

Relative importance of climate vs local factors in shaping the regional patterns of forest plant richness across northeast China

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Northeast (NE) China covers three climatic zones and contains all the major forest types of NE Asia. We sampled 108 forest plots in six nature reserves across NE China to examine the influence of climate and local factors (canopy seasonality, successional stage, topography and forest structure) on geographic patterns of plant richness. We analyzed the relative effects of different factors at two spatial scales: the regional scale (across both latitude and altitude) and the local scale (along the altitudinal gradient within site). Our results showed that the relative importance of climate vs local factors differed remarkably depending on scale and functional group. While total and tree species richness were mainly limited by climate, herb and shrub richness was more related to local factors (especially at the local scale). In the climatic factors, heat sum was the major correlate of tree, shrub and total species richness, while herb richness was more associated with winter coldness. Precipitation was not a limiting factor for forest plant richness in NE China. Climate accounted for 34–76% of variation in richness at the regional scale, but explained only 0–44% at the local scale. Among the local factors, shrub species richness was sensitive to seasonal canopy openness, with higher richness in deciduous forests than in the evergreen needle-leaf forest. On the other hand, herb richness was sensitive to forest successional stage, with higher richness in middle- successional forests than in the early and late-successional forests. Local topography (aspect and position on slope) and forest structure (tree density) also showed remarkable influence on species richness. Our results suggest the importance of including local factors when examining large scale diversity gradient (especially for understory species), and the necessity of comparing diversity patterns among functional groups at different spatial scales.

Understanding the underlying causes of geographic diversity gradients, especially in hyper-diverse ecoregions, is important for the conservation and sustainable use of biodiversity (Gaston 2000, Grytnes 2003). It is widely observed that species richness varies systematically with both latitude and altitude for a variety of taxa (Hillebrand 2004, Rahbek 2005). Though many mechanisms for these changes have been suggested, climate is widely reported to be closely correlated with species richness, and thus some authors suggested climate as the first-order predictor for species richness (O'Brien 1993, Francis and Currie 2003, Hawkins et al. 2003). The relative importance of particular climatic factors might, however, vary geographically. For instance, temperature generally accounts for more variation in richness in cold regions, while water availability is more important for areas with high energy inputs (O'Brien 1993, Hawkins et al. 2003, Kreft and Jetz 2007).

Temperate East Asia has long been a focus in broad-scale diversity studies (Latham and Ricklefs 1993, Qian and Ricklefs 2000). Significantly higher taxonomic richness in this area than other temperate regions in the world

has been repeatedly reported at different taxon levels. This Asian bias is hypothesized to be related to: 1) a longer history of direct connection with rich tropical species pools; 2) greater environmental heterogeneity; 3) higher beta diversity; and 4) less extinction during historical glaciations (Qian and Ricklefs 2000, Qian et al. 2005). However, most studies on broad-scale diversity patterns in East Asia have been conducted only for species richness within large grain sizes (i.e. areas $>10 \text{ km}^2$; Qian and Ricklefs 2000, Ricklefs et al. 2004). Data at more local scales, especially from the rich floras of temperate China, are urgently needed for comparisons with other temperate regions (Ricklefs et al. 2004).

Diversity gradients may differ remarkably among plant groups, reflecting differences in the determinants for different groups (Pausas 1994, Austin et al. 1996, Leathwick et al. 1998). Comparisons among ecological or taxonomic groups are necessary to gain a more comprehensive understanding of diversity patterns (Lomolino 2001, Pausas and Austin 2001). Diversity at plot scale (e.g. 1 m^2 – 1 ha) is affected by a variety of local factors in

addition to climate, such as disturbance, canopy openness, topography, forest structure and biotic interactions (Pausas 1994, Saha 2003, Quigley and Platt 2003, Laughlin et al. 2005). These local factors are particularly important for understory plants (Svenning and Skov 2002, Laughlin et al. 2005, Laughlin and Grace 2006). However, the relative roles of local environments have seldom been quantified systematically along both latitudinal and altitudinal gradients (but see Austin et al. 1996, Harrison et al. 2006). A major objective of this study was to examine the relative importance of climate vs local factors in shaping the geographic richness gradients, emphasizing the differences among tree, shrub and herb species.

The processes determining diversity are scale dependent, and thus it is crucial to examine the relative roles of different factors at different scales (Rahbek 2005, Harrison et al. 2006). Accordingly, we examined the effects of various variables at two spatial scales: 1) the regional scale of northeast China (along both latitudinal and altitudinal gradients); 2) the local scale within study site (along the altitudinal gradient).

In this analysis, we sampled 108 plots from six nature reserves across northeast (NE) China to examine the following three specific questions: 1) what are the relative roles of different climatic and local factors in limiting species richness in NE China? 2) Are patterns different

between the regional and the local scales? 3) Are patterns similar for tree, shrub and herb growth forms?

