, and alter belowground communities and their metabolic products (Jackson & Colmer, 2005). Therefore, heat and flood stress might be one of the physiologically limiting factors that shape the distribution of oaks in some regions.

Our results show that the variation in diversity–energy relationships was influenced by water availability. This finding is consistent with previous studies on plant distributions and diversity–climate relationships (Liu *et al.*, 2013; O'Brien, 1998; Sommer *et al.*, 2010). For example, recent studies suggest that when water and other factors are not limiting, the growth rate of four *Quercus* trees from tropical/subtropical North America are usually positively correlated with temperature, which could be one of the limitations for the northward and southward distribution of these species (Koehler *et al.*, 2012). In contrast, in the arid Loess Plateau of China, the growth of *Quercus liaotungensis* was found to be negatively correlated with spring and summer temperature (Du *et al.*, 2007). Likewise, the negative oak diversity–energy relationship in the Southern Mediterranean region as shown by our study (Fig. 2c) might also be attributed to summer drought. Unlike diversity–energy relationships, our results suggest that the variation in diversity–water relationships may not depend on energy availability, which is inconsistent with Francis & Currie's (2003) study on angiosperm family diversity. This might be attributed to the relatively high

tolerance of some *Quercus* species to water stress (Abrams, 1990) relative to other plant taxa.

Although physiological tolerance can limit species distributions and influence patterns of species diversity (Sakai & Weiser, 1973; Grace, 1987; Root, 1988; Koehler *et al.*, 2012), other processes also contribute to the spatial variation in species diversity, namely speciation, extinction and dispersal (Nilsson & Nilsson, 1978; Cain *et al.*, 2000; Primack & Miao, 2002; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007; Svenning *et al.*, 2008; Rabosky, 2010). Svenning *et al.* (2009) found that the geographical heterogeneity in plant diversity–environment relationships in Europe was affected by past climate change such that past climate change has constrained source pool size. In a non-plant example, Hortal *et al.* (2011) found that the heterogeneity in the dung beetle diversity–climate relationship was influenced by evolution in climatically stable areas and dispersal in areas subject to pronounced climatic fluctuations during the Pleistocene. Obviously we think that fundamental processes like speciation, extinction and dispersal have influenced the current distribution of *Quercus* spp. on the planet. However, the extent to which they influence the heterogeneity of oak diversity–climate relationships remains an interesting, and open, question.

In sum, we assessed the statistical effects of water and energy availability on species diversity by examining the relationships between species diversity and water/energy availability. Our results suggest that the statistical effects of water and energy on species diversity are weak in wet and warm regions but strong in dry and cold regions at global scales. However, the effects of energy availability on species diversity depended on local water availability, which suggests that the effects of future climatic warming on oak diversity could vary geographically, with especially pronounced effects in arid regions.

ACKNOWLEGEMENTS

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SUPPORTING INFORMATION

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

Appendix S1 List of oak species and their distributions.

Appendix S2 Literature used to construct the oak distribution database.

Appendix S3 Supplementary results and analyses.

BIOSKETCH

Xiaoting Xu is a postdoctral researcher at Peking University. She is broadly interested in global patterns of plant diversity and the underlying evolutionary and climatic mechanisms.

Author contributions: X.X, and Z.W. conceived the ideas. X.X. collected the data and performed data analyses. All authors contributed to the writing.

Editor: Len Gillman