forests

Article

Relationships between Plant Species Richness and Terrain in Middle Sub-Tropical Eastern China

Chuangye Song [1,*] and Mingchang Cao [2]

[1] Institute of Botany, Chinese Academy of Sciences, Nanxincun 20, Haidian, Beijing 100093, China
[2] Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection, Jiangwangmiao Street 8, Xuanwu, Nanjing 210042, China; caoming@163.com
* Correspondence: songcy@ibcas.ac.cn

Academic Editor: Timothy A. Martin
Received: 16 June 2017; Accepted: 4 September 2017; Published: 14 September 2017

Abstract: The objective of this research was to study the relation between species richness and topography in the middle sub-tropical area of Eastern China. A species richness survey was conducted along altitude in Kaihua County, Zhejiang Province, Eastern China. Topographic variables, such as altitude, slope, aspect, terrain roughness, relief degree and the topographical wetness index, were extracted from the digital elevation model. The Generalized Additive Model (GAM), the linear model and the quadratic model were used to fit response curves of species richness to topographic variables. The results indicated that altitude and the topographical wetness index have a significant relation to species richness. Species richness has a unimodal response to altitude and a linear response to the topographical wetness index. However, no significant correlations were observed between slope, aspect and species richness. The predicted species richness by GAM is significantly correlated with the observed species richness, whereas the prediction error tends to increase with the increment of species richness. This study furthered insights into the relationship between topography and plants' diversity in the middle sub-tropical area of Eastern China.

Keywords: evergreen broad-leaf forest; altitude; slope; aspect; topographic wetness index

1. Introduction

Species richness is one of the important biodiversity measures [1]. The relation between species richness and the influencing factors has always been one of the focuses in biodiversity and ecology research [1,2]. Topography was regarded as the important factor for governing the biodiversity pattern at landscape and regional scales [3–5]. Topographic variables, such as altitude, slope and aspect, were often used as predictors to analyze the biodiversity-topography association [6–10]. In recent years, instead of incorporating topographic metrics as predictors to analyze the relationship between species richness and topography, geodiversity was used as a comprehensive indicator to represent environmental heterogeneity [11–13]. Although geodiversity was considered as an important correlate of biodiversity at regional and landscape scales [11,12,14] and contributed more than topographic variables accounting for species richness [13], the limitation of data availability influenced the widespread application of geodiversity in biodiversity and ecology research. Topographic variables still possess great value in biodiversity pattern analysis [11].

Numerous research works were conducted to study the relation between species richness and topography at the regional scale. However, there still exist conflicting views on the relations between species richness and topographic variables. For example, at least three patterns of species richness along altitude were reported: negative [6,15], positive [16,17] and hump-shaped [7–10,18]. Recently, some research works provided quantitative proof to underpin positive Environmental Heterogeneity (EH) -species richness relationships across EH subject areas, habitat types, taxonomic groups and spatial scales [19,20]. Some research works presented explanations of the negative and humped EH-species richness relationships. They considered that fragmentation might be the driver of negative and humped EH-species richness relationships [21,22]. Given the complexity and context dependence of the EH-species richness relationship, more attention should be paid to assess the influences of the spatial grain and spatial extent on the EH-species richness relationship in further studies [19], and more comparative studies should be performed across more habitats, particularly in tropical and arid regions, to analyze the influences of EH on species richness [19,23]. Furthermore, non-linear statistical approaches are required to better understand EH-species richness relationships [19].

The evergreen broad-leaf forest of the sub-tropical area is a regional vegetation of China. It is one of the most important biodiversity centers of the globe. However, due to the long-term human disturbance, the area of evergreen broad-leaf forest in China dropped greatly in the past decades [24]. Species diversity conservation of evergreen broad-leaf forest has become among the crucial actions of biodiversity conservation and maintenance in the sub-tropical area of China. Kaihua County lies in the west of Zhejiang Province, Eastern China. There still exist a large area and well-protected evergreen broad-leaf forest in this county, especially evergreen broad-leaf forest dominated by *Castanopsis eyrei*. In recent years, Kaihua County was selected as the experimental area of ecological function conservation by Zhejiang Province and the Ministry of Environmental Protection, China. Furthermore, Kaihua County was approved as an experimental county of national park construction by the National Development and Reform Commission, China. Therefore, the conservation of ecology and biodiversity has become the most important issue for Kaihua County. In this research, based on the generalized additive model, and the digital elevation model, we studied the relation between the species richness and the topographic variables of evergreen broad-leaf forest in Kaihua County and predicted the spatial distribution of species richness. This will help us to explore the characteristics of the evergreen broad-leaf forest in the middle sub-tropical area of Eastern China. This research will also help us to make a scientific assessment of the evergreen broad-leaf forest and provide a theoretical basis for the effective and sustainable management of vegetation and biodiversity in the middle sub-tropical area of Eastern China.

2. Study Area

Kaihua County (28°54′–29°30′ N; 118°01′–118°37′ E) is located in the west of Zhejiang Province, Eastern China (Figure 1). It is the source area of the Qiantang River. It was recognized as one of nine important ecological function regions in the Qiantang River basin by Zhejiang Province, China.

There exists the primary evergreen broad-leaf forest of the middle sub-tropical area in Kaihua County. The forest has the characteristics of complex structure, old origin, species richness and unique flora. It is the important ecological function region of the hilly area in the west of Zhejiang Province and the ecological barrier for Eastern China. It also provides important ecological services, such as biodiversity maintenance, ecological protection, soil and water conservation.