Materials and methods

Study area

Northeast China ($115^{\circ}37' - 135^{\circ}5'E$, $38^{\circ}43' - 53^{\circ}34'N$) consists of Heilongjiang, Jilin, Liaoning provinces and the eastern part of Inner Mongolia Autonomous Region, covering an area of 1 240 000 km². The climate is controlled by high latitude East Asia monsoons, changing from warm temperate, temperate to cool temperate zones from south to north, and from humid, semi-humid to semiarid zones from east to west. These climatic gradients drive variation in vegetation types, from deciduous broadleaf forest over needle-leaf and broadleaf mixed forest to boreal forest and from forest over forest steppe to steppe, respectively (Zhou 1997). Geographically, NE China is characterized by plains separated by three major mountain systems (Changbai-Zhangguangcai Mountains, Xiaoxing'an Mountains, and Daxing'an Mountains; Fig. 1). With these great gradients in climate and topography, NE China is a major biodiversity center in East Asia (Chen 1998), and thus provides an ideal region for examining large scale diversity patterns across many taxa and their underlying causes.

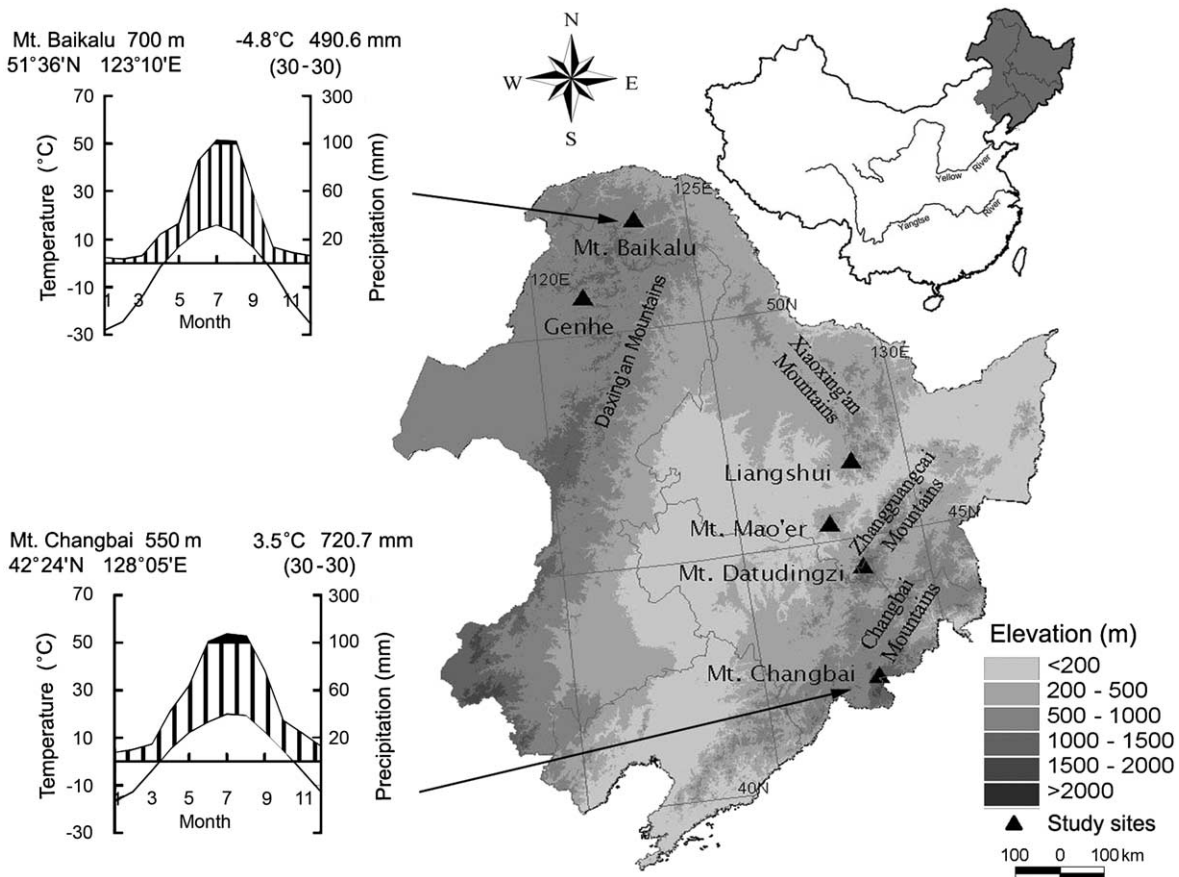


Figure 1. Location of study sites in NE China, together with two climatic diagrams (Mt. Changbai and Mt. Baikalu). The study sites include six nature reserves: Mt. Changbai, Mt. Datudingzi, Mt. Mao'er, Liangshui, Mt. Baikalu and Genhe. The "(30-30)" in the climatic diagrams means that the temperature and precipitation were both means of 30 yr records.

Data collection

The study sites were located in six well-protected nature reserves across the forest region of NE China: Mt. Changbai in Changbai Mountains, Mt. Mao'er and Mt. Datudingzi in Zhangguangcai Mountains, Liangshui in Xiaoxing'an Mountains, and Genhe and Mt. Baikalu in Daxing'an Mountains (Table 1, Fig. 1).

