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Response of pteridophyte richness to water-energy dynamic hypothesis under climate change in China

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Abstract Typical water–energy dynamics hypothesis assumes that the effects of water and energy on species richness vary geographically, and there is a latitudinal shift from water dominated to energy dominated. However, the effects of available water and energy on species richness patterns might be influenced by local climate change. In this study, geographically weighted regression was used to quantitatively analyze the relationship between pteridophyte species richness and water as well as energy. The effect of local climate conditions on richness was estimated by establishing the energy and water model. The results showed that the relationship between Chinese pteridophyte richness and water was stronger than that with energy across the country. There was no latitudinal transition line from water dominance to energy dominance in China. Furthermore, the sensitivity of pteridophyte richness to the changes in ambient climatic factors increased with the decrease in water and energy availability. Overall, pteridophyte richness is more dependent on available water than energy, and the decrease of water and energy availability is crucial for limiting pteridophyte richness. As global climate change intensifies, the threat to pteridophyte richness in cold and arid regions will become more severe, and more attention should be given to the monitoring and conservation of species diversity in these regions.

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Introduction

The mechanism controlling the large-scale distribution pattern of biodiversity is one of the most critical issues in ecological research (Gaston 2000). As one of the most important indicators of biodiversity (Willig and Presley 2018; Nagalingum et al. 2015), species richness usually presents a gradually decreasing distribution pattern from the equator to the poles (Willig et al. 2003; Gaston 2000). This latitudinal richness gradient can be observed in nearly all kinds of organisms (Willig and Presley 2018; Brown 2014). Many hypotheses have been proposed to explain this phenomenon (Willig and Presley 2018; Willig et al. 2003). These explanations have usually been centered around "historical" or "ecological" influences on the latitudinal diversity gradient of species (Brown 2014). Historical hypotheses suggest that species richness patterns are the result of past geological, climatic and evolutionary events (Ferrer-Castán et al. 2016; Qian et al. 2015; Hortal et al. 2011), most of which occurred millions of years ago or more. Ecological hypotheses, unlike historical hypotheses, assume that abiotic environmental factors (such as temperature and precipitation) on the Earth's surface, play major roles in the formation and maintenance of species richness patterns (Lobos-Catalán and Jiménez-Castillo 2019; Sosa and Loera 2017; Chen et al. 2015). Several studies have reported that species richness could be significantly affected by climate (Whittaker et al. 2007; Hawkins et al. 2003), especially water-energy dynamics (Eiserhardt et al. 2011; O'Brien 1998).

The water-energy dynamic hypothesis is one version of the energy hypothesis based on climate factors (Wang et al. 2009). It was proposed by O'Brien (O'Brien 1993) and its core principle is that large-scale patterns of species diversity can be determined by water and energy together (Hawkins et al. 2003). The energy in this hypothesis refers to heat energy (O'Brien 1993), usually expressed as temperature (Wang et al. 2009). Brown (2014) argued that temperature plays a crucial role in species diversity, with the relatively high temperatures in the tropics producing and sustaining a high diversity. Moisture is essential in the physiological activities of living organisms, for example the movement of liquid water provides the power for plants to absorb and transport nutrients (Nobel 2009). Water in plant was induced to form ice nuclear when temperatures close to 0 ℃, leading to biomembranes rupture and electrolyte leakage (Banerjee and Roychoudhury 2016, 2017). Excessive temperature could affect the physiological structure and function of plant, such as reducing photosynthetic activity by destroying PSII and thylakoid membrane (Ahmad et al. 2019), which could limit plant growth (Xu et al. 2016). The combination of water and energy determines the intensity of plant photosynthesis and biomass accumulation, which further affects the pattern of plant diversity (Xu et al. 2016). At a specific locality, water and energy usually have unequal effects on species richness. Previous studies have shown that the relative importance of water and energy on plant richness shifts from an energy dominance in cold temperate zones to a water dominance in the tropics (Whittaker et al. 2007; Hawkins et al. 2003). Eiserhardt et al. (2011) found that the species richness and distribution responded strongly to water and energy, and the explanatory power of water decreased while the explanatory power of energy increased along with latitude in American palms. It remains unclear whether such a latitudinal shift of dominant factors generally exists in terrestrial plant species. Xu et al. (2016) analyzed oak diversity data in Asia and concluded that there was no geographical transition line for water and energy dominance along the latitudinal gradient, with the relative importance of each being related to the original climate of the species. Therefore, quantifying the relative importance of water and energy on species richness is necessary to study the mechanism of water-energy dynamics on species distribution.