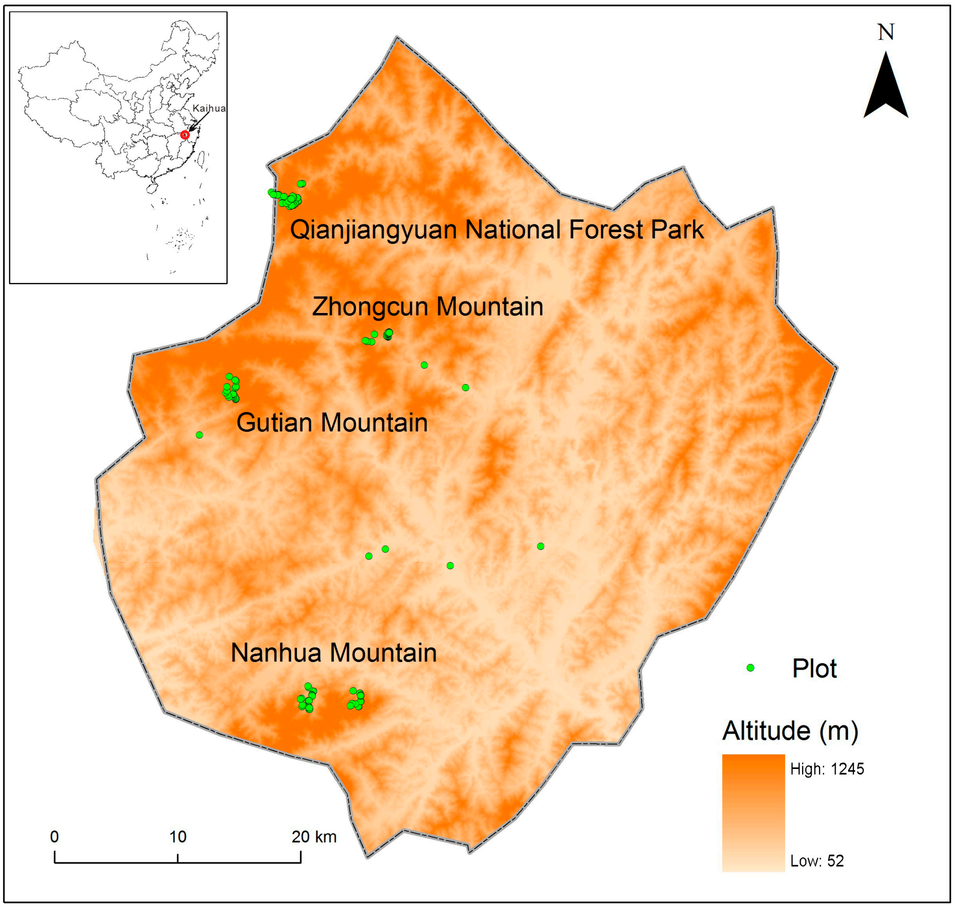

Figure 1. Location of the study area and the distribution of the surveyed plots.

3. Method

3.1. Plant Species Investigation

In this research, we selected four survey regions in Kaihua County to implement the investigation of plant species richness: Qianjianyuan National Forest Park, Gutian Mountain, Nanhua Mountain and Zhongcun Mountain. Figure 1 shows the location of Kaihua County in China and the location of the four survey regions in Kaihua County.

The plant species investigation was performed from July to October 2015. In each survey region, investigation sites were set along the altitude gradient. At each site, three to four plots (10 × 10 m) were set to make the species richness investigation. The species name and the number of plants were recorded in each plot. A total of 125 plots were investigated, and 423 species, 238 genera and 111 families were recorded. Among these 125 plots, 90 plots were randomly selected to fit the Generalized Additive Model (GAM) to portray relations between species richness and topographic variables, the remaining 35 plots were used to validate the fitted GAM.

3.2. Topographic Data

The ASTER GDEM at 30 m spatial resolution [25] (Advanced Spaceborne Thermal Emission and Reflection Radiometer, Global Digital Elevation Model, released by Japanese Ministry of Economy, Trade, and Industry and the American National Aeronautics and Space Administration) of the study area was used to calculate altitude, slope, aspect, relief degree and terrain roughness by ArcGIS software. We transformed the aspect into continuous variables (ranging from 0° to 180°) according to the approach of Wang (1997) [26]: the north slope was set as 0°, and the south slope was set as

180°, both the east and west slope were set as 90°; with the change of the aspect from north to south, the degree of aspect increased from 0° to 180°, and when the aspect changed from south to north, the degree decreased from 180° to 0°.

The Topographical Wetness Index (TWI) could provide information of the soil properties and quantify the drainage of water and air masses [27]. Therefore, TWI was selected as the predictor to explain the spatial pattern of species richness. TWI was calculated according to the following algorithm [28].

$$w = \ln(\frac{\alpha}{\tan\beta})$$

where w is the topographic wetness index, α is the area of flow accumulation and β is the slope (°).

3.3. Data Analysis

3.3.1. Correlation Analysis between Topographic Variables

In order to reduce the impacts of high correlations between pairs of topographic variables on the fitting of GAM, we set 0.7 as the maximum correlation coefficient allowed between topographic variables [29]. From Table 1, we can see that correlation coefficients between slope and relief degree, slope and terrain roughness, relief degree and terrain roughness are higher than 0.7. Therefore, the relief degree and terrain roughness were omitted in the analysis. Altitude, slope, aspect and TWI were used to perform the analysis on the relations between species richness and topographic variables.

Table 1. Correlation coefficients between pairs of topographic variables.

	Altitude	**Aspect**	**Relief Degree**	**Terrain Roughness**	**Slope**	**TWI**
Altitude	1	−0.04	−0.25 *	−0.26 *	−0.20 *	0.17
Aspect	−0.04	1	0.28 **	0.24 *	0.35 **	−0.27 **
Relief Degree	−0.25 *	0.28 **	1	0.94 **	0.95 **	−0.35 **
Terrain Roughness	−0.26 *	0.24 *	0.94 **	1	0.94 **	−0.30 **
Slope	−0.23 *	0.35 **	0.95 **	0.94 **	1	−0.35 **
TWI	0.17	−0.27 **	−0.35 **	−0.30 **	−0.35 **	1

* Correlation is significant at the 0.05 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed). TWI is the Topographical Wetness Index.