These nature reserves cover all the ten major forest types of NE China, including: 1) *Betula ermanii* forest, a typical timberline forest in humid NE Asia; 2) *Larix olgensis* forest in the Changbai Mountains; 3) *Picea jezoensis* forest and 4) *Abies nephrolepis* forest in subalpine and upper montane of humid NE Asia; 5) *Pinus koraiensis* forest and 6) *Pinus koraiensis* and broadleaf mixed forest, the zonal forests of temperate NE Asia; 7) *Betula platyphylla* forest and 8) *B. platyphylla*-*Populus davidiana* mixed forest that occur widely; 9) deciduous broadleaf forest in the lower montane zone, a forest type dominated by *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica*, *Tilia mandshurica* etc.; and 10) *Larix gmelini* forest, the zonal vegetation of cool-temperate NE Asia (Zhou 1997). For details on the species composition of these forests, see Wang et al. (2006b).

In each of the six sites, we placed plots along the altitudinal gradient to cover all the vertical forest zones, with an altitudinal interval between plots of 50–100 m. A total of 108 plots were sampled during the summers of 2000–2003. The number of plots at each study sites differed depending on forest types and altitudinal ranges (Table 1). In each plot (20 × 30 m), vascular plant species were recorded and divided into tree, shrub and herb species. Nomenclature follows Fu (1995). Diameter at breast height (DBH) and tree height were measured for trees with DBH ≥ 3 cm. Latitude, longitude, altitude, aspect, position on the slope (POS), and slope for each plot were measured in situ. Aspect was measured in degrees to real north, and transformed into the nine categories in Table 2. POS was recorded as four categories (Table 2).

Climatic variables

We estimated climatic variables for each of the plots using a well-established method (Tang and Fang 2006, Wang et al. 2006a). Monthly mean temperature and precipitation were estimated based on linear models using latitude, longitude and altitude as predictors. Details for the models and model validation have been described in an earlier study and thus not presented here (Wang et al. 2006a).

Climatic indices were calculated for each plot using the estimated monthly temperature and precipitation. Heat sum, water supply and winter coldness are commonly

suggested as crucial climatic limitation for plant biological activity, and thus, may be important in affecting species richness (Woodward and Rochefort 1991, Hawkins et al. 2003). Accordingly, the following three indices were selected for this study: 1) warmth index (WI, °C × month), an index of growing season heat sum. WI is defined as the sum of mean monthly temperatures above 5°C for the months with a temperatures higher than 5°C (Kira 1945); 2) mean temperature for the coldest month (MTCM, °C), a surrogate for absolute minimum temperature (Prentice et al. 1992); and 3) annual precipitation (AP, mm).

Other indices, including mean temperature for the warmest month (MTWM), cold index (Kira 1945), annual potential and actual evapotranspiration (PET and AET, respectively), and the moisture index of Thornthwaite (1948), were also estimated for each plot. However, they were highly correlated with one of the three indices mentioned above (e.g. $r > 0.99$ between WI, PET and MTWM). Thus they were excluded from subsequent statistical analyses to avoid collinearity. PET was equal to AET for all our plots, suggesting no water deficit in our study region (Thornthwaite 1948, Francis and Currie 2003).

Data analysis

Total, tree, shrub and herb species richness and 12 explanatory variables were used in data analyses, including geographic, climatic, topographical, forest structural and forest type variables (Table 2). Tree density and biomass were used as forest structural parameters (Pausas 1994). Biomass for each plot was estimated with DBH and tree height using site and species specific allometric relationships (Wang et al. 2008). We classified the 10 forest types into four categories to examine the effect of seasonal canopy openness on species richness: evergreen needle-leaf forest, needle-leaf and broadleaf mixed forest, deciduous needle-leaf forest and deciduous broadleaf forest. We also classified the 10 forest types into early, middle and late successional forests to examine the influence of successional stages (Table 2).

Species richness, slope and tree density were square-root transformed, while biomass and altitude were log-transformed prior to analyses. WI, AP, MTCM and latitude were not transformed, for transformation could not reduce skewness and kurtosis (Table 2). For each model, we further used diagnostic plots to check the normality and homoscedasticity of residuals.

The effects of climatic and local factors on species richness were analyzed with general linear models (GLMs) and F-tests, using sequential (type-1) sums of squares

Table 1. Geographic, climatic and vegetation outlines of the six sites sampled in northeast China. Abbreviations: AMT, annual mean temperature; AP, annual precipitation.

Site	Latitude (°N)	Longitude (°E)	Altitude (m)	AMT (°C)	AP (mm)	Number of plots
Mt. Changbai	41°23'–42°36'	126°55'–129°0'	500–2691	–7.3–4.9	600 ~ 1340	65
Mt. Datudingzi	44°24'	128°12'	350–1669	2–4	550 ~ 650	8
Mt. Mao'er	45°20'–45°25'	127°30'–127°34'	300–805	2.8	724	6
Liangshui	47°07'–47°14'	128°48'–128°56'	280–707	–0.3	680	13
Mt. Baikalu	51°36'	123°04'	450–1460	–5.6––1.2	360 ~ 500	10
Genhe	50°49'–50°51'	121°30'–121°31'	780–1142	–5.4	450 ~ 550	6

Table 2. Descriptive statistics for species richness and explanatory variables used in the study. For variables that were square-root (*) or log (**) transformed in subsequent analysis, skewness and kurtosis were given for transformed data. Abbreviations: SD, standard deviation. WI, warmth index; AP, annual precipitation; MTCM, mean temperature for the coldest month; POS, position on slope.