The sensitivity of species richness to water-energy changes may not be the same everywhere due to geographical variations in water and energy availability (Hawkins et al. 2003). Zhang et al. (2019) found that there was strong spatial heterogeneity in the sensitivity of species richness to ambient climate change in Theaceae species. Such spatial heterogeneity likely results from the significant influence of water-energy interaction on water-richness or energy-richness relationships (Francis and Currie 2003). For example, the impact of water on species diversity probably increases as the limitations of water and energy become stronger (Rangel and Diniz-Filho 2005; Janzen 1967). Xu et al. (2016) found that available water and energy interactions affected the oak diversity-energy relationship at the regional scale, but did not affect the diversity-water relationship. The effects of water and energy availability on the sensitivity of richness to climate change may vary widely in different taxa because of the different physiological tolerance limits to water and energy in species (O'Brien 2006, 1998; Currie et al. 2004).

Pteridophytes (i.e., ferns and fern allies) can be used as a suitable taxon to analyze the role of water and energy in determining species richness gradients (Qian et al. 2012). Compared with most terrestrial vertebrates and seed plants, the distribution of pteridophytes is considered to have greater consistency with current climatic balances (Aldasoro et al. 2004). There are obvious differences in pteridophyte species richness with variations in the surrounding environment (Kreft et al. 2010). Due to various climatic conditions and high species diversity, China is considered an ideal region for studying broad-scale richness-environment relationships. About 2300 pteridophyte species have been recorded in China (The Biodiversity Committee of Chinese Academy of Sciences 2008), accounting for nearly one-fifth of the global total, which is around 12,000 species (Aldasoro et al. 2004). In recent decades, a large number of floristic inventories have been conducted throughout China (Chen et al. 2011). These investigations have produced an abundance of data that can be used to accurately describe the spatial distribution patterns of pteridophytes in China and support for the statistical analysis of the relationship between species richness and environment. Therefore, pteridophytes were used to distinguish the effects of water and energy availability, as well as their interactions, on the species richness pattern in this study. Our aims were to: (1) quantify the relative importance of water and energy on pteridophyte species richness in China; (2) determine whether there was a latitudinal transition from water dominance to energy dominance; and (3) clarify how water and energy affect the sensitivity of pteridophyte richness to climate change.

Materials and methods

Species presence and climatic data

In this study, pteridophyte species distribution across China was compiled from the published lists of species in the national nature reserves of China (http://www.papc.cn/html/folder/13100752-1.htm, accessed in January 2018). Nature reserves are suitable locations for studying the relationships between plant species richness and climatic variables, due to their high biodiversity and weak human influence (Zhang et al. 2017). The complete species lists in the nature reserves are carried out regularly by professional botanists who are asked to collect data, which makes it possible to obtain accurate local species richness data (Pyšek et al. 2002). In this study, 116 national nature reserves were initially examined, among which 63 reserves containing pteridophytes were selected. To avoid disturbances from abnormal data, nature reserves including less than 10 kinds of pteridophyte species were removed from the study. Finally, a total of 48 eligible natural reserves were selected for analysis (Table S1).

To test the effects of available water and energy on species richness, a suite of frequently used water and ambient energy variables was selected (Zhang et al. 2019). These climatic variables included 19 bioclimatic predictors (1950–2000), which were obtained from the WorldClim database (http://www.worldclim.org/), with a spatial resolution of 2.5 × 2.5 arc minutes. Bioclimatic variables, which are calculated from the monthly temperature and rainfall values, are commonly used in researches about species distribution model and other ecological models. Among these predictors, 11 climate factors such as annual mean temperature (Bio01) were used to characterize available energy, and the other 8 factors represent water availability (Table 1). To match the species distribution data, the "Extract by Mask" function in ArcGIS 10 was used to extract climate variable values based on the midpoint of longitude and latitude for each nature reserve (Tables S2, S3). Principal component analysis (PCA) was performed using the water and energy variables (19 bioclimatic predictors) to avoid collinearity among variables. The first axes for both energy (EPC1) and water variables (WPC1) were extracted according to the broken-stick stopping rule (Jackson 1993).

