

Environmental factors driving tree richness at multiple spatial scales in temperate forests, Northeast China

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November 9, 2022

Abstract

Aim: Uncertainty remains in revealing the determinants of plant diversity over regional and larger scales. Both plant diversity and the effects of environmental factors on it are scale dependent. This study aims to integrate and analyse the variations in the ecological mechanisms by which environmental factors drive plant diversity. **Location:** Montane forests, Northeast China **Taxon:** Tree **Methods:** In this study, we used field survey data from 3,078 sample plots in temperate forest ecosystems. First, we partitioned the species–area curve into different area scales with segmented models to explain changes in the dominant factors affecting tree richness. Then, we quantified the contribution of environmental factors to tree richness with gradient boosted model (GBM) and fitted their correlations at different spatial scales. Finally, we partitioned the contribution of climate, topography and both to tree richness with redundancy analysis (RDA) and analysed how the driving mechanisms varied with spatial scale. **Results:** Two area scales (small scale A_1 and large scale A_2) were segmented in regional temperate forests. The correlations between environmental contributions and spatial scale at the A_2 scale were better than those at the A_1 scale. The effects of environmental factors driving tree richness varied spatially nonlinearly. Tree richness at the A_1 scale was determined by both climate and topography and climate alone, while it was determined by climate alone at the A_2 scale. **Main conclusion:** Spatial heterogeneity affected the effects of environmental factors on tree diversity, especially at the A_1 scale. Environmental factors exerted a dominant control at different spatial scales. Environmental filtering determined tree diversity at the A_1 scale, and dispersal limitation determined tree diversity at the A_2 scale for temperate forests. The spatial heterogeneity and collinearity of climate and topography prevented us from drawing consistent conclusions.

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Funding information

National Key Research and Development Program of China, Grant/Award Number: 2016YFA0600804.

Natural Science Foundation of Liaoning Province, Grant/Award Number: 2019-BS-262.

Academy of Changbai Mountain Science, Grant/Award Number: 2017-03.

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Keywords: Plant diversity, Environmental heterogeneity, Climate, Topography, Collinearity, Ecological mechanism

1 INTRODUCTION

The spatial scale dependence of biodiversity has become a hot topic in recent years (Rolls et al., 2018; Bhatta et al., 2018; Malanson et al., 2018; Keil & Chase, 2019). What affects regional patterns in the number of species living at different sites, and how do the important factors drive plant diversity change? Studies across different spatial scales are important for understanding variations in plant diversity, and many ecological mechanisms are closely related to spatial scale (Crawley & Haral, 2001; McGill, 2010). Therefore, exploring changes in the driving mechanisms is important to understanding the effects of spatial scale on plant diversity. However, there is still a lack of consensus about the determinants of regional plant diversity changes across spatial scales.

The most fundamental question is that the number of species increases nonlinearly with area (Storch, 2016). The spatial patterns of diversity observed at small spatial scales are usually different from those at large

spatial scales (Rahbek, 2005; Chase & Knight, 2013) and differ from place to place (Tuomisto et al., 2017). Different spatial scales, study sites or both can lead to significant variations in species diversity influenced by mechanisms and spatial heterogeneity (Cavieres et al., 2014; Gavilan & Callaway, 2017; Rahbek, 2005). However, whether this nonlinear relationship can be segmented across a spatial scale and the determinate mechanism can be successfully partitioned remain unclear.

Furthermore, the important obstacle to answering the fundamental issue is that the different factors driving plant diversity also vary with spatial scales and geographic regions (Hillebrand & Blenckner, 2002; Nogués-Bravo et al. 2008; Keil & Chase, 2019; Wang et al. 2009; Zhang et al., 2017). Climate has a stronger impact on diversity than other abiotic factors at a large regional scale (Harrison et al., 2020; Malanson et al., 2018). Diversity at the montane scale emphasizes the importance of topographical factors, especially altitude (Naud et al., 2019). Spatial patterns of broad-ranged species tend to be more correlated with the climatic gradient on larger spatial scales, while narrow-ranged species are often sensitive to habitat heterogeneity (especially the terrain) at the local scale (Jetz & Rahbek 2002; Qian & Kissling, 2010). Moreover, the relative contribution of environmental factors to species richness may change nonlinearly with study scale. Temperature impacts species diversity at multiple spatial scales but is less important at small local scales (Schweiger & Beierkuhnlein, 2016), as it has a weak correlation with species diversity at microscales (Field et al., 2009). The floristic composition has been found to be significantly related to environmental variables, and the correlation may vary with spatial scale (Auestad et al. 2008; Siefert et al. 2012). Studies about the relative contribution of environmental factors to plant diversity are common, but little is known about how they change across continuous spatial scales.

