Tree species richness in northeastern China: geographical variation and minimum areas

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Abstract: The geographical patterns of tree species richness in forest communities have been studied widely, but little is known about the geographical variation of the estimated species richness and minimum areas using species-area curves. A differential technique based on the species-area relationships (SAR) was developed for estimating the minimum area (A_{min}) capturing 60-80% of the species in each plot, which is an important characteristic of a forest community. The relationship between estimated species richness (ESR) from the SAR and the corresponding minimum area is described by the linear model $ESR = 0.0051 \times A_{min}$ ($R^2 = 0.98$, $p < 0.0001$). Both the ESR and the minimum area exhibit similar geographical variations with a significant increase along altitudinal and a decrease along latitudinal gradients. The spatial variations of the ESR were partitioned into three geographical components and their combined effects. Altitude accounted for 40% and 45% of the total variation in the ESR and the minimum area, respectively. While latitude accounted for 69% and 61% of the total variation in the ESR and the minimum area, respectively. Thus, latitude is the main determinant which influences the geographical variation of the ESR. As far as we know, this study presents the first report of the geographical patterns of the minimum area in temperate forests.

Abbreviations: ESR–Estimated Species Richness; OSR–Observed Species Richness; SAR–Species-Area Relationship.

Introduction

Based on an investigation of species diversity within delimited research plots, Arrhenius (1921) concluded that the number of species increases continuously as the area of a habitat increases. That so-called species-area relationship (SAR) shows the rate at which species diversity increases with increasing area (Hubbell 2001, McGill 2003). The SAR is often represented graphically by a curve and the shape of the species-area curve has been used to determine the minimum area that captures all species in a particular plant community (Cain 1938, Cain and de Oliveria Castro 1959). This "minimum area" has adequately been defined as the smallest area within which the species composition of a community is adequately represented (Mueller-Dombois and Ellenberg 1974).

The "minimum area" concept has been applied and studied by many scholars (Barkman 1989, Cannone 2004, Gadow and Hui 2007, Cristaudo et al. 2015). The main problem with the species-area curve approach is that the number of species never reaches an asymptote due to the natural heterogeneity of the site and the spatial distributions of individual species (Williamson et al. 2002, Dengler 2009). Some researchers therefore believe that the minimum area concept is not a useful one because it does not present new information about ecological communities (Hawkins and Harmoll 1980, Greig-Smith 1983).

The reported minimum areas may vary widely among research sites. For example, the minimum sample area may only be 500-600 m^2 in temperate mixed broadleaf-conifer forests (Hao 2000, Fang et al. 2012) while adequate sample plot areas for capturing the majority of species ranged from 1000 m^2 to 2500 m^2 in tropical rainforests (Kent and Coker 1994, Drees 1954, Rice and Westoby 1983, Taylor and Dunlop 1985). These examples from the literature show that about 1000 m^2 may be regarded as a sample plot area which would include most, if not all, of the tree species in the temperate forests in Northeastern China.

The latitudinal variation of species diversity, where species richness tends to peak near the equator and to decline towards the poles, has been widely recognized by biologists (Peet 1978, Wang et al. 2006). Longitudinal variations in species richness have been documented for birds (Jetz and Rahbek 2001), marine organisms (Gray 2001) and vascular plants (Qian 1999). Species richness tends to increase with increasing altitude creating a diversity "bulge" at mid-range altitudes and then decreases again. The altitudinal effect thus represents a "hump-shaped" gradient (Rahbek 2005, Grytnes 2003, McCain 2005, Wang and Fang 2012).

Table 1. Names, localities, areas and vegetation types of the 21 observational plots.