Table 1 The loadings and cumulative sum of variance of the first two principal components (PC) in the principal component analysis (PCA) of energy and water predictors

Climatic variables	Code	PC1	PC2
Energy			
Annual mean temperature	Bio01	0.993	0.050
Mean diurnal range	Bio02	−0.738	−0.358
Isothermality	Bio03	0.312	−0.823
Temperature seasonality	Bio04	−0.798	0.594
Max temperature of warmest month	Bio05	0.650	0.695
Min temperature of coldest month	Bio06	0.990	−0.107
Temperature annual range	Bio07	−0.888	0.412
Mean temperature of wettest quarter	Bio08	0.692	0.518
Mean temperature of driest quarter	Bio09	0.977	−0.193
Mean temperature of warmest quarter	Bio10	0.776	0.605
Mean temperature of coldest quarter	Bio11	0.977	−0.207
Cumulative sum of variance		67.69%	90.79%
Water			
Annual precipitation	Bio12	0.983	0.127
Precipitation of wettest month	Bio13	0.895	0.403
Precipitation of driest month	Bio14	0.925	−0.353
Precipitation seasonality	Bio15	−0.846	0.373
Precipitation of wettest quarter	Bio16	0.908	0.397
Precipitation of driest quarter	Bio17	0.924	−0.359
Precipitation of warmest quarter	Bio18	0.813	0.506
Precipitation of coldest quarter	Bio19	0.925	−0.309
Cumulative sum of variance		81.67%	95.17%

Statistical analysis

Ordinary least square (OLS) regression and geographically weighted regression (GWR) were used to examine the relationships between pteridophyte species richness and climate variables. The OLS regression assumed a global relationship between the species richness and predictors over geographical space (Jetz et al. 2005). This relationship was stationary and constant. In contrast, the GWR could evaluate the spatial variation in the richness–energy and richness–water relationships (Svenning et al. 2009; Keil et al. 2008).

GWR was used to explore the relationships between species richness and energy as well as water for pteridophytes in China. In the GWR models, the local r^2 values represented the local explanatory power of energy (r_E^2) or water (r_W^2) on pteridophyte richness at specific localities. The difference between energy and water r^2 was calculated as follows:

$$r_{diff}^2 = r_E^2 - r_W^2 \quad (1)$$

where r_{diff}^2 means the relative importance of energy and water in shaping species richness in different localities. For a given locality, the contribution of energy and water to the species richness pattern was considered to be similar when the values of r_{diff}^2 were between − 0.05 and 0.05 (Xu et al. 2013). When $r_{diff}^2 > 0.05$, energy was the most important factor controlling species richness patterns, while $r_{diff}^2 < -0.05$ indicated that water played the dominant role.

The local slope value for each specific nature reserve estimated by the GWR represented the statistical effects of local climatic conditions on richness and denoted how many species would be gained or lost via changes in a unit of energy or water availability (Xu et al. 2016). The local slope values were calculated by establishing the GWR energy and GWR water model, and were recorded as Eslopes and Wslopes, respectively. Linear models were then used for the regression analysis of Wslopes against WPC1 and Eslopes against EPC1. To determine the interaction of energy and water on richness–energy (or richness–water) relationships at the local scale, two other linear models were constructed using Eslopes (or Wslopes) as dependent variables, and EPC1, WPC1, and their interactions as the independent variables in the models (Zhang et al. 2019). The results of the influence of energy and water interaction on pteridophyte species richness were shown using contour plots.

To assess whether the area of nature reserves might have potential bias the relationships between pteridophyte species richness and climate variables, GWR models including and excluding area were constructed for the species richness–climate relationship. The result showed that area was not a significant predictor for species richness because the difference in the corrected Akaike information criterion (AIC_c) value was <3 (Xu et al. 2013) (Table S4). Therefore, area was excluded from the analysis.

The PCA analyses and linear models were conducted in SPSS 13.0. The OLS and GWR analyses were conducted and maps were created in ArcGIS 10. The contour plots were generated with JMP 13.

Results

Geographical patterns of climate variables and species richness

The proportion of variance explained by the first axis was 67.69% for energy groups and 81.67% for water groups (Table 1). The annual mean temperature (Bio01) had the largest positive loading on EPC1, and the annual precipitation (Bio12) having the largest positive loading on WPC1. This suggested that energy and water availability increased with the increasing values of EPC1 and WPC1, respectively. A trend was observed, in which energy availability decreased with increasing latitude in the geographical patterns of EPC1 (Fig. 1a). The spatial pattern of WPC1 showed that water availability was negatively related to the distance from the ocean (Fig. 1b).