The collinearity among these environmental factors may affect their explanation of diversity. Changes in both altitude and latitude gradients can alter temperature and precipitation in space and further affect the pattern of plant diversity at different spatial scales (Currie et al., 2004; Naud et al., 2019). Areas with warm and humid climates support more species than those with cold or dry climates (Cowles et al., 2018), while some adjacent low-temperature areas may also maintain higher species richness than high-temperature areas; for example, plant richness varies with altitudinal gradients in humps (Paudel et al., 2016; Steinbauer et al., 2018). Moreover, it is difficult to separate the biophysical interactions of temperature and precipitation on regional plant diversity (Kikvidze et al., 2011; Peyre et al., 2019). Climate warming tends to reduce plant diversity in areas with relatively limited water resources (Pfeifer et al., 2016), but this negative effect can be offset by increased precipitation (Cowles et al., 2018). Comparing studies among single spatial scales or sites may lead to unmatched results and hinder synthetic analyses (Keil & Chase, 2019; Stein et al., 2014). Methods accounting for multiple spatial scales are suitable for the simultaneous analysis of complex ecological variations (Li et al., 2020). However, analyses simultaneously integrating plant diversity and environmental drivers at multiple continuous spatial scales are rare.

The montane forests in Northeast China are the most species-rich temperate ecosystems in the world and contain complex ecological information. In this study, we first segmented the species-area curve to examine the changes in potential mechanisms across spatial scales. We then quantify the contribution of environmental factors at different scales. The goals of our study are to integrate and analyse the variations in the ecological mechanisms by which environmental factors affect plant diversity. We tested the following hypotheses regarding plant diversity in temperate forests: (1) the species-area relationship can segment variations in dominant mechanisms; (2) different environmental factors may exert a dominant control in driving plant richness at different spatial scales; and (3) collinearity of climate and topography can impact their effects on tree richness at different spatial scales.