No.	Plot name	Forest type	Plot area (m²)	Longitude (°E)	Latitude (°N)	Altitude (m)
1	Liangshui1	OGF	200×260	128.8803	47.1700	400
2	Liangshui2	OGF	200×260	128.8798	47.1736	375
3	Liangshui3	OGF	200×260	128.8801	47.1718	381
4	Liangshui4	OGF	200×260	128.8796	47.1754	380
5	Jiaohe1	OGF	200×260	127.7392	43.9745	704
6	Jiaohe2	OGF	200×260	127.7382	43.9716	622
7	Jiaohe3	OGF	200×260	127.7613	43.9663	731
8	Jiaohe4	OGF	200×260	127.7565	43.9688	628
9	Jiaohe5	HMF	200×260	127.7392	43.9745	469
10	Jiaohe6	HMF	200×260	127.7407	43.9725	483
11	Jiaohe7	HMF	200×260	127.7367	43.9736	461
12	Jiaohe8	NMF	200×260	127.7162	43.9664	444
13	Jiaohe9	NMF	200×260	127.7187	43.9697	493
14	Jiaohe10	MF	200×260	127.7404	43.9660	492
15	Jiaohe11	MF	200×260	127.7416	43.9635	494
16	Jiaohe12	MF	200×260	127.7427	43.9611	498
17	Jiaohe13	MF	200×260	127.7369	43.9652	471
18	Jiaohe14	MF	200×260	127.7380	43.9627	468
19	Jiaohe15	MF	200×260	127.7392	43.9602	470
20	Mt.Changbai1	HMF	200×260	128.1287	42.3202	899
21	Mt.Changbai2	NMF	200×260	128.1300	42.3487	748

OGF indicates old-growth forest; MF indicates mature forest; NMF indicates near-mature forest; HMF indicates half-mature forest.

Numerous theoretical and empirical studies have been devoted to revealing the underlying reasons for the aforementioned geographical variations. Species-richness responses to geographical gradients are commonly driven by climate, topography and soil chemistry (Dix and Smeins 1967, Turner 2004, Thornthwaite 1948). Mid-geographical zones usually have high humidity and moderate temperatures and they may still be suitable, albeit marginal habitats for species adapted to extremely cold or dry conditions. These middle range zones permit the co-existence of taxa which otherwise have high-, mid- or low-geographical centers of distribution (Kessler 2001, Bhattarai et al. 2004, Santamaría et al. 2003).

The observed species richness (OSR) from field surveys was commonly related to specific geographical regions, but little is known about the geographical variation of the estimated species richness (ESR) from SAR, in particular regarding forest communities. The minimum area may represent the species composition of a very specific forest community. Thus, we hypothesize that the ESR and the minimum areas both respond to geographical variability. To test this hypothesis 21 large research plots located in different regions were pooled to detect the effects of geographical variables on the ESR and the minimum area of forest communities in Northeastern China.

Materials and methods

Field observation and data collection

The observations used in this study were collected in 21 research plots in three protected nature reserves (Fig. 1). The experimental sites are located between 42-48°N and 127-129°E, where altitudes range from 375 to 899 m above sea level. The mean annual temperature in the plots varies from -4.35 to 1.06°C, the annual precipitation from 618 to 1209 mm. In each of the 21 plots, all trees with a diameter at breast height (dbh) of 1 cm or more were identified, measured and mapped. Species richness varies from 21 to 42 species per plot (Table 1). Based on the previous studies mentioned above, the 5.2-ha area is large enough to establish a SAR in each field plot.

Simulating species-area curves

To develop species-area curves, ten thousand independent square cells of side length d (1, 2…200 m) were randomly simulated in each study plot. The average number of species (S) for all cells of a given size d was plotted over the cell area ($A = d^2$).

The resulting SAR may be described by various mathematical models. The first mathematical descriptions of the species-area relationship were proposed using a power function and an exponential model (Gleason 1922). He and Legendre, who developed a generalized species-area model, advocate that species-area relationships should follow a saturation function (He and Legendre 1996). In this analysis, we adopt the logistic model:

$$S = (a\,A^c) / (1 + bA^c),$$

where S is the number of species, A is the area of a square cell used in this study, and *a*, *b* and *c* are parameters. When the parameter c = 1, the model will be that proposed by Monod (1950). The parameters which were estimated using the "nls" function of the R software are shown in Table 2.

Table 2. Estimated parameters of the logistic model, estimated species richness (ESR) and minimum area (A_{min}) of 21 research plots within three protected nature reserves.