3.3.2. Analysis between Species Richness and Topographic Variables Based on Generalized Additive Model

GAM is a generalization of the classical least square regression. The link function is used to build the relation between the expected value of the response variable and the predictive variable. The mathematical formula is described as follows:

$$g(u) = \boldsymbol{\beta}_0 + \sum_{i=1}^{k} f_i(x_i)$$

where $g(u)$ is the link function, β_0 is the intercept and $f_i(x_i)$ is the non-parametric function, which is used to describe the relation between $g(u)$ and the ith predictive variable. In this research, the smoothing spline method was selected to smooth the predictive variables. The link function is log, and the family of responsible variable is a Poisson distribution. Deviance explained (D^2) and adjusted R^2 were used to test the fitness of GAM:

$$D^2 = \frac{ND - RD}{ND}$$

where ND is the null deviance, RD is the residual deviance that cannot be explained by the model and $ND - RD$ is the explained deviance. A D^2 value of 1 indicates that there is no residual deviance and that the deviance could be explained completely by the model.

In GAM, the degree of freedom of the smooth function has important influence on the parameter estimation and model stability. Therefore, the key step in model fitting is the determination of the degree of freedom of the smooth function. In this research, the deviance of generalized cross-validation was used to determine the degree of freedom and then to select the best GAM for species richness estimation. This approach is the simplification of the least mean square error.

Multi-factor GAM was fitted to describe the relationship between species richness and topographic variables. We also fitted the relation between species richness and each topographic variable by using the linear model and the quadratic model. This aims to verify the result of the fitted GAM.

3.3.3. Prediction of Species Richness Based on Generalized Additive Model

Based on the fitted multi-factor GAM, we predicted the spatial distribution of species richness in the study area. The Pearson correlation coefficient and RMSE (Root Mean Square Error) between the observed and predicted species richness were calculated to estimate the predictive ability of fitted GAM.

We also performed an analysis of the relation between the prediction error and observed species richness based on linear regression. This aimed to evaluate the performance of GAM on different areas with varied biodiversity.

4. Results

4.1. GAM Analysis on Species Richness-Topography

Tables 2 and 3 present the parameters of fitted GAM. These parameters were divided into two groups: one was the hypothesis test on the intercept (Table 2), and the other one was the hypothesis test on the smooth function (Table 3).

Table 2. Parameters of Intercept of the fitted Generalized Additive Model (GAM) between species richness and topographic variables.

	Estimate	Standard Error	*t*-value	Pr (>|z|)
Intercept	3.40	0.02	179.2	$<2 \times 10^{-16}$

Table 3. Approximate significance of smooth terms.

Smooth Terms	Edf	Ref.df	F	*p*-Value
s(altitude)	1.96	2.00	9.16	0.00033
s(aspect)	3.61	4.46	1.61	0.16
s(slope)	1.00	1.00	1.64	0.20
s(TWI)	1.00	1.00	6.67	0.01

Edf, Ref.df and TWI are respectively the Estimated degree of freedom, the Reference degree of freedom and the Topographical Wetness Index; "s" in "s(altitude)" is the symbol of spline smoothing curve.

Altitude and TWI were found to have a significant relation with species richness (Table 3) ($p < 0.05$), whereas there was no significant correlation between aspect, slope and species richness ($p > 0.05$) (Table 3). Variations of the estimated degree of freedom showed that the relation between species richness and altitude and the TWI are quite different (Table 3, Figure 2). The degree of freedom of the altitude was higher than one (Table 3, Figure 2). This indicated that there existed a non-linear relationship between species richness and altitude. The degree of freedom for TWI was one (Table 3). This means that species richness was linearly correlated with TWI (Figure 2).