2 MATERIALS AND METHODS

2.1 Study region and sample sites

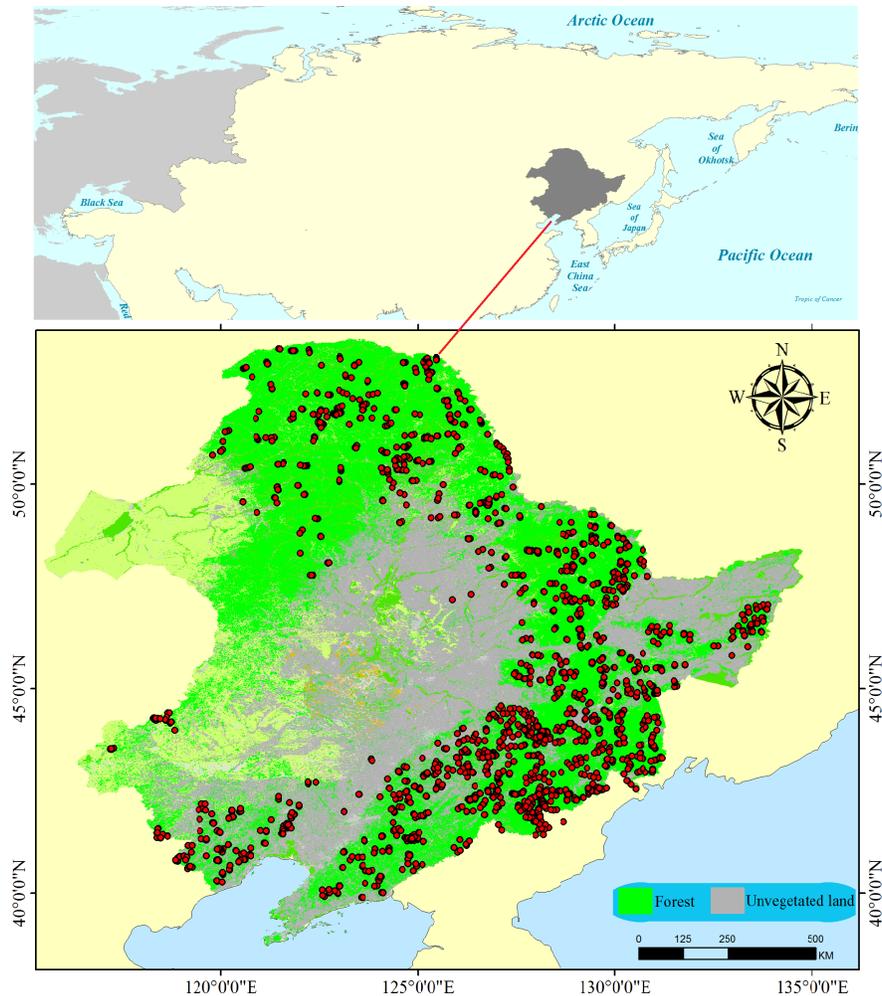


Figure 1 Distribution of 3,078 sampling plots covering the mountainous area in Northeast China. [colour figure can be viewed in the online edition].

The study focused on the natural forests in Northeast China, including 9 mountain systems—the western Liaoning, Longgang, Hadaling, Changbai, Wanda, Zhangguangcailing, Laoyeling and Greater and Lesser Khingan Mountains—as well as 14 natural reserves. The survey area extends from 39-54° N and 117-135° E (Figure 1).

The study area is a mountainous monsoon forest within a temperate continental climate zone. There are four distinctive seasons throughout the year, with warm, rainy summers and cold, dry winters. The annual mean temperature varies by more than 10°C between the north and the south. The annual precipitation decreases from approximately 1,100 mm in the southeastern region to less than 400 mm in the northwestern region. Most of the rainfall occurs between June and September of each year. The elevation ranges from 30 to 2100 m, and the slope ranges from 0 to 45°. The vegetation types include temperate deciduous broad-leaved forest, temperate mixed coniferous and broad-leaved forest, temperate coniferous forest and cold temperate coniferous forest (Gu et al., 2020).

In the summer of 2008-2016, we investigated a total of 3,078 plots with an area of 900 m² (30 m×30 m). These plots were the basic unit of the different sampling grids in the subsequent analysis. We recorded the longitude and latitude at the centre of the plot and measured the elevation (m), aspect and slope (°).

We surveyed all trees with a diameter at breast height (DBH) > 5 cm in the plot. The plant names were standardized according to the Flora of China (Chinese Academy of Sciences, 1999). Finally, we collected a total of 289,124 individual trees and 155 tree species, and the number of species in 3078 plots varied from 1 to 21 (Supporting Information Appendix S1). All descriptive statistics were performed using the R version (University of Auckland, NZ).

2.2 Data scaling

The validity of results on species diversity gradients and their dominant factors at regional scales crucially depend on spatial representation and methodological consistency of sampling at the local scale (Tuomisto et al., 2017). The sampling method of this study was the contiguously arrayed grids as the Type II curves of Scheiner (2003). The difference from Scheiner’s Type II approach was that our sampling grids were constituted with the basic 3078 plots. First, we converted the spherical coordinates (longitude and latitude, °) of the plots into plane coordinates (geographic distance, km) with the “geosphere” R package. Then, we divided the plane into sampling grids of different area scales, level by level (Supporting Information Appendix S2).

Figure 1 clearly shows that the 3078 plots were not evenly distributed across the study region. This uneven sampling coverage could potentially bias the tree richness analysis in this study. For example, grids with larger numbers of plots and more widely dispersed plots had higher species richness. To minimize this problem, (1) we excluded the grids with < 36 plots because the gradient boosted model (GBM) could obtain stable operation with approximately 36 plots; (2) we retained the grids with an area of the sample plots accounting for more than 1/2 of the grid area.