Pteridophyte species diversity was highest in the tropical and subtropical areas of China, and presented a decreasing trend northward (Fig. 2a). Pteridophyte richness was higher in the mountainous ecozones in southern China and lower in the Inner Mongolia Plateau and arid areas of northwestern China. The species diversity of pteridophytes was associated with available energy ($R^2_{adj}=0.49$) and water ($R^2_{adj}=0.53$) in the OLS results. The spatial variation of energy ($R^2_{adj}=0.63$) and water ($R^2_{adj}=0.66$) had better explanatory power on the pattern of pteridophyte species diversity in the GWR results. There were significantly higher values of R^2_{adj} in the GWR models than in the OLS models, and the AIC_c values in the GWR models were significantly smaller than in the OLS models (Table 2). Furthermore, there were clear geographical patterns of residuals in the OLS models, indicating that the relationships between richness and energy, and richness and water had an obvious spatial heterogeneity (Fig. 2b, c). Thus, the results of the GWR models were retained for further analysis.

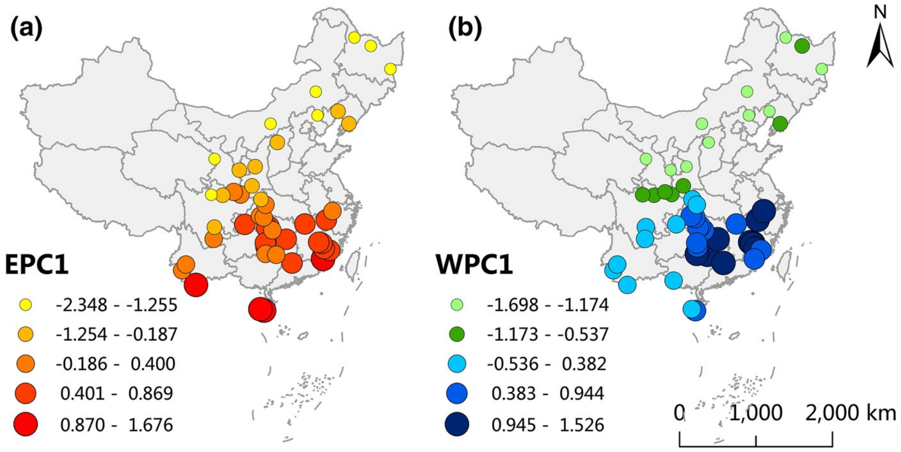

Fig. 1 The first axes of the principal component analysis (PCA) for **a** energy variables (EPC1) and **b** water variables (WPC1)

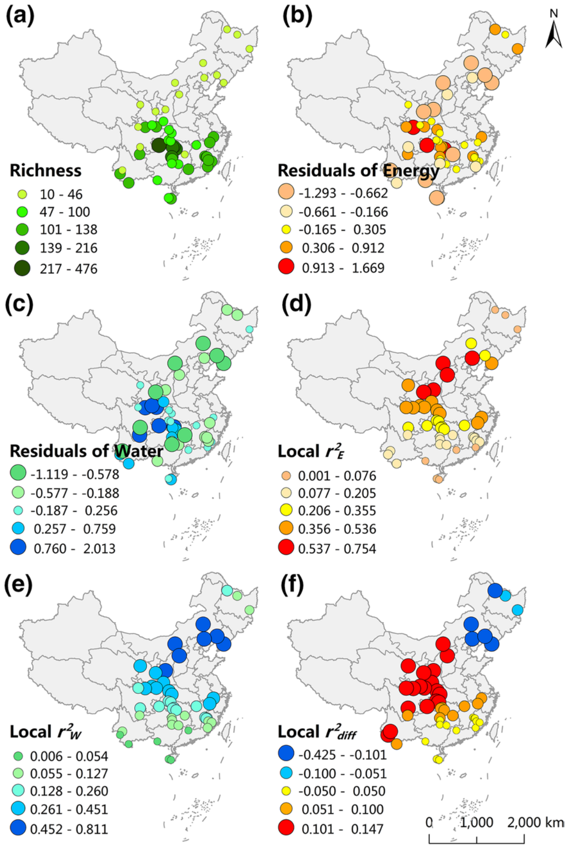

Fig. 2 The pattern of pteridophyte richness in relation to climate. **a** Species richness of pteridophytes in Chinese national nature reserves. The residuals of the OLS regression between pteridophyte richness and available energy (**b**) and water (**c**). Species richness was natural logarithm transformed in the OLS regressions. The geographical variation of local r^2_E values for energy and local r^2_W values for water are shown in (**d**) and (**e**), respectively, and the differences (r^2_{diff}) between water and energy models for pteridophytes are shown in (**f**). The size of the dots indicates the strength of the GWR models in (**d**) and (**e**). In **f**, the colours of the dots indicates whether the effects of water limitation (blue) or energy limitation (red) predominates (yellow suggests that water and energy contribute equally to species richness)

Table 2 Corrected Akaike information criterion (AICc) values of the ordinary least-squares (OLS) regressions and geographically weighted regressions (GWR) for pteridophyte species richness—climate models