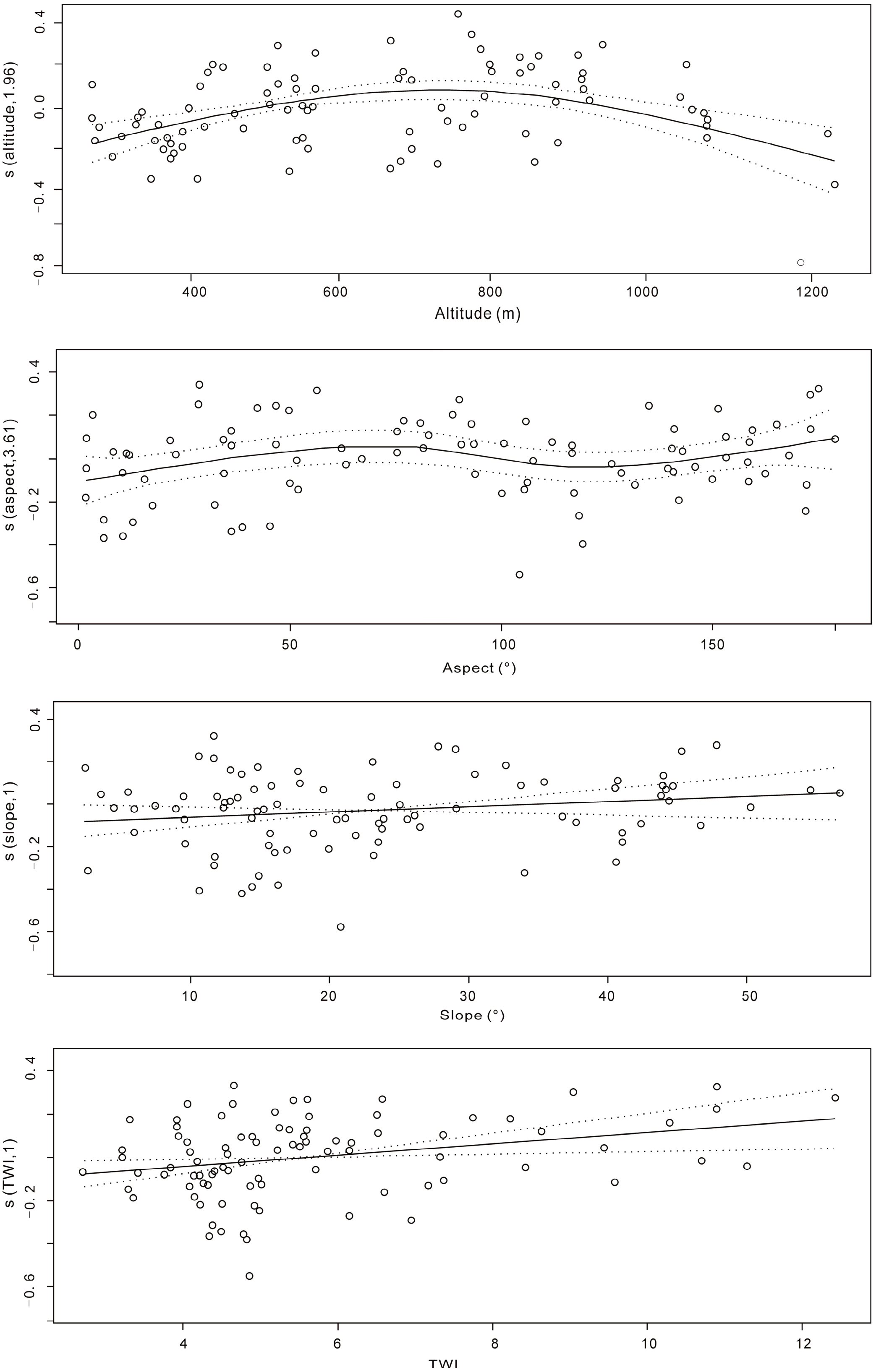

Figure 2. Estimated response curves by GAM, which portrays relations between species richness and topographic variables. Vertical axes are log scaled, based on partial residual and indicate the relative influence of the topographic variable on the estimation of species richness; s is the symbol of the spline smoothing curve; numbers in brackets are the estimated degree of freedom; the dashed line indicates two times the point-wise standard errors for each curve; TWI is the Topographical Wetness Index.

The parametric coefficients of the intercept indicated that the intercept had significant influence on fitted GAM ($p < 0.001$) (Table 2). The Generalized Cross-Validation (GCV) indicated that the performance of the fitted GAM reached its optimum at 0.04 (Table 4). Adjusted R^2 and D^2 showed that part of the deviances were not explained by the fitted GAM (Table 4).

Table 4. Performance parameters of the fitted GAM between species richness and topographic variables.

	N	Adjusted R^2	D^2	GCV
Model Performance	90	0.24	0.31	0.04

N is the number of samples used to fit the Generalized Additive Model; D^2 is the deviance explained; GCV is the deviance of generalized cross-validation. Adjusted R^2 is the proportion of the variation in the dependent variable accounted by the explanatory variables.

4.2. Regression Analysis Based on Linear and Quadratic Models

Figure 3 presents the relation between species richness and each topographic variable estimated by the linear model. Species richness is significantly positively related to TWI (p = 0.012). However, there are no significant relations detected between species richness and altitude, nor aspect and slope ($p > 0.1$).

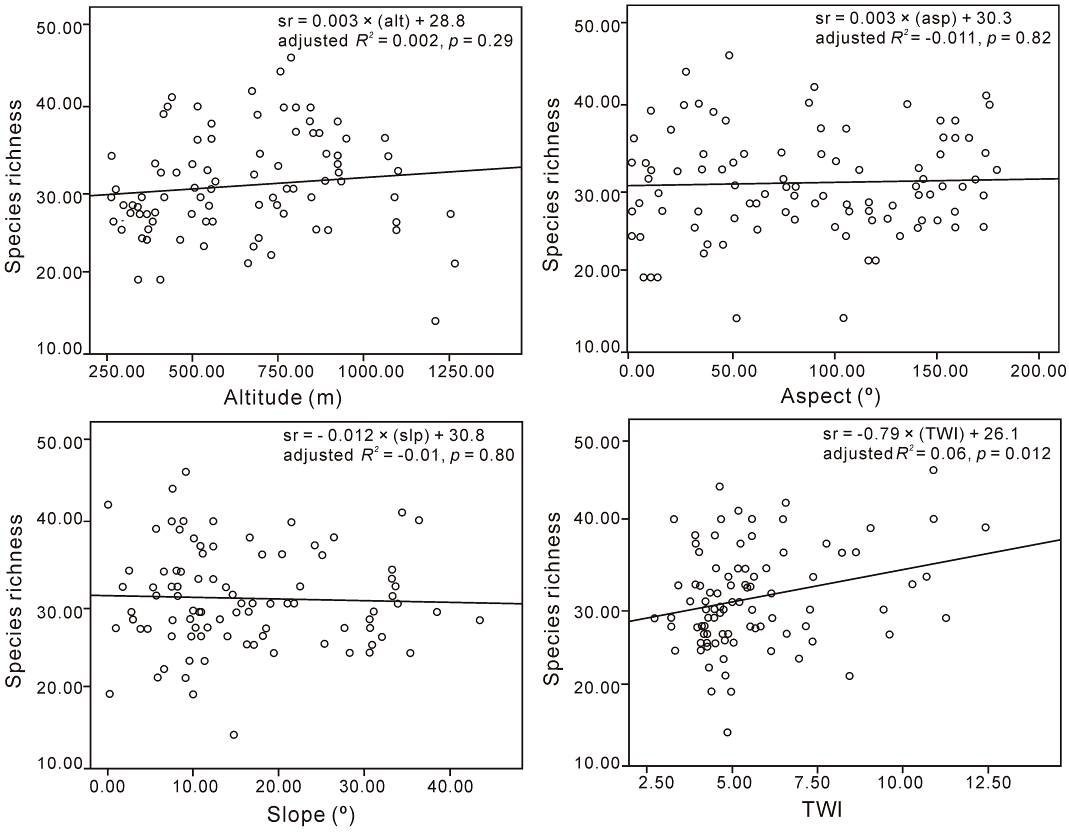

Figure 3. Estimated response lines of species richness (sr) to altitude (alt), aspect (asp), slope (slp) and the Topographical Wetness Index (TWI) based on the linear model.