2.3 Scaling effect of tree richness

The species–area relationship is one of the most investigated ecological patterns. The shape of a species–area curve reflects the changes in species richness with the sampling area. In many species–area models, the segmenting model provides a satisfactory statistical test to determine the inflection point (threshold point) in the species–area curve (Muggeo, 2010). This model was shown to be ecologically relevant in segmenting the process of increasing species richness with area (Lomolino, 2000), as it can detect the threshold point of the spatial scales at which the species number changes. The discontinuous segment model was used to identify different processes of increased species richness as the sampling area increased (Gao and Perry, 2016). In contrast, a continuous segmented model was shown to be more consistent with the actual increase in species richness with area (Dengler, 2010). Therefore, we chose the continuous segmented model in this study. The model fitting was based on the “segmented” package (Muggeo, 2008). We simultaneously fitted two segmented models to verify the reliability of this sampling method (Figure 2).

2.4 Contribution of environmental variables

We chose 12 environmental variables to explain tree richness, including climate and topography (Table 1). The correlation of these environmental factors is shown in Supporting Information Appendix S3. We obtained 8 climate variables from the website of the China Meteorological Administration (<http://www.cma.gov.cn/>), including the annual mean temperature (AMT), seasonal temperature (ST), mean temperature of warmest quarter (MTWQ), mean temperature of coldest quarter (MTCQ), annual precipitation (AP), seasonal precipitation (ST), precipitation of wettest quarter (PWQ) and precipitation of driest quarter (PDQ). We chose 4 topographic variables, including elevation (EL), aspect (AS), slope (SL) and soil moisture index (SMI). The SMI is the water holding capacity of soil related to topography. We calculated the cosine of the slope aspect to eliminate collinearity.

Table 1 Twelve environmental variables were used to explain tree richness.

Variables	Mean	Minimum	Maximum	Unit
Climate				
Annual mean temperature	3.78	-5.42	11.33	
Seasonal temperature	1418.00	1104.00	1742.00	

Variables	Mean	Minimum	Maximum	Unit
Mean Temperature of Warmest Quarter	19.91	13.44	24.50	
Mean Temperature of Coldest Quarter	-14.96	-26.31	-4.18	
Annual precipitation	676.10	380.10	1112.10	mm
Seasonal Precipitation	97.75	69.18	151.43	mm
Precipitation of Wettest Quarter	166.12	83.49	331.98	mm
Precipitation of Driest Quarter	0.93	-12.24	13.33	mm
Topography				
Elevation	527.80	30.00	2073.00	m
Aspect	-	-	-	-
Slope	10.41	0.00	50.00	°
Soil Moisture Index	107.10	66.02	142.00	

We used a gradient boosted model (GBM) to quantify the relative contributions of each variable to species richness. The GBM can produce reliable coefficient estimates and robust interpretation when considering the collinearity of environmental variables (Elith et al., 2006; Friedman, 2001; Leathwick et al., 2006). This model 1) can gradually add regression trees and reweight data to compensate for the improper fitting of previous regression trees and 2) minimizes the impact of extreme outliers (Zhang et al., 2014). When fitting the GBM models, it is necessary to specify two main parameters (learning rate and tree complexity). The learning rate adjusts the weight of each regression tree. The smaller this value is, the more regression trees there are. Tree complexity controls the interaction depth of each regression tree (Connell, 1978). This parameter can partition the collinearity among environmental variables. We fitted three GBMs with a learning rate value of 0.001 and tree complexity value of 2. The other parameters of the model are default values. Finally, we averaged the relative contributions of the three models. The model used the "dismo" R package and "gbm" scripts to estimate the contribution of each predictive variable.

These 12 environmental variables were used to partition the total variation in tree richness into individual components by climate alone, climate and topography jointly and topography alone. We carried out redundancy analysis (RDA) using the "varpart" function in the R package vegan. There was no need to remove collinearity of the explanatory variables in RDA, as the topographical gradient of each climatic variable and the R^2 values of the relationships between such variables were used to evaluate the correlation of tree richness with these variables (Legendre & Legendre, 2012, Zhang et al., 2020).