	Max	Min	Mean	SD	Skewness	Kurtosis
Richness (/plot)*						
Total	72	9	38.7	14.18	-0.23	-0.24
Tree	23	1	8.7	4.93	-0.41	-0.80
Shrub	17	1	8.6	4.15	-0.66	-0.11
Herb	49	2	21.7	9.73	-0.32	0.74
Geographic variables						
Latitude (°N)	51.9	42.1	44.5	3.35	1.21	0.02
Altitude (m)**	1945	344	964.6	464.82	-0.10	-1.08
Climate						
WI (°C month ⁻¹)	59.5	17.8	40.3	13.52	-0.15	-1.52
AP (mm)	1132.4	469.6	787.6	190.00	0.07	-0.98
MTCM (°C)	-16.6	-29.2	-20.6	3.67	-1.19	0.49
Forest structure						
Tree density (hm ⁻²)*	3116.7	383.3	1250.9	548.07	0.26	0.15
Biomass (mg hm ⁻²)**	663.7	56.1	260.4	122.56	-0.19	0.32
Topography						
Slope (°)*	30.0	0.0	5.7	7.36	0.50	-0.72
Aspect	Nine categories: N, NE, E, SE, S, SW, W, NW and flat land with no aspect					
POS	Four categories: bottom, lower, middle and upper slope					
Forest type						
Canopy seasonality	Four categories: evergreen need-leaf, needle-leaf and broadleaf mixed, deciduous needle-leaf, and deciduous broadleaf forest ¹					
Successional stage	Three categories: early, middle and late successional forest ²					

¹Evergreen need-leaf forests: *Picea jezoensis* forest and *Abies nephrolepis* forest; needle-leaf and broadleaf mixed forests: *Pinus koraiensis* forest and *P. koraiensis* and broadleaf mixed forest; deciduous needle-leaf forest: *Larx olgensis* forest and *L. gmelini* forest; and deciduous broadleaf forest: other forest types.

²Early successional forest: *Betula platyphylla* forest and *B. platyphylla*-*Populus davidiana* mixed forest; middle successional forest: deciduous broadleaf forest; and late successional forest: other forest types (Zhou 1997).

(Schmid et al. 2002). We first analyzed the influence of different factors on regional-scale richness pattern (along both latitude and altitude gradients). The variables entering the model were selected by a forward stepwise procedure (Pausas 1994, Austin et al. 1996). We did not include interactions between variables and the quadratic terms of continuous variables (Austin et al. 1996, Krefl and Jetz 2007) in our final analyses, because many of them were not significant and only explained a very small amount of variation.

In a second analysis, we entered site (the six study site) into GLMs before other variables to examine the roles of climatic and local factors in explaining the within-site variation of species richness (Schmid et al. 2002). In the present study, the within-site variation of richness was mainly caused by the altitudinal gradient, for we sampled plots along altitude in each site. We used this method to examine whether the within-site effects of the predictors were different from that at the regional scale. The variables entering the model were selected by the same procedure described above, except that this time we started forward selection from a model including site (instead of a null model in the first analysis) and added variables after site.

Our plots were samples from six spatially separated study sites (Fig. 1). Hence, we also analyzed the data with linear mixed models, using site as random effect. However, the results were nearly the same as the GLMs fitting site before other variables (Supplementary material, Appendix S1 and S4–S6), and thus we used GLMs in the final analyses.

Spatial autocorrelation in geographic diversity data can inflate type I errors in statistical analyses (Lennon 2000, Diniz-Filho et al. 2003). Hence, for bivariate relationships, we tested the significance using the modified t-test of Dutilleul et al. (1993). For multivariate models, Dutilleul's method was used to correlate the observed and estimated richness for each model to test the overall statistical significance of the model (Hawkins et al. 2007). We also calculated Moran's I values for both species richness data and the residuals of the models, to examine how the spatial autocorrelation in species richness was explained by the predictor variables (Hawkins and Porter 2003, Diniz-Filho et al. 2003). Since the model residuals did not contain significant positive spatial autocorrelation at the short distances, the influence of spatial autocorrelation on F-tests was very slight (Hawkins and Porter 2003).

The analyses were conducted with the software R 2.6 (R Development Core Team 2007), SAM 3.0 (Rangel et al. 2006) and the Mod_t_test program (Legendre 2000).

Results

Regional patterns of species richness

A total of 421 species were recorded in the 108 plots, belonging to 72 families and 205 genera, of which 137 were woody species (25 families and 55 genera), and 284 were herb species (50 families and 149 genera). The 137 woody species included 50 tree species (13 families and 22 genera) and 87 shrub species (18 families and 36 genera).

A correlation analysis showed that, species richness generally decreased with increasing altitude and latitude (Table 3). However, shrub richness did not change remarkably with latitude, while herb richness was not significantly correlated with altitude.