Figure 4 is the curves estimated by the quadratic model. We can see that species richness had a significant unimodal response to altitude (p = 0.01) and a significant positive relation with TWI (p = 0.036). However, the correlation between species richness and slope, as well as aspect is not significant ($p > 0.1$).

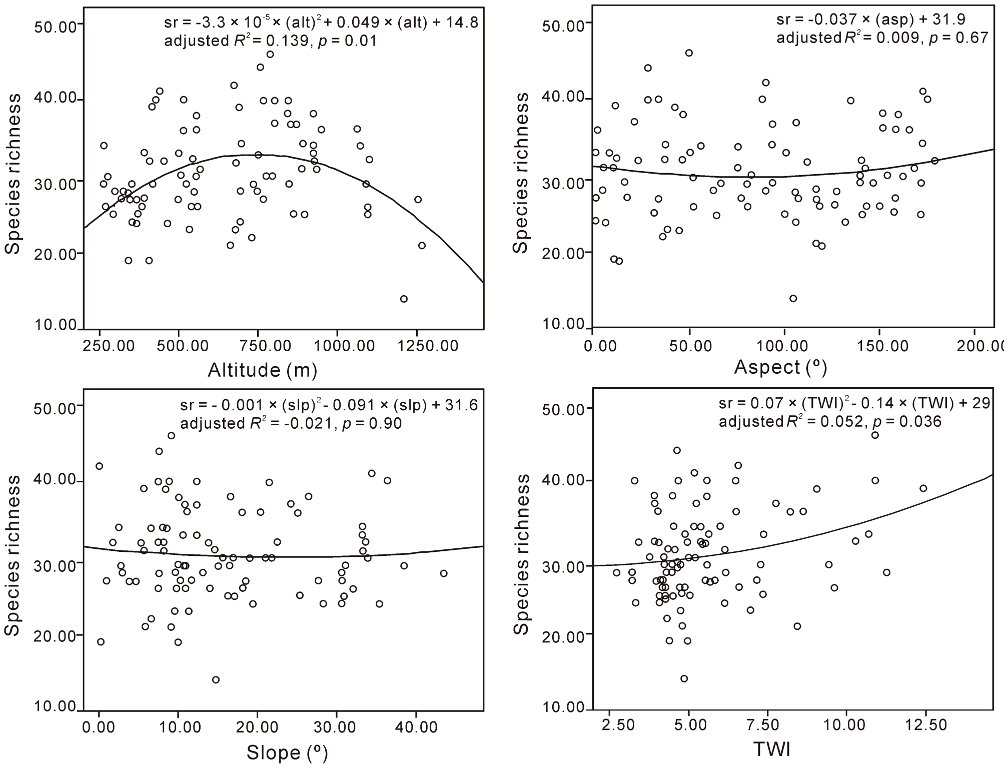

Figure 4. Estimated response curves of species richness (sr) to altitude (alt), aspect (asp), slope (slp) and the Topographical Wetness Index (TWI) based on the quadratic model.

4.3. Spatial Prediction of Species Richness Based on Generalized Additive Model

Based on the fitted multiple-factor GAM, we made a spatial prediction of the species richness in Kaihua County (Figure 5). The Pearson correlation coefficient between the observed and predicted species richness was 0.72 (RMSE = 7.1, p = 0.000, Figure 6). This indicated that the predicted species richness was significantly correlated with the observed species richness.

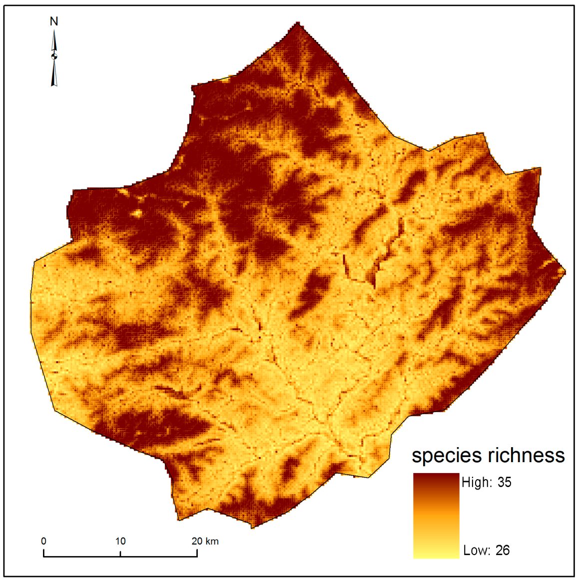

Figure 5. Spatial distribution map of predicted species richness in the study area (the pixel size is 240 m × 240 m).