3 RESULTS

3.1 Partitioning spatial scale with species–area relationship

The spatial dependence of tree richness increased with area, as shown with the power model. In segmented model, the threshold ($L=4.76$ and $L=4.59$) partitioned the species–area curve into two different spatial scales (A_1 and A_2) as the tree richness increased with area (Figure 2). The explained total deviance (R^2) of the two models were 0.72 and 0.51, respectively.

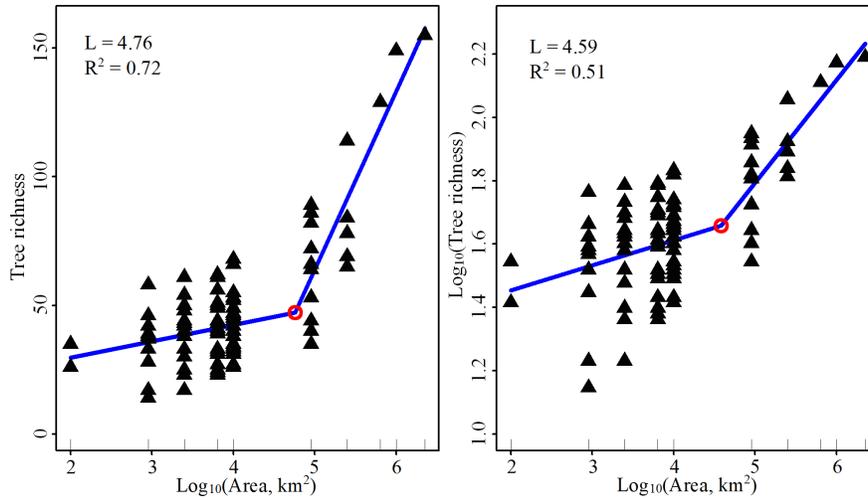


Figure 2 Species–area relationship for tree richness according to the power model segmented model. Area is the spatial scale of the sampling grid. The red dot is the threshold (L_1). [colour figure can be viewed in the online edition].

3.2 Scaling effect of environmental factor contributions

The relationship between the contribution of each environmental variable and area scales was fitted with general linear models (considering A_1 and A_2 , respectively) (Table 2) and local polynomial regression (Figure 3). The scaling effect of environmental variables driving tree richness varied nonlinearly with area scale, but this effect was affected by spatial heterogeneity, especially at the A_1 scale. In general, the environmental variables and the A_2 scale correlated more than those of A_1 , except for ST. The correlation ranged from -0.45 to 0.45 (\cdot , $p < 0.1$).

Table 2 General linear analysis of the correlation between environmental variables and the two spatial scales. Spearman correlations were conducted for each fitted model.

Variable	Scale	Correlation (r)
AMT	A1	-0.25*
	A2	0.45·
ST	A1	0.24*
	A2	-0.04
MTWQ	A1	0.13
	A2	0.27
MTCQ	A1	0.14
	A2	0.38
AP	A1	-0.03
	A2	0.34
SP	A1	0.09
	A2	0.17
PWQ	A1	0.20·
	A2	-0.33
PDQ	A1	0.07
	A2	-0.24
EL	A1	0.07
	A2	0.17

Variable	Scale	Correlation (r)
AS	A1	-0.15
	A2	-0.30
SL	A1	-0.12
	A2	-0.45
SMI	A1	-0.08
	A2	-0.41

Note: AMT = annual mean temperature (°C); ST = seasonal temperature; MTWQ= mean temperature of warmest quarter (°C); MTCQ= mean temperature of coldest quarter (°C); AP = annual precipitation (mm); SP = seasonal precipitation; PWQ = precipitation of wettest quarter (mm); PDQ = precipitation of driest quarter (mm); EL = elevation (m); AL = aspect; SL = slope (°); SMI = soil moisture index. A₁, area < 10^{4.76} km²; A₂, area > 10^{4.76}km². *, $p < 0.05$; ·, $p < 0.1$.