	Richness-energy model	Richness-water model
OLS	99.27	95.12
GWR	88.70	87.56

Explanatory power of water and energy for species richness

It was found that the explanatory power of energy (r^2_E) and water (r^2_W) for pteridophyte richness varied with the distribution of available water and energy (Fig. 2d, e). Both of them generally showed a higher trend of explanatory power with increasing latitude, except for northeast China. The values of the local r^2 were between 0 and 1, with a higher value indicating stronger explanatory power for pteridophyte richness. At the national scale, the explanatory power of energy for pteridophyte richness ranged from 0.001 to 0.754 (Fig. 2d), while the explanatory power of water for pteridophyte richness ranged from 0.006 to 0.811 (Fig. 2e). The local r^2_{diff} values between $-$ 0.050 and 0.050 were noticed in southern China (Fig. 2f), meaning that water and energy contributed equally to species richness in this region. The local r^2_{diff} increased from 0.051 to 0.147 from southeast coast to northwest inland, indicating that the relative importance of energy to pteridophyte species richness increased gradually (Fig. 2f). The local r^2_{diff} values ranged from $-$ 0.051 to $-$ 0.425 in northeast China (Fig. 2f), indicating that water was predominate variable contributing to pteridophyte richness in this area. In GWR models, there was no latitudinal transition zone of water–energy for pteridophytes.

Effects of water-energy on the sensitivity of richness to climate change

The local slopes of the richness-energy (Eslopes) and richness-water (Wslopes) relationships could reflect the sensitivity of species richness to ambient climate change. There was a significant spatial variation in Eslopes and Wslopes (Fig. 3a, b). The results supported the expectation that water availability (WPC1) considerably influenced the richness-water (Wslopes) relationship. In particular, Wslopes values decreased significantly with increasing WPC1 (Fig. 4a, $P < 0.05$). Similarly, energy availability (EPC1) also affected Eslopes (Fig. 4b). The water×energy interaction significantly influenced the changes in Eslopes (Table 3), suggesting that Eslopes would be greatly influenced by WPC1 during the decrease along the EPC1 gradient. Unlike Eslopes, the water×energy interaction had no effect on Wslopes, indicating that the decrease

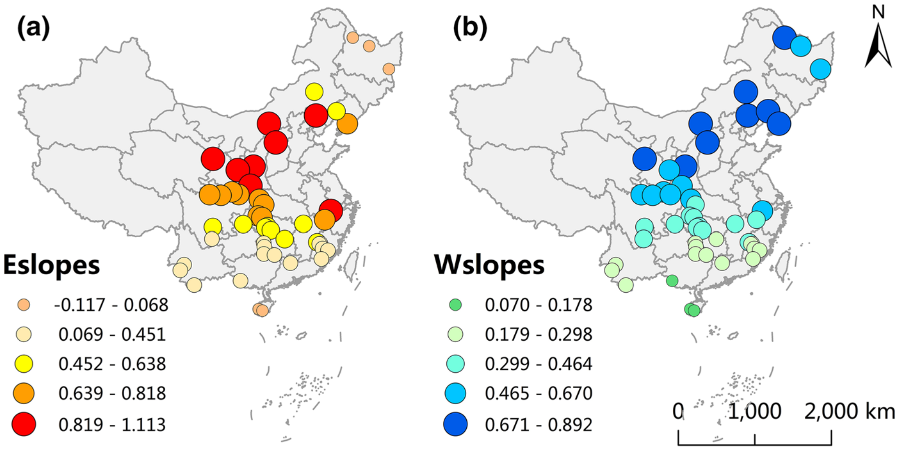

Fig. 3 The local slope values for a specific nature reserve estimated by the **a** GWR energy model (Eslopes) and **b** GWR water model (Wslopes)

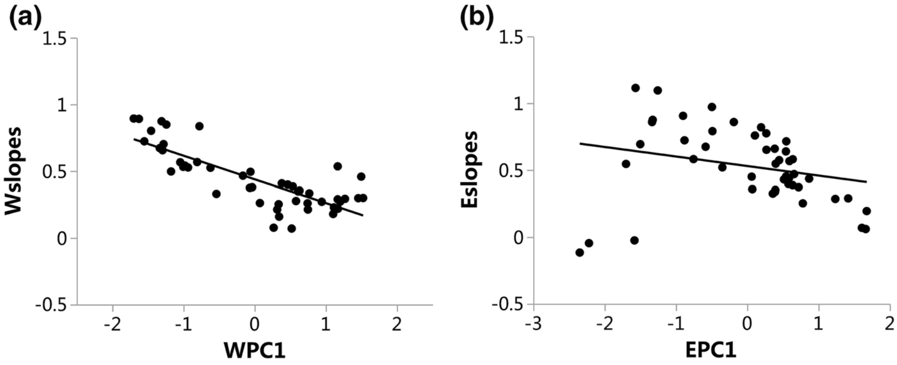

Fig. 4 Local slope values of the GWR models decreased along both water and energy gradients. **a** The local slopes of the pteridophyte richness-water relationship (Wslopes), and **b** the local slopes of richness-energy relationship (Eslopes)