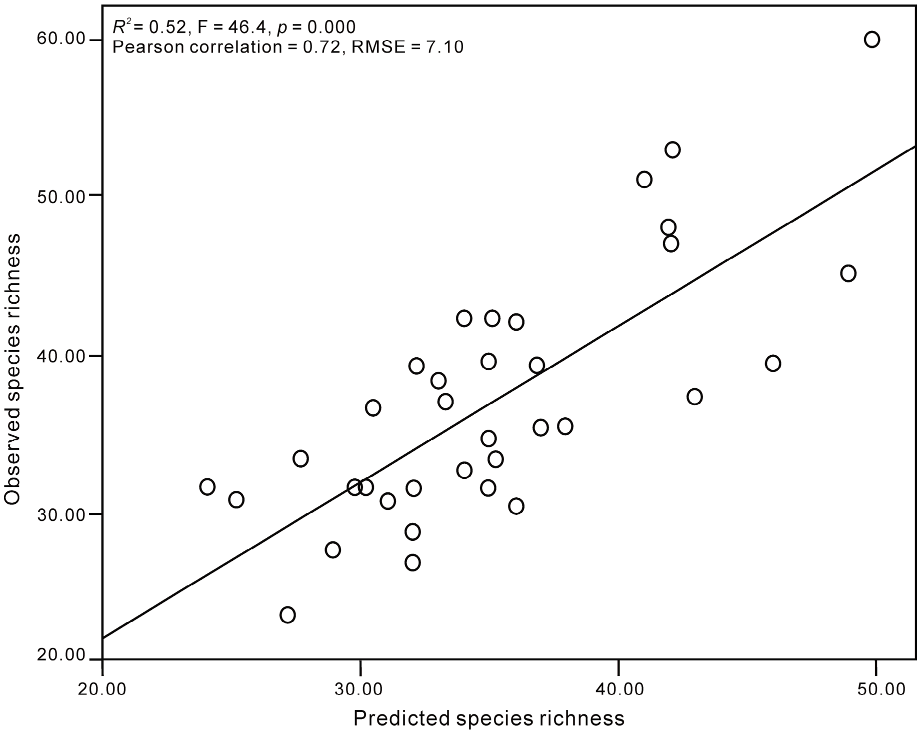

Figure 6. Relation between the observed species richness and the predicted species richness.

From Figure 7, we can see that the prediction error is positively linearly related to the observed species richness. This indicates that the prediction error increased with the increment of the observed species richness.

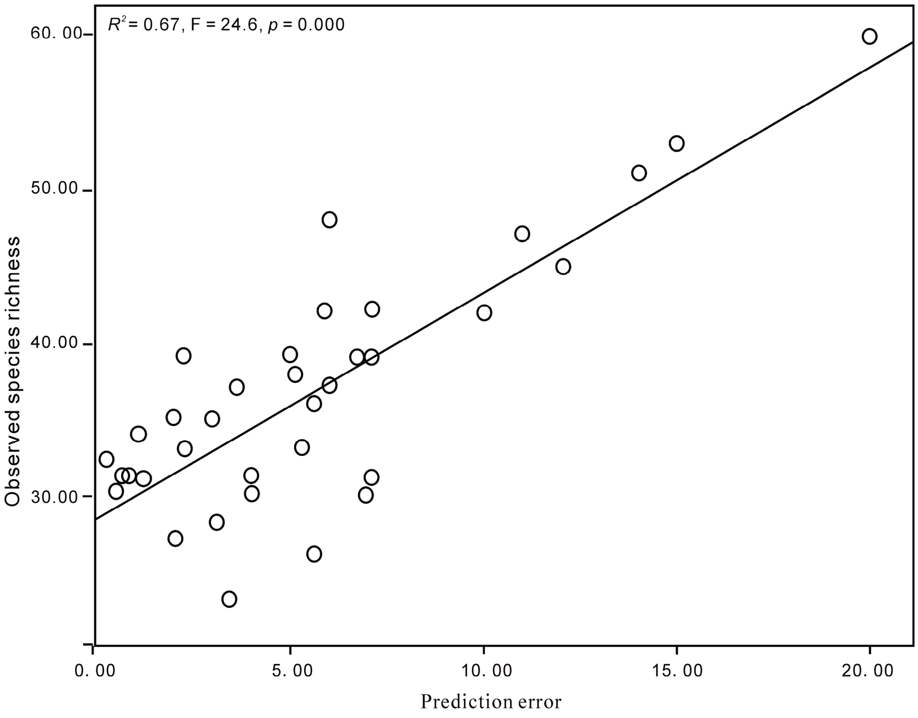

Figure 7. Relation between the observed species richness and the prediction error.

5. Discussion

5.1. Relation between Species Richness and Altitude

The altitude of the surveyed area ranges from 260 m to 1200 m. This provides multiple habitats for plant species. In the lower area (altitude ranging from 260 m to 500 m), *Cyclobalanopsis glauca* forest, *Michelia skinneriana-Castanopsis tibetana* forest and *Daphniphyllum oldhamii-Castanopsis eyrei* forest are predominant community types. These habitats are characterized by a thin soil layer and medium humidity. Exposed rocks can be often found in these habitats. Species recorded ranges from 24 to 30 in one surveyed plot. In the higher area (altitude ranging from 450 m to 650 m), *Quercus phillyraeoides-Cyclobalanopsis glauca* forest often occurs on the hillside. This habitat is characterized by a thin soil layer and low humidity. Exposed rocks and gravel can be observed everywhere. Around 30 plant species were recorded in one surveyed plot. *Castanopsis fargesii* forest is located in a ravine with altitude ranging from 500–600 m. This habitat is characterized by a deep soil layer and high humidity. Exposed rocks and gravel can seldom be found in this habitat. The habitat quality is better than that of the *Quercus phillyraeoides-Cyclobalanopsis glauca* forest, and the number of species is higher than that of the *Quercus phillyraeoides-Cyclobalanopsis glauca* forest. In regions with an altitude ranging from 500 m to 850 m, *Castanopsis eyrie* forest is the most important community, which can often be observed on the hillside. This habitat is characterized by a deep soil layer and a steep slope. Species richness is high, and more than 30 species were recorded in one surveyed plot. In areas with an altitude higher than 900 m, *Pinus taiwanensis* forest is the main community type that occurs on the top area of the mountain. There are around 26 species recorded in one plot. The habitat of *Pinus taiwanensis* forest is characterized by a deep soil layer and low humidity.