The impact of AMT on tree richness decreased significantly across the A₁ scale ($r = -0.25^*$) and then increased across the A₂ scale (Figure 3). The ST varied with the area scale into a hump shape, and the MTWQ changed across A₁ as a double hump and then smoothed across the A₂ scale. The MTCQ increased with area scale in an ascending ladder type, and AP, SP and EL had similar variations. The PWQ and PDQ showed hump-type across the A₁ scale and then decreased across the A₂ scale. The changes in SL and SMI were found to be a declining ladder type.

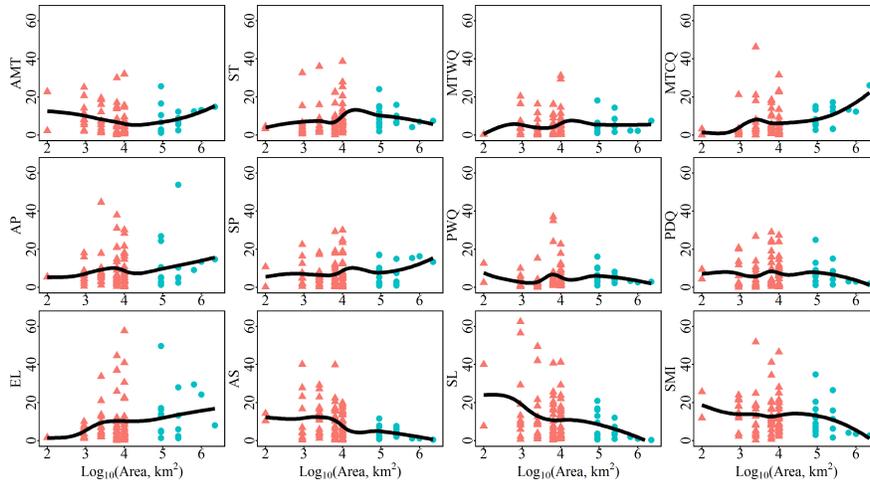


Figure 3 The contribution of each environmental variable to tree richness and area scale fitted by local polynomial regression. ⁱsthesecondareascale(A₁), and ^{*} isthethirdareascale(A₂).[colour figurecanbeviewedintheonlinedition].

The contributions of climate, topography and both affect plant diversity across spatial scales in a nonlinear relationship (Figure 4). For these three factors, climate influenced the most on tree richness overall, followed by both and topography. The contribution of both has an alternately strong influence as climate on tree richness at a small scale across A₁. The contribution of climate increased with spatial scale, and the jointly explained contribution decreased with spatial scale. The contribution explained by topography alone changed with spatial scale into a hump shape, increasing across A₁ and decreasing across A₂.

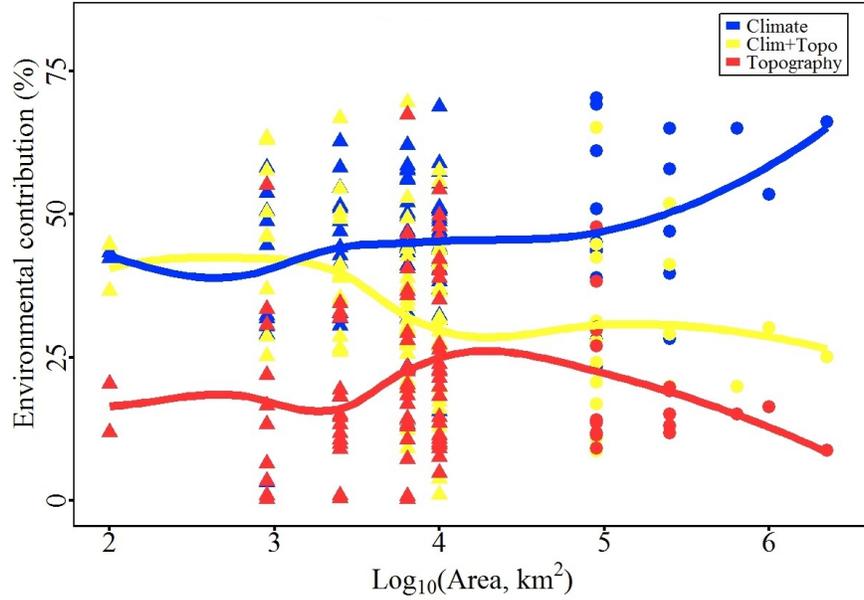


Figure 4 Contributions of climate, topography and both varying with spatial scales. The blue line is the contribution explained by climate alone. The yellow line is the contribution jointly explained by climate and topography. The red line is the contribution explained by topography alone. A_1 area $< 10^{4.76} \text{ km}^2$; A_2 area $> 10^{4.76} \text{ km}^2$. [colour figure can be viewed in the online edition].