Table 3 The relationships between local slope values in pteridophyte richness-climate GWR models and available water (WPC1), available energy (EPC1) as well as the water-energy interaction (WPC1 × EPC1) were analyzed with a variance analysis. Wslopes and Eslopes were the local slopes of pteridophyte richness-water and richness-energy relationships, respectively

Wslopes–WPC1 × EPC1				Eslopes–EPC1 × WPC1			
Factors	d.f	*F*	*P*	Factors	d.f	*F*	*P*
WPC1	1	9.194	0.004	EPC1	1	1.526	0.223
EPC1	1	13.555	0.001	WPC1	1	2.374	0.131
WPC1 × EPC1	1	0.053	0.820	EPC1 × WPC1	1	6.894	0.012

of Wslopes along with WPC1 gradient would not be affected by EPC1 (Table 3). The Wslopes values were highest in dry areas (Fig. 5a). With an increase in available water, Wslopes values gradually decreased and the lowest value was reached in hot and wet regions. In dry and cold conditions, the Eslopes values decreased faster than in other areas (Fig. 5b). Pteridophyte species richness was higher in areas with more sufficient water and energy (Fig. 5c). The pteridophyte richness reached a peak when the availability of both energy and water was high, and where the local slopes of the GWR water model were relatively low (Fig. 5d).

Discussion

The relative importance of available energy and water for pteridophyte species richness was evaluated

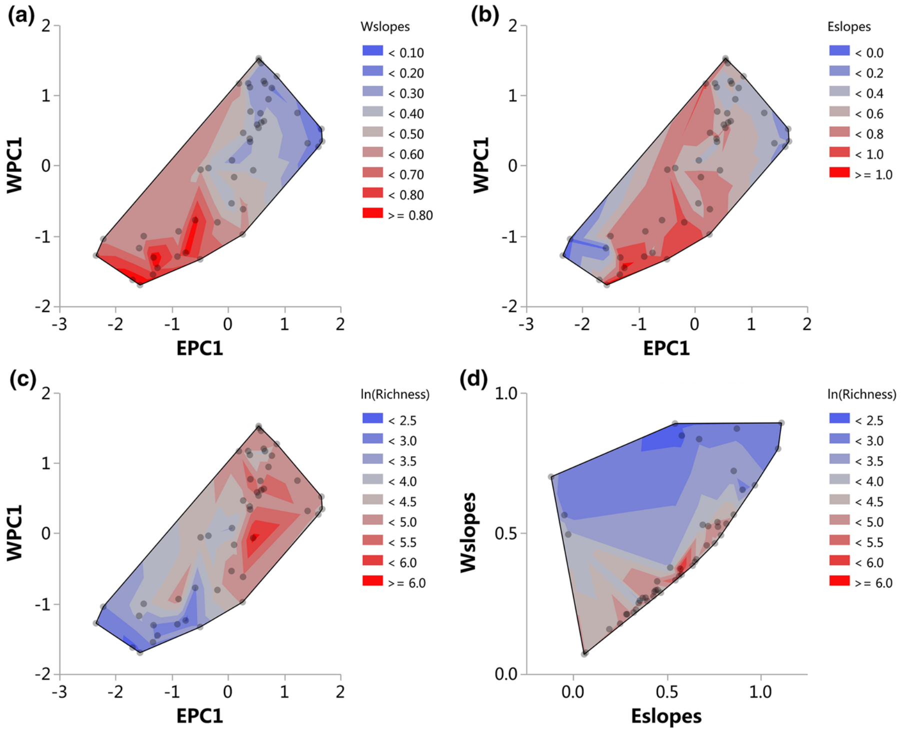

Fig. 5 Variation of the local slopes for the pteridophyte richness–climate relationship in GWR along water (WPC1) and energy (EPC1) gradients. **a** The local slopes for the richness–water relationship (Wslopes); **b** The local slopes for the richness–energy relationship (Eslopes); **c** Variation of pteridophyte species richness along the EPC1 and WPC1 gradients; **d** Variation of pteridophyte species richness along the Eslopes and Wslopes gradients