Relative effects of climate vs local factors at the regional scale

We first examined the influence of different factors on species richness at the regional scale (along both latitude and altitude). Results of both correlation analysis and GLMs suggested that (Table 3 and 4, Supplementary material, Appendix S2), growing season warmth (WI) was the major correlate of total, tree and shrub species richness, which accounted for 66, 72 and 34% of variation, respectively (Fig. 2). However, winter coldness (MTCM) was more powerful in explaining herb richness (34%). Precipitation showed only a weak effect on species richness.

Climatic factors accounted for 73–76% of variation in total and tree richness, and ca 34% for shrub and herb species (Table 4). Local factors together explained only 13–15% of variation in total and tree species richness, but explained 36–38% for shrub and herb species.

Relative effects of climate vs local factors at the local scale

By fitting site before other variables, we examined the effects of climate and local factors on the within-site variation of species richness (i.e. along altitudinal gradient) (Table 4, Supplementary material, Appendix S3). WI was the only climatic variable entering the models, and explained 35, 44 and 17% of variation in total, tree and shrub species richness, respectively. Interestingly, no climatic variable entered the model for herb species. Local factors together accounted for 16, 5, 16 and 41% of variation in total, tree, shrub and herb species richness,

Table 3. Correlations between geographic and climatic variables and species richness. Adj. p, p values corrected for spatial autocorrelation, WI, warmth index; AP, annual precipitation; MTCM, mean temperature for the coldest month.

Richness	Latitude		Altitude		WI		AP		MTCM	
	r	Adj. p	r	Adj. p	r	Adj. p	r	Adj. p	r	Adj. p
Total	-0.40	<0.001	-0.57	0.040	0.81	0.002	-0.09	0.719	0.66	<0.001
Tree	-0.44	0.010	-0.56	0.039	0.85	0.001	-0.09	0.741	0.71	<0.001
Shrub	0.19	0.090	-0.68	0.008	0.60	0.021	-0.53	0.016	0.08	0.321
Herb	-0.46	0.021	-0.22	0.303	0.48	0.025	0.18	0.417	0.58	0.001

Table 4. Summary for the effects of climate and local factors on species richness at two scales: the regional scale vs the local scale. This table was summarized from the models in Supplementary material, Appendix S2–S3. For each variable, percentage of sum of squares explained (%SS) was reported. Slope and biomass were excluded from all the models and thus not presented. Abbreviations: WI, warmth index; MTCM, mean temperature for the coldest month; AP, annual precipitation, POS, position on slope.

%SS	Total			Climatic variables pooled			WI			MTCM			AP		
	Region	Local	Total	Region	Local	Total	Region	Local	Total	Region	Local	Total	Region	Local	Total
Total	87.5	51.8	72.7	72.7	35.4	65.5	65.5	35.4	7.2	0.0	0.0	0.0	0.0	0.0	0.0
Tree	88.2	48.9	75.5	75.5	43.9	71.5	71.5	43.9	0.0	0.0	0.0	0.0	4.0	0.0	0.0
Shrub	71.5	33.0	34.0	34.0	17.3	34.0	34.0	17.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Herb	69.3	41.2	33.8	33.8	0.0	0.0	0.0	0.0	33.8	0.0	0.0	0.0	0.0	0.0	0.0
	Local factors pooled			Canopy seasonality			Successional stage			Topography (aspect and POS)			Tree density		
	Region	Local	Total	Region	Local	Total	Region	Local	Total	Region	Local	Total	Region	Local	Total
Total	14.8	16.4	1.2	1.2	7.3	11.3	11.3	7.3	7.1	1.0	0.8	1.0	1.0	0.8	0.8
Tree	12.7	5.0	2.5	2.5	1.1	3.6	3.6	1.1	0.0	4.5	1.4	4.5	4.5	1.4	1.4
Shrub	37.5	15.7	7.6	7.6	0.0	13.8	13.8	0.0	8.1	0.0	0.0	8.1	0.0	0.0	0.0
Herb	35.5	41.2	3.0	3.0	25.8	18.7	18.7	25.8	9.8	4.0	2.6	9.8	4.0	2.6	2.6

respectively. The within-site effects of all variables (except successional stage) were lower than that at the regional scale, especially for climatic variables (Table 4).

Influence of local factors on species richness

Canopy seasonality explained 24 and 8% of variation in shrub richness at the regional and local scales, respectively (Table 4). However, it showed only weak effects on herb richness. To visualize the influence of canopy seasonality, we used the residuals of richness fitted to climatic variables (Supplementary material, Appendix S2) to analyze the difference among forest groups (Schmid et al. 2002). The results showed that, shrub richness was significantly lower in evergreen forest than in the deciduous forests when the effect of climate had been accounted (Fig. 3), suggesting a remarkable effect of seasonal canopy opening. However, no significant difference was observed for other species groups ($p > 0.05$ in all cases).

Successional stage accounted for 9 and 26% of variation for herb richness (Table 4). However, it explained little variation (<1.1%) for tree and shrub species. Middle successional forest had a significantly higher richness for total and herb species than the late and early successional forests (when the effect of climate had been accounted). However, this difference among successional stages was not observed for woody (tree and shrub) species at $p < 0.05$ (Fig. 3).