The changes in the explained total deviance (R^2) of GBM and RDA showed similar variation (Figure 5). Both varied with area scale in a declining wave type, and the humps were mainly concentrated at the A_1 scale.

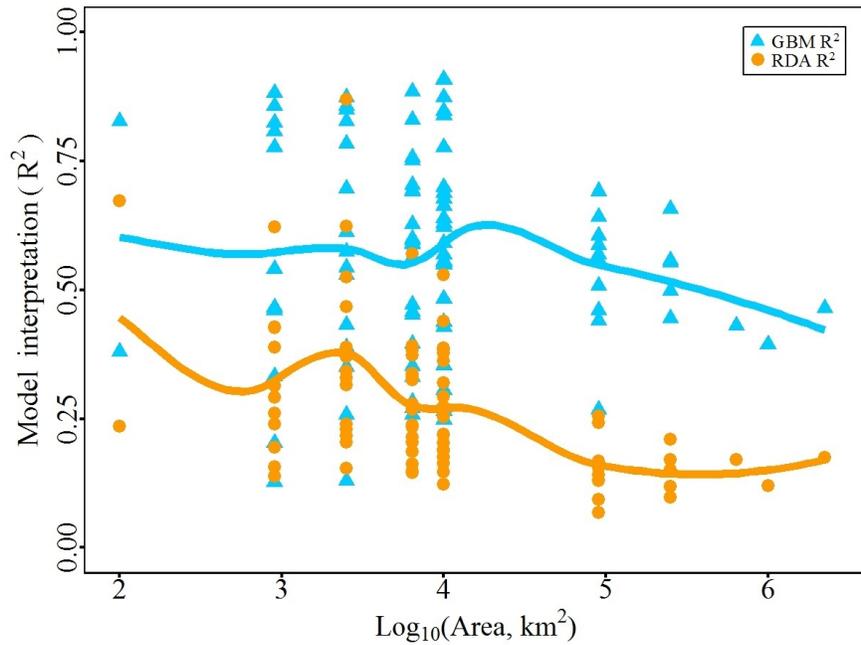


Figure 5 The interpretation of the total deviance (R^2) of GBM and RDA across the area scale. a are R^2 of GBM; and * are R^2 of RDA. [colour figure can be viewed in the online edition].

4 DISCUSSIONS

To explain changes in the dominant mechanism of tree richness, we partitioned the species–area curve into two area scales with segmented models. Previous research showed that plant species in different segments have different adaptability to the environment and the demand for spatial resources (Gao & Perry, 2016). Therefore, we fitted the correlations and variations between the contributions of environmental factors to tree richness and two spatial scales.

Our results showed that these correlations increased with the spatial scale. Studies have shown that species richness patterns depend on complex cross-scale effects (Hillebrand & Blenckner, 2002; Zhang et al., 2014; Zhang et al., 2017). Large regions with high species richness, such as China, could have historically accumulated species that survived in climate refuges (Svenning & Skov, 2004) or segregated by complex physiological heterogeneity with relatively small spaces (Qian & Ricklefs, 2000). This would increase the regional richness but contribute less to local richness, which would lead to stronger regional effects at larger scales than at smaller scales (Keil & Chase, 2019). In addition, spatial heterogeneity affected the dependence of tree diversity on environmental factors, especially on a small scale. Niche theory considers that the ecological and biological characteristics of plant species determine their life history strategy, and species occupy their respective ecological niches with different approaches to utilize natural resources (Connell, 1978; Silvertown, 2004). Regions with greater local environmental differences can support more species with different niches (Fernandez-going et al., 2013; Harrison & Cornell, 2008; Kallimanis et al., 2010).