Plot	Parameters			ESR	OSR	A_{min}	ESR/OSR
	a	b	c				
Liangshui1	0.4957***	0.0203***	0.5856***	16	22	2577	0.7273
Liangshui2	0.5331***	0.0208***	0.5121***	14	21	2754	0.6667
Liangshui3	0.7081***	0.0268***	0.4857***	15	24	2662	0.6250
Liangshui4	0.7017***	0.0227***	0.4443***	14	23	2929	0.6087
Jiaohe1	0.2402***	0.0059***	0.6721***	27	36	5557	0.7500
Jiaohe2	0.4364***	0.0115***	0.5642***	22	32	4686	0.6875
Jiaohe3	0.8316***	0.0151***	0.4556***	24	37	5727	0.6486
Jiaohe4	1.2617***	0.0137***	0.3797***	26	42	6613	0.6190
Jiaohe5	0.7789***	0.0151***	0.4825***	26	36	5752	0.7222
Jiaohe6	0.7856***	0.0185***	0.4839***	22	32	4628	0.6875
Jiaohe7	0.8176***	0.0192***	0.4412***	18	29	4163	0.6207
Jiaohe8	1.1435***	0.0258***	0.5130***	29	37	4533	0.7838
Jiaohe9	0.5566***	0.0119***	0.5999***	32	41	5521	0.7805
Jiaohe10	0.6859***	0.0174***	0.5318***	24	33	4488	0.7273
Jiaohe11	0.7503***	0.0183***	0.4894***	22	33	4486	0.6667
Jiaohe12	0.5345***	0.0161***	0.5794***	22	30	3771	0.7333
Jiaohe13	0.6242***	0.0156***	0.5103***	21	31	3877	0.6774
Jiaohe14	0.7913***	0.0182***	0.5213***	26	35	4891	0.7429
Jiaohe15	1.0060***	0.0207***	0.4828***	27	38	5263	0.7105
Mt.Changbai1	0.8279***	0.0178***	0.5585***	31	40	5079	0.7750
Mt.Changbai2	0.8927***	0.0180***	0.5414***	33	42	5507	0.7857

Significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.
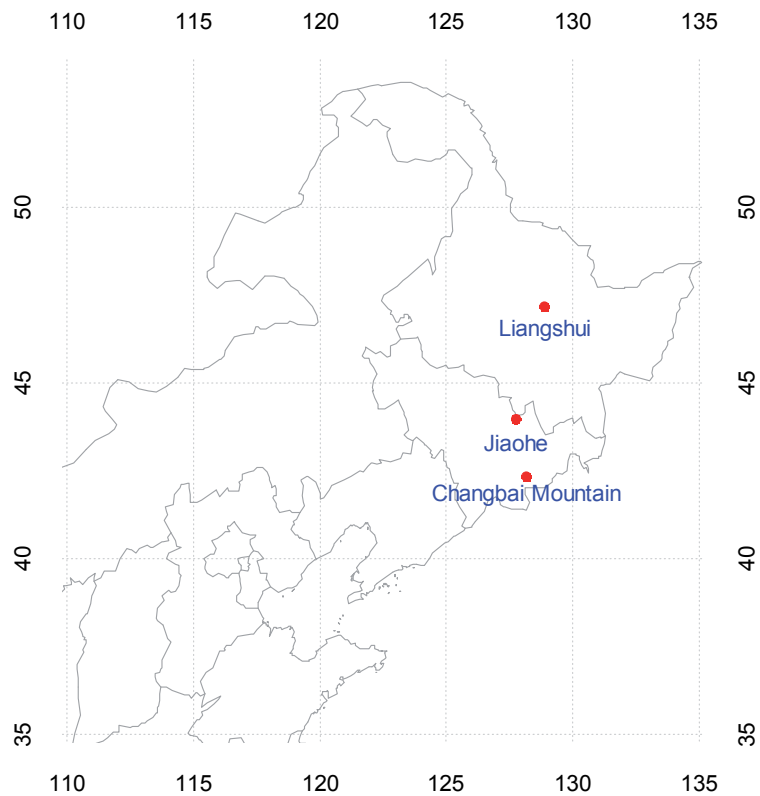
Figure 1. Map showing the relative positions of three nature reserves in Northeastern China.