Local topographical factors (aspect and POS) accounted for 7–19% of variation in total, shrub and herb species richness, but had only weak effect on tree species. Slope did not show any explanatory power for species richness (Table 4, Supplementary material, Appendix S2–S3).

Tree density showed a positive effect on tree richness but a negative effect on herb and total species richness (Supplementary material, Appendix S2–S3). Biomass of the tree layer had no effect on richness for all species groups.

Spatial autocorrelation in species richness

Species richness showed strong positive spatial autocorrelation at the short distance classes, and showed negative or positive autocorrelation at intermediate distance (Fig. 4). Climatic variables (Supplementary material, Appendix S2) reduced most of the spatial autocorrelation for tree and total species richness, but significant autocorrelation still remained for herb at some distance classes. Adding the local factors into the models significantly reduced the remaining spatial autocorrelation, especially for herb species (Fig. 4).

Discussion

Species richness in relation to climate

Many authors have pointed out that species richness is often strongly correlated with climate (O'Brien 1993, Francis and Currie 2003, Hawkins et al. 2003, Kreft and Jetz 2007). However, most of the previous studies at a large scale were based on species richness within geographic grids (but see Gentry 1988, Austin et al. 1996, Leathwick et al. 1998,

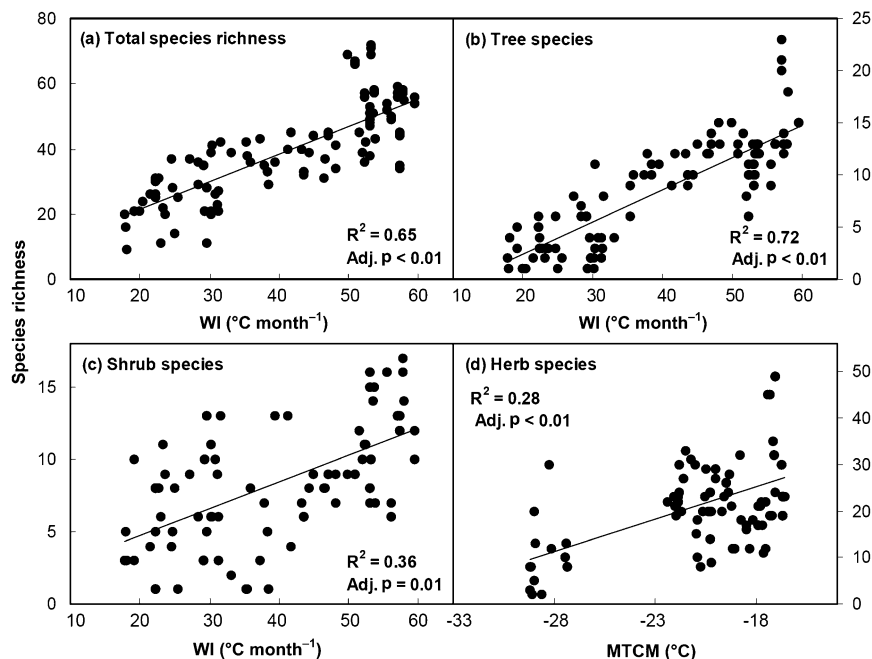


Figure 2. Relationships between species richness and climatic indices. WI, warmth index; MTCM, mean temperature for the coldest month; Adj. p, significance corrected for spatial autocorrelation.

Harrison et al. 2006). In this analysis, we used data at plot scale to examine geographic diversity patterns in relation to climate. We found that most of the variation in total and tree species richness was explained by climatic variables at the regional scale (73–76%; Table 4). Of the climatic variables, heat sum was the major correlate of total and woody species richness both at the regional and the local scales, while herb richness was more related to winter coldness than heat sum. Contrary to other studies (Hawkins et al. 2003, Krefl and Jetz 2007), water availability is not a limiting factor for forest diversity in the cold humid forest region of NE China (Table 3, 4). These results support the hypothesis that species richness is more closely correlated with energy availability in regions without water deficit

(Pausas and Austin 2001, Hawkins et al. 2003, Krefl and Jetz 2007).

There are two versions of the energy hypothesis: the productivity hypothesis and the ambient energy hypothesis (Hawkins et al. 2003). The former proposes that plant richness is primarily constrained by the limitation of solar energy and water availability on productivity, while the latter suggests that higher biological activity and lower winter mortality at higher temperatures are major mechanisms for more species (see reviews in Hawkins et al. 2003). In this study, total and woody species richness were the most closely associated with WI (Table 3, 4). WI is a direct measure of ambient temperature and thus the result supports the ambient energy hypothesis (Hawkins et al. 2003). At the same time, WI is highly correlated with forest productivity in humid East Asia (Ohsawa 1995) and the result can also support the productivity hypothesis. However, herb richness was more related to winter coldness than heat sum (Table 3, 4), and thus our results provide more support to the ambient energy hypothesis.