Different environmental factors exerted a dominant control on driving tree richness at different spatial scales, and they varied with spatial scale in a complex nonlinear pattern. The aspect, slope and soil moisture index dominated tree richness at the A_1 scale, while the mean temperature of the coldest quarter, annual precipitation, seasonal precipitation and elevation determined tree richness at the A_2 scale. Topographic heterogeneity has clear barriers over large areas, such as mountain ranges and deep valleys, limiting colonization (Quintero & Jetz, 2018) or creating refuges for species persisting in adverse environments (Stein et al., 2014). Furthermore, elevation can promote diversification of species by increasing the environmental gradient in the same area. At a large scale, studies have shown that variations in plant richness patterns represent overlapping differences in dispersal range, whereas the edge of dispersal limits individuals to tolerating and occupying an environment that is influenced by macroscopic climate (Gu et al., 2020; O’Brien, 1998).

The annual mean temperature affected tree richness more at $< 10^3 \text{ km}^2$ and $> 10^6 \text{ km}^2$ than at middle scales. This may be because the difference in temperature was mainly caused by aspect and slope at a small scale, while it was caused by altitude and latitude at a large scale. However, this effect would be found only when the difference in climate was significant across the spatial scales (Grace et al., 2016). The seasonal temperature operated more at middle scales, which may be caused by the combined effects of topography and climate. From the perspective of geomorphological metrics, topography, associated with elevation, slope, and aspect, could affect the local water and energy budgets by increasing habitat heterogeneity at small scales and then indirectly regulate regional plant distribution and species richness (Yu et al., 2015).

We showed that climate alone and both (climate + topography) explained a major portion of tree richness at the A_1 scale. At a small spatial scale, studies on diversity emphasize the importance of topography (Bruun et al., 2006; Rose & Malanson, 2012), and the influence of climate is weaker (Schweiger & Beierkuhnlein, 2016). This is inconsistent with our result because differences in climate caused by topography are also important at the A_1 scale. Tree richness explained by both may generate the conclusion that environmental filtering affects plant diversity more than dispersal limitation for temperate forests (Zhang et al., 2020). A possible source of this difference is the collinearity between climate and topography, which may prevent us from detecting the scale dependence of climatic effects. In other words, climatic factors also tend to be topographically distinct at the A_1 scale. This collinearity weakens our ability to partition the relative

importance of climate versus topography. Given this covariation, we cannot clearly draw conclusions as to whether climatic or topographic effects are more determinate in driving patterns of tree richness. This collinearity is likely the reason for the inconsistent results in many studies.

The contribution to tree richness explained by climate alone was much higher than that explained by both climate and topography at the A_2 scale. Many studies show that climate significantly affects plant diversity at large regional scales, and this impact far exceeds those of other environmental factors (Harrison et al., 2020; Malanson et al., 2018), which is consistent with our results. The regional effect of climate is more positive than its local effect because climate controls species diversity by regulating the regional species pool (Cornell & Harrison, 2014), as gamma diversity has a cross-scale effect on alpha diversity (Ricklefs, 1987; Grytnes & Birks, 2003).

The explained total deviance (R^2) of GBM and RDA declined with area scales. This may indicate that some factors we do not consider are emerging and dominate tree diversity at large regional scales. On the other hand, the spatial autocorrelation of tree species may weaken the interpretation of tree richness accounted for by environmental predictors. However, we had no direct evidence verifying this.

ACKNOWLEDGEMENTS

This work was supported by the National Key Research and Development Program of China (No. 2016YFA0600804), the Natural Science Foundation of Liaoning Province (No. 2019-BS-262) and Academy of Changbai Mountain Science (No. 2017-03).

CONFLICT OF INTEREST

All the authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the research data are not shared.

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BIOSKETCH

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Author contributions: Shijie Han and Junhui Zhang designed and conceived the field study; Yue Gu, Yue Feng, Zhuo Li and Yanshuang Guo processed the data for statistical analysis. Yue Gu and Guoqiang Shi analysed the data. Yue Gu accomplished the original draft and review of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

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