through the analysis of the pteridophyte species diversity pattern. Several aspects of the species distribution were apparent: (1) the number of pteridophyte species in the southern regions was higher than that in the north, and pteridophytes preferred to live in the environments with sufficient rainfall and moderate temperature; (2) in general, the distribution pattern of pteridophyte species diversity in China was more obviously affected by water availability than energy; (3) there was no geographical transition zone indicating the relative dominance of water and energy along latitude for pteridophytes; (4) pteridophyte species richness was most sensitive to water and energy availability changes in arid environments. This study supported the relationship between the richness of regional pteridophyte species and local climate variables, and the relationship varies geographically along environmental gradients. Regions with the highest pteridophyte species richness do not exactly coincide with the tropics where have the most energy (Kreft et al. 2010; Aldasoro et al. 2004), although tropics are generally considered to be the most biologically diverse regions on Earth (Brown 2014).

Pteridophytes tend to grow in warm and moist forest environments which often have good water and energy conditions. The geographical distribution of pteridophytes in China is uneven, and the number of pteridophytes in each nature reserve varies greatly (Fig. 2a). The pteridophyte diversity in China was highest in tropical and subtropical regions, and decreased with increasing latitude. It has been observed in previous studies that pteridophyte species richness peaks in warm and wet forests (Qian et al. 2012; Kreft and Jetz 2007). Chen et al. (2011) found that fern species richness decreased with increasing latitude. Temperature is usually the main climate variable that changes with latitude (Aldasoro et al. 2004), with the overall radiant energy increasing gradually as the latitude decreases. Zhao and Fang (2006) found that the relationships between pteridophyte species richness and mean annual temperature was more positive than the corresponding relationships for gymnosperms and angiosperms at the national scale. It could be inferred that the distribution of pteridophytes was more likely to be affected by environmental energy than that of seed plants, because the energy model of ferns had 49.2% explanatory power, whereas it only had 33.4% for seed plants in a previous study (Chen et al. 2011). The positive relationship between radiation and pteridophyte diversity suggested that available energy was a limiting factor (Weigand et al. 2020; Khine et al. 2019), conforming to the species-energy hypothesis. Several studies have pointed that more sufficient energy could support higher productivity (Khine et al. 2019; Brown 2014). Kessler et al. (2014) found positive links between fern species richness and both the number of fern individuals and fern productivity at the regional scale, which was probably due to the increasing number of fern individuals and niche availability. However, radiation alone is not sufficient to explain the distribution mechanism of pteridophyte species diversity. In this study, the energy input of northeast China was lower than that of north China (− 1.496 vs − 1.460), but the pteridophyte species number in the former region was higher than in the latter (21.40 vs 14.25) (Fig. 1a; Table S1). Therefore, energy alone was not the main predictor of pteridophyte richness (Zhao and Fang 2006), and other influencing factors need to be considered.

Water seemed to have a greater effect on pteridophyte species diversity than energy. In this study, the effect of water (0.006–0.811) on pteridophyte richness was greater than that of energy (0.001–0.754) in China. Similar results were found in Australia, where variables of water availability were more correlated with pteridophyte richness than available energy variables (Bickford and Laffan 2006). Another study of ferns in China showed that the water model could explain 63.5% of the pteridophyte richness, which was more powerful than the energy model (51.3%) (Chen et al. 2011). Qian et al. (2012) suggested that annual precipitation was more important than mean annual temperature in determining pteridophyte species richness. Previous research has shown that water-related variables (including single water and water-energy balance) performed higher correlations with pteridophyte richness, while variables only reflecting energy had little effects on pteridophyte richness around the world (Kreft et al. 2010). Pteridophytes show a strong dependence on water because their gametophytes and sporophytes generally need water to survive and reproduce (Hernández et al. 2013). They are dependent on liquid water for fertilization and the process needs a water film of sexual fertilization by the free-motile spermatozoids (Qian et al. 2012). Another possible reason for the strong water dependence is that the lack of vascular tissue in the small gametophytes of pteridophytes results in poorly developed or non-existent cuticles, restricting their ability to store water internally (Kreft et al. 2010). Because of quite dependent on water during their life cycle (Nagalingum et al. 2015), pteridophyte distribution is particularly limited by ambient water availability (Bickford and Laffan 2006).