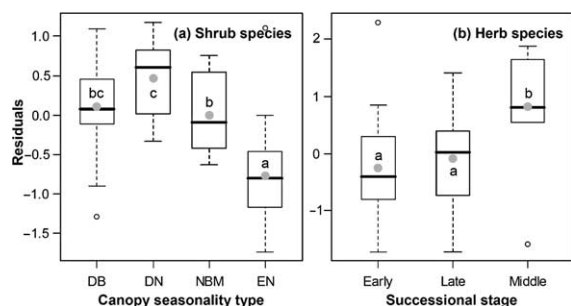


Figure 3. Effects of (a) canopy seasonality and (b) successional stage on understory species richness. Residuals of richness fitted to climatic variables (Supplementary material, Appendix S2) were used for analyses to examine the difference among forest groups when the effect of climate on richness had been accounted (Schmid et al. 2002). Grey dots indicate mean values. Forest groups that shared a same letter were not different at $p < 0.05$ (p value adjustment method: Bonferroni). Abbreviations: DB, deciduous broadleaf forests; DN, deciduous needle-leaf forests; NBM: needle-leaf and broadleaf mixed forests; EN: evergreen needle-leaf forests.

Differences among growth forms

Pattern of species richness is different for different functional groups (Pausas 1994, Pausas and Austin 2001). Differences among growth forms in this study can be summarized as the following three aspects.

1) Difference in geographical patterns. While total and tree species richness changed with both latitude and altitude, shrub richness did not change with latitude and herb richness did not vary with altitude significantly (Table 3). With higher latitudes in NE China, heat sum decreases, while climatic continentality increases (Zhou 1997). The latter leads to an increasing seasonal canopy opening, which in turn results in higher shrub diversity (Fig. 3) (Specht and

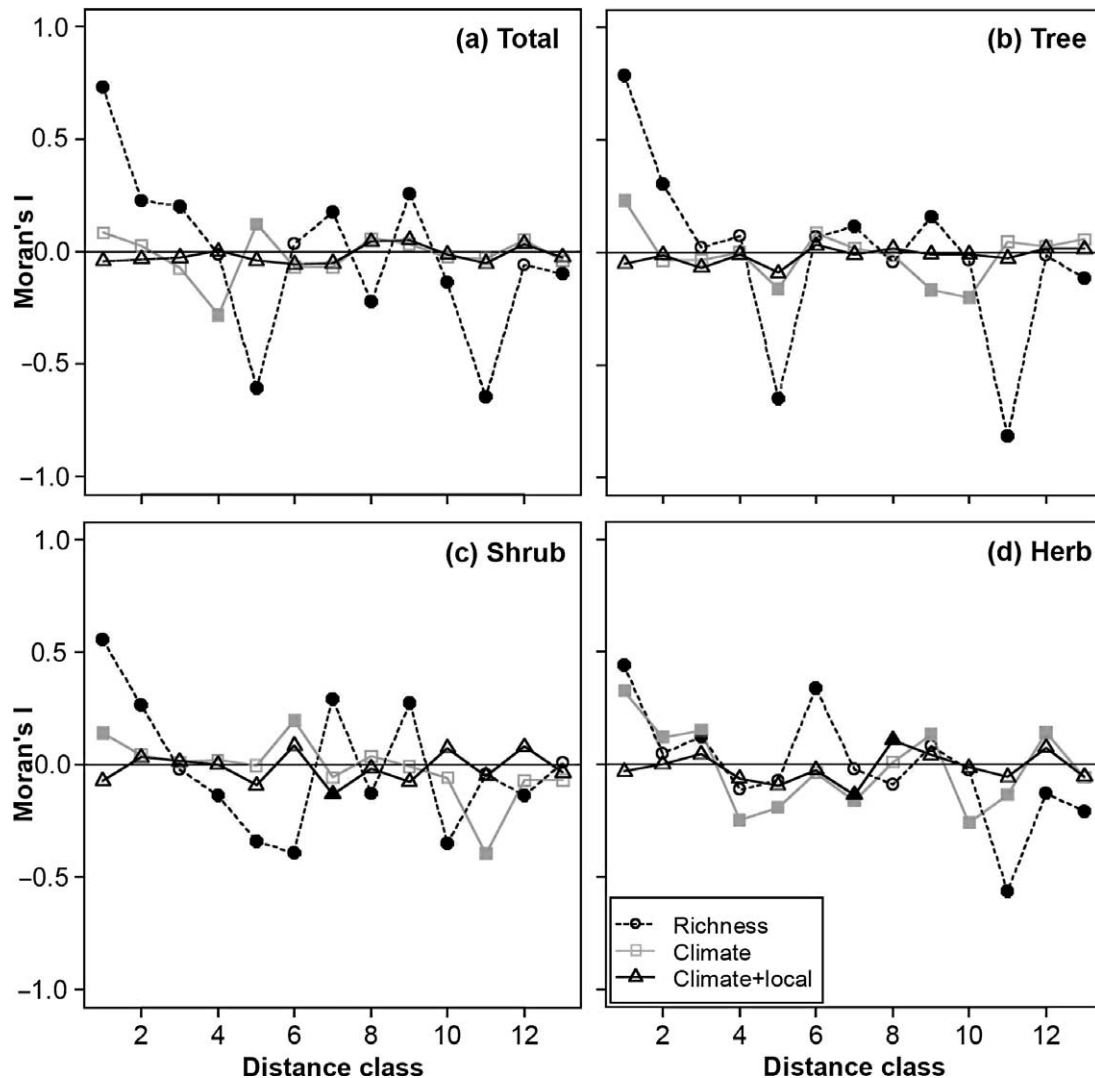


Figure 4. Correlograms of Moran's I showing patterns of spatial autocorrelation of species richness and residual autocorrelation after sequentially adding climatic variables and local factors (local) into the models. For variables used, see Supplementary material, Appendix S2. Filled circles (squares or triangles) indicate significant Moran's I values ($p < 0.05$), while open circles (squares or triangles) denote non-significant values.