Based on these discussions, we can see that dominant species and species composition change with the increment of altitude. Additionally, species richness reaches the maximum at an altitude around 800 m and then falls gradually with the increase of altitude. Therefore, we concluded that species richness had a unimodal response to altitude in this study area. This conclusion is consistent with the result of the GAM (Figure 2). The unimodal response of species richness to altitude in this study was well portrayed by the fitted GAM.

5.2. Topographical Wetness Index

Moeslund et al. (2013) [23] performed a review of research works on the topography-biodiversity relationship, and they suggested that more functional topographic variables should be used to study the association of topography and species richness, instead of simple topographic measures. The topographical wetness index, derived from the digital elevation model, is a functional topographic variable that could be used to simulate the status of soil moisture [30]. Soil moisture is an important factor that has great influence on species richness [31]. Soil moisture not only has direct impacts on the survival of plants, but also has an influence on soil pH, nitrogen mineralization, uptake and utilization [32]. This could affect the adoption of available nutrients and then impact the growth and distribution of plants [33]. Our research found that the topographical wetness index has a significant relation with species richness ($p < 0.05$). This proved the practicality of the topographical wetness index in studying the response of species richness to the environment.

5.3. Performance of Generalized Additive Model

In this research, through the approach of GAM, altitude and TWI were found to have a significant relation with species richness, and predicted species richness was significantly correlated with observed species richness. These indicated that GAM is an effective tool for estimating the response of species richness to topographic variables. However, we need to realize that part of the deviance was not explained by the fitted GAM (Table 4), and there exists an obvious gap between predicted species richness and observed species richness (Figure 6). The unexplained deviance and prediction error might be due to the following reasons: (1) The limited data amount used for model-fitting: Only 90 plots were used to calibrate the GAM. We believe that the increment of the data amount could reduce the data noise and improve the model performance. (2) The topographic variables employed cannot represent all of the abiotic factors related to the species richness pattern. More factors, such as solar energy, soil and wind, should be included to study the relation between species richness and environment. (3) Biotic factors, such as biological evolution, community succession and biological interactions, were not included in the analysis. These factors might have great impacts on the pattern of species richness [34,35].

In this research, the prediction error was found to have a positive relation with observed species richness (Figure 7). One reason might be sampling bias. For accessibility, more plots might be set in a relatively flat area with low species richness. Therefore, GAM performed better on the low richness area than on the high richness area. Another reason is that stronger interspecific and intraspecific competitions might exist in communities with high species richness [36]. Biotic factors play an important role in shaping the species richness pattern in high richness areas. Therefore, the interpretability of topographic variables decreased, and the prediction error increased with the increment of species richness.

6. Conclusions

Altitude and the topographical wetness index were found to have a significant relation with species richness, whereas the relations between species richness and slope and aspect were not significant. Species richness had a unimodal response to altitude and a positive linear response to the topographical wetness index. The predicted species richness was significantly correlated with the observed species richness. However, the prediction error tended to increase with the increment of species richness.

Acknowledgments: This study was funded by the Ministry of Sciences and Technology (The National Key Research and Development Program of China, 2016YFC500100, 2017YFC0503800) and Chinese Academy of Sciences (Science and Technology Service Network Initiative, KFJ-SW-STS-168).

Author Contributions: Chuangye Song and Mingchang Cao conceived and designed the experiments; Chuangye Song performed the experiments and analyzed the data; Mingchang Cao contributed analysis tools; Chuangye Song wrote the paper.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Gaston, K.J. Global patterns in biodiversity. *Nature* **2000**, *405*, 220–227. [CrossRef] [PubMed]
2. Chi, X.L.; Tang, Z.Y.; Fang, J.Y. Patterns of phylogenetic beta diversity in China's grasslands in relation to geographical and environmental distance. *Basic Appl. Ecol.* **2014**, *15*, 416–425. [CrossRef]
3. Grytnes, J.A. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* **2003**, *26*, 291–300. [CrossRef]
4. Field, R.; Hawkins, B.A.; Cornell, H.V.; Currie, D.J.; Diniz-Filho, J.A.F.; Guegan, J.F. Spatial species-richness gradients across scales: A meta-analysis. *J. Biogeogr.* **2009**, *36*, 132–147. [CrossRef]
5. Sanders, N.J.; Rahbek, C. The patterns and causes of elevational diversity gradients. *Ecography* **2012**, *35*, 1–3. [CrossRef]
6. Mallen-Cooper, J.; Pickering, C.M. Linear declines in exotic and native plant species richness along an increasing altitudinal gradient in the Snowy Mountains, Australia. *Austral Ecol.* **2008**, *33*, 684–690. [CrossRef]
7. Nogués-Bravo, D.; Araújo, M.B.; Romdal, T.; Rahbek, C. Scale effects and human impact on the elevation species richness gradients. *Nature* **2008**, *453*, 216–219. [CrossRef] [PubMed]
8. Roland, C.A.; Schmidt, J.H. A diverse alpine species pool drives a 'reversed' plant species richness–elevation relationship in interior Alaska. *J. Biogeogr.* **2015**, *42*, 738–750. [CrossRef]
9. Rai, H.; Khare, R.; Baniya, C.B.; Upreti, D.K.; Gupta, R.K. Elevational gradients of terricolous lichen species richness in the Western Himalaya. *Biodivers. Conserv.* **2015**, *24*, 1155–1174. [CrossRef]