In this study, it was found that there was no obvious water-energy conversion zone along latitude (i.e., Hawkins' conjecture (Xu et al. 2013) in the distribution pattern of pteridophyte species diversity (Fig. 2f). There was an obvious pattern of limited pteridophyte diversity in the central arid interior regions of the continent, while there were hot spots in the humid tropical areas, which agreed with the results of previous studies of the large scale distribution of pteridophytes (Nagalingum et al. 2015; Qian et al. 2012; Chen et al. 2011; Kreft et al. 2010). With the enhancement of drought, the effects of water and energy availability on pteridophyte species richness gradually increased (Fig. 2d, e). The typical water-energy dynamics hypothesis is that the influence of water decreases while the importance of energy becomes more significant with increasing latitude at the global scale (Hawkins et al. 2003). An analysis of species richness in five European taxa (plants, mammals, birds, amphibians, and reptiles) also found a shift from water to energy variables, supporting the proposition that water was more limiting in southern Europe, while energy was the limiting factor in the north (Whittaker et al. 2007). However, some studies have suggested that the ancestral climatic niche influences the relative importance of water and energy in species richness patterns. Xu et al. (2013) investigated the differences in water-energy dynamics between two subgenera of Asian oak with different evolutionary histories, and concluded that the departure of contemporary climate from their ancestral climatic niches significantly affected species richness. A previous study of Theaceae species originated in warm environments found that the species distribution pattern was mainly due to the increase in frost filtration intensity for tropical species along with latitude at the regional scale (Zhang et al. 2019). Whether water or energy dominates during the spread of pteridophytes from tropical and subtropical to temperate zones depends on the availability of water and energy in the surrounding environment. It could be inferred that this is related to the evolutionary history of pteridophyte species. Pteridophytes are generally thought to have originated under tropical humid conditions; thus, it is necessary to evolve greater environmental tolerance for colonization of and diversification to other areas (Kreft et al. 2010). Nagalingum et al. (2015) found these adaptations in only two of the 89 genera examined in a study of Australian ferns. This pattern also fits the niche conserved hypothesis, in which the species richness of clades decreased with the deviation of environmental climatic conditions from the ancestral climatic niche (Qian et al. 2015; Hortal et al. 2011).

The results also showed that the sensitivity of pteridophyte richness to climate change was enhanced with decreasing water and energy availability (Zhao and Fang 2006), and species richness was most affected by ambient climate change in low temperature and drought conditions. Xu et al. (2016) mapped the global distribution pattern of oaks and found that the species richness due to a unit variation in water or energy availability increased significantly as available water and energy decreased. A study analyzing pteridophyte richness showed that the response of plants to climate was strongly influenced by the interaction of energy and water (Qian et al. 2012). From a plant physiology perspective, that is probably because low temperature or drought could limit net photosynthesis in leaves, resulting in a decrease in leaf size, stem extension, and water use efficiency (Anderegg and HilleRisLambers 2016). At the same time, pteridophytes are extremely dependent on water because of their own physiological characteristics. Temperatures too high or too low could limit the efficiency of water use in pteridophytes. There is a consensus that climate factors are more closely related to pteridophyte species richness than that of seed plants (Tanaka and Sato 2014). In a study of African ferns, it was found that the fern distribution agreed with the recent climate evolution data in Africa (Aldasoro et al. 2004). Our results showed that water variations could cause dramatic changes in species richness in arid regions. With an increase of available water, the sensitivity of pteridophyte diversity to water changes decreased. In addition, pteridophyte species diversity was also very strongly linked to energy changes under extremely dry and cold conditions. Therefore, the risk of local extinction for pteridophytes in arid and cold inland areas will increase with more intense climate change. It is necessary to carefully consider the impact of climate change on species diversity in these areas and to strengthen conservation measures where needed.

Conclusion

In this study, geographically weighted regression was used to accurately quantify the relative importance and statistical effects of water and energy availability on pteridophyte richness in Chinese nature reserves, and the relationship between water and energy interactions and the pteridophyte diversity pattern was clarified on a broad scale. It was found that the effects of energy and water on pteridophyte richness had spatial heterogeneity, and water had more explanatory power than energy. In addition, the sensitivity of pteridophyte diversity to climate change gradually increased with the enhancement of drought severity. These results suggested that the water-energy dynamics could explain the pteridophyte species richness in China, and pteridophytes tended to live in areas similar to their ancestral climatic niches. Against the background of global climate change, drought may lead to an increased risk of local pteridophyte extinction, and global warming could have an adverse effect on species diversity, especially in arid areas.

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Data availability The pteridophyte species distribution data are available from the published lists of species in the national nature reserves of China (http://www.papc.cn/html/folder/

13100752-1.htm). The climatic variables data are available from the WorldClim database (http://www.worldclim.org/).

Declarations

Conflict of interest The authors declare no competing financial interests.

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