Specht 1993, Quigley and Platt 2003). On the other hand, decreasing heat leads to lower species richness (Fig. 2). The opposite effects of heat sum and continentality may explain why shrub richness does not show a significant change along the latitudinal gradient.

2) Difference in the relative effects of climate vs local factors. From our results, it is clear that total and tree species richness are mainly limited by climate, while herb richness is more related to non-climatic factors (especially at the local scale; Table 4). The influence of climate on understory richness is mediated by the tree layer. Local scale studies have revealed that abiotic factors and disturbance affected understory richness via tree layer through various pathways, with the relative effects of different mechanisms changed with forest structure and tree species (Weiher 2003, Laughlin et al. 2005, Laughlin and Grace 2006). Thus it is natural that understory richness is much less related to climate compared with tree richness. Coincide with this, our results also showed that, climate was the main cause of spatial autocorrelation in tree richness, while the

spatial structures in shrub and herb richness were shaped by both climate and local factors (Fig. 4).

3) Difference in the relative effects of different local factors. An interesting finding of this study is that, while shrub richness was sensitive to seasonal canopy openness, herb richness was sensitive to forest successional stage (Fig. 3). Canopy seasonality is an important mechanism affecting plants under canopy in addition to gap dynamics (Quigley and Platt 2003), and we also observed significant difference between deciduous and evergreen forests for shrub species richness. The lack of sensitivity of herb richness to canopy seasonality may be caused by the fact that deciduous forests generally possess a denser shrub layer (unpubl.). Consequently, herb species can not benefit from seasonal canopy opening.

Herb and total species richness was the highest in the middle-successional forests, consistent with other studies along the successional gradients (Pausas and Austin 2001, Saha 2003) and the hypothesis that community richness is higher under a medium disturbance (Connell 1978).

However, it remains unclear why shrub and tree richness were not different among successional stages in our study, which deserves further investigation. Some authors suggested that the remarkable increases of herb abundance caused by disturbance is an important mechanism affecting understory richness, and found that annual herb richness are more sensitive than richness of other species groups to habitat heterogeneity created by fire (Laughlin et al. 2005, Laughlin and Grace 2006). Pausas et al. (1999) also showed that herb species had a higher beta diversity than woody species in post-fire shrublands. It seems that different functional groups differ in their sensitivity to disturbance and successional stage, and these differences may be scale dependent.

Tree density showed a positive effect on tree richness (Supplementary material, Appendix S2–S3), reflecting remarkable influence of sampling effect on species richness. However, tree density had a negative effect on herb richness, which reflect the effect of canopy tree shading and perhaps also other factors associated with tree density, e.g. water and mineral resources and litter depth (Laughlin and Abella 2007). However, the influence of trees on understory plants is very complex. For an example, Laughlin et al. (2005) found that understory richness was negatively related to subalpine fir basal area, but positively related to Engelmann spruce basal area. These complex effects may be a reason why tree layer biomass had no explanatory power for species richness in this study.

The importance of local factors on geographic diversity gradients

Climate has long been recognized as major correlate for large scale diversity patterns, and it is also well known that community richness is affected by a variety of local factors at the local scale. However, the relative importance of climate vs local factors has rarely been quantified systematically at a large scale (but see Austin et al. 1996, Harrison et al. 2006). Our results showed that local factors played an important role in explaining geographic diversity gradients, especially for understory species (Table 4).

At the local scale, no climatic variable entered the model for herb species (Supplementary material, Appendix S3). Though we can not conclude that climate has no effect on herb richness along the altitudinal gradient, it is clear that the influence of local factors is far more powerful. This result is consistent with our previous findings that herb richness generally did not change significantly with altitude, and was more related to local factors (e.g. tree density) rather than estimated temperature (Zhao et al. 2004, Feng et al. 2006). In New Zealand, Ohlemüller and Wilson (2000) also found that both latitude and altitude had no explanatory power for herb richness, while the difference in dominant canopy trees showed a significant effect. Even for tree species, Austin et al. (1996) had demonstrated that local environment should not be ignored in any analysis of geographic richness patterns (see also Table 4). Our results, together with these studies, suggest the importance of examining diversity patterns using multivariate gradients to compare the differences among functional groups (Pausas and Austin 2001). We also suggest more studies on

community richness to be conducted across both latitude and altitude to examine the relative roles of different mechanisms at different scales (Austin et al. 1996, Grytnes 2003, Harrison et al. 2006).

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