10. Brummer, T.J.; Byrom, A.E.; Sullivan, J.J.; Hulme, P.E. Alien and native plant richness and abundance respond to different environmental drivers across multiple gravel floodplain ecosystems. *Divers. Distrib.* **2016**, *22*, 823–835. [CrossRef]
11. Hjort, J.; Heikkinen, R.K.; Luoto, M. Inclusion of explicit measures of geodiversity improve biodiversity models in a boreal landscape. *Biodivers. Conserv.* **2012**, *21*, 3487–3506. [CrossRef]
12. Lawler, J.J.; Ackerly, D.D.; Albano, C.M.; Anderson, M.G.; Dobrowski, S.Z.; Gill, J.L.; Weiss, S.B. The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conserv. Biol.* **2015**, *29*, 618–629. [CrossRef] [PubMed]
13. Bailey, J.J.; Boyd, D.S.; Hjort, J.; Lavers, C.P.; Field, R. Modelling native and alien vascular plant species richness: At which scale is geodiversity most relevant? *Glob. Ecol. Biogeogr.* **2017**, *26*, 763–776. [CrossRef]
14. Tukiainen, H.; Bailey, J.J.; Field, R.; Kangas, K.; Hjort, J. Combining geodiversity with climate and topography to account for threatened species richness. *Conserv. Biol.* **2016**, *31*, 364–375. [CrossRef] [PubMed]
15. Stevens, G.C. The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* **1992**, *140*, 893–911. [CrossRef] [PubMed]
16. Baruch, Z. Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan páramos. *Vegetatio* **1984**, *55*, 115–126.
17. Rahbek, C. The elevational gradient of species richness: A uniform pattern? *Ecography* **1995**, *18*, 200–205. [CrossRef]
18. Grytnes, J.A.; Vetaas, O.R. Species richness and altitude, a comparison between simulation models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.* **2002**, *159*, 294–304. [CrossRef] [PubMed]
19. Stein, A. Environmental heterogeneity-species richness relationships from a global perspective. *Front. Biogeogr.* **2016**, *7*, 168–173.
20. Stein, A.; Gerstner, K.; Kreft, H. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **2014**, *17*, 866–880. [CrossRef] [PubMed]
21. Tamme, R.; Hiiesalu, I.; Laanisto, L.; Szava-Kovats, R.; Pärtel, M. Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J. Veg. Sci.* **2010**, *21*, 796–801. [CrossRef]
22. Laanisto, L.; Tamme, R.; Hiiesalu, I.; Szava-Kovats, R.; Gazol, A.; Pärtel, M. Microfragmentation concept explains non-positive environmental heterogeneity-diversity relationships. *Oecologia* **2013**, *171*, 217–226. [CrossRef] [PubMed]
23. Moeslund, J.E.; Arge, L.; BØcher, P.K.; Dolgaard, T.; Svenning, J.C. Topography as a driver of local terrestrial vascular plant diversity patterns. *Nord. J. Bot.* **2013**, *31*, 129–144. [CrossRef]
24. Zhang, B.; Yang, Y.S.; Zepp, H. Effect of vegetation restoration on soil and water erosion and nutrient losses of a severely eroded clayey Plinthudult in Southeastern China. *Catena* **2004**, *57*, 77–90. [CrossRef]
25. NASA JPL. ASTER Global Digital Elevation Model [Data set]. NASA JPL. 2009. Available online: https://doi.org/10.5067/aster/astgtm.002 (accessed on 12 August 2016).
26. Wang, X.A. Multivariate analysis and environmental interpretation of plant communities in Maqu, South Gansu Province. *Acta Ecol. Sin.* **1997**, *17*, 61–65. (In Chinese)
27. Pouteau, R.; Rambal, S.; Ratte, J.P.; Goge, F.; Joffre, R.; Winkel, T. Downscaling MODIS-derived maps using GIS and boosted regression trees: The case of frost occurrence over the arid Andean highlands of Bolivia. *Remote Sens. Environ.* **2011**, *115*, 117–129. [CrossRef]
28. Moore, I.D.; Gessler, P.E.; Nielsen, G.A.E.; Peterson, G.A. Soil attribute prediction using terrain analysis. *Soil Sci. Soc. Am. J.* **1993**, *57*, 443–452. [CrossRef]
29. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carre, G.; Marquez, J.R.G.; Gruber, B.; Lafourcade, B.; Leitao, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46. [CrossRef]
30. Qin, C.Z.; Yang, L.; Zhu, A.X.; Li, B.L.; Pei, T.; Zhou, C.H. Computation Method of Topographic Wetness Index in Low Relief Area. *Prog. Geogr.* **2006**, *25*, 87–93. (In Chinese)
31. Hettenbergerova, E.; Hajek, M.; Zeleny, D.; Mikulaskova, L.; Jirouskova, J.; Mikulaskova, E. Changes in species richness and species composition of vascular plants and bryophytes along a moisture gradient. *Preslia* **2013**, *85*, 369–388.
32. Loiseau, P.; Louault, F.; Le Rouxl, X.L.; Bardy, M. Does extensification of rich grasslands alter the C and N cycles, directly or via species composition? *Basic Appl. Ecol.* **2005**, *6*, 275–287. [CrossRef]

33. Moeslund, J.E.; Arge, L.; Bocher, P.K.; Dalgaard, T.; Ejrnaes, R.; Odgaard, M.V.; Svenning, J.C. Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodivers. Conserv.* **2013**, *22*, 2151–2166. [CrossRef]
34. Araujo, M.B.; Luoto, M. The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* **2007**, *16*, 743–753. [CrossRef]
35. Kissling, W.D.; Rahbek, C.; Bohning-Gaese, K. Food plant diversity as broad-scale determinant of avian frugivore richness. *Proc. R. Soc. B Biol. Sci.* **2007**, *274*, 799–808. [CrossRef] [PubMed]
36. Soliveres, S.; Maestre, F.T.; Ulrich, W.; Manning, P.; Boch, S.; Bowker, M.A.; Prati, D.; Delgado-Baquerizo, M.; Quero, J.L.; Schoning, I.; et al. Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett.* **2015**, *18*, 790–798. [CrossRef] [PubMed]