Calculating the minimum area

Barkman (1968) suggested the use of a "differential curve" in which the increase in species number (ΔS), instead of species number S, is plotted over the area. A similar approach is adopted in our study. The species-area curve is expressed mathematically as $S = f(A)$, where S is the number of species and A is the area of a square cell. S increases with increasing A, until an asymptotic value of S is reached. If A $= A_0$, then $S_0 = f(A_0)$. If $A = A + A_0$, then $S_t = f(\Delta A + A_0)$. Thus, the change rate of the number of species is equal to $\Delta S = S_t - S_0 = f(A_0 + \Delta A) - f(A_0)$.

A problem with this method is the fact that the significance of certain discrete steps in the declining rate ΔS is difficult to test. Thus, an iterative process was adopted. The S0 was calculated with A_0 ranging successively from 1 to 40000 m^2 at 1 m^2 intervals. S_t was then calculated with the area increasing at
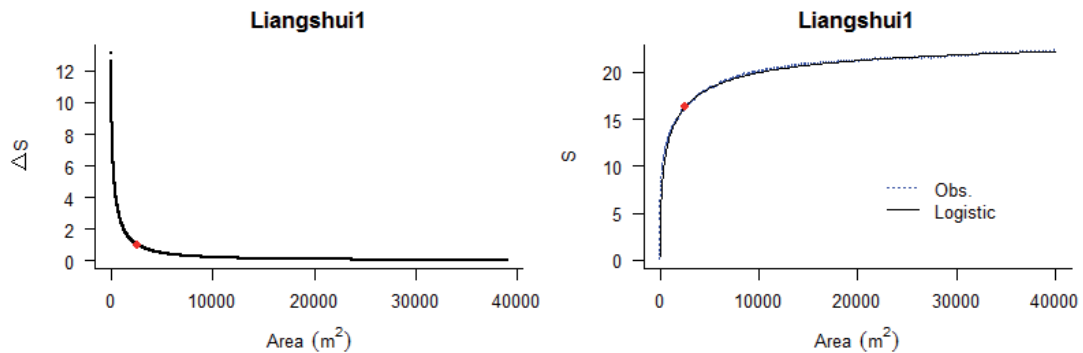
Figure 2. An example of calculating the minimum area for Liangshui1 research site. A circle in each diagram shows the cut-off point where ΔS equals one and the corresponding area is the minimum area. S indicates the estimated number of species.

a constant lag ΔA, the relationship between ΔS and A_0 being affected by the size of ΔA (Figure A1 in Appendix). ΔA can be regarded as a unit of area that contains a certain number of species. In this particular study, each step of ΔA is set equal to 1000 m² which represents an effective area which would include most tree species in the research forests in Northeastern China, as discussed in the introduction.

The next step involved plotting ΔS against A_0, thus indicating the discrete rate of change in the number of species per increasing ΔA at different sampled areas in each plot. If the number of species reaches an absolute maximum ("complete saturation") with increasing sampling area, then the species change rate approaches zero: ΔS ≈ 0. Although the increase in the number of species in an unbounded area does not stop, it usually slows down. Thus, we define the minimum area (A_{min}) as that area A_0 where the area increase produces exactly one new species (ΔS = 1). Then, the ESR corresponding to the minimum area can then be calculated from the logistic model which was fitted to each field plot.

Variation partitioning method

The variation of the response variables can be partitioned into several components accounted for by different explanatory variables and their combined effects (Borcard et al. 1992, Legendre and Legendre 2012). The ESR and the minimum area are our two response variables. We use three explanatory variables altitude, longitude and latitude which form the expanded data table. In this approach, the adjusted R^2 is used to assess the partitions which are explained by the explanatory variables and their combinations. Peres-Neto et al. (2006) found that this is an unbiased method for variation partitioning. In this study, the variation of each of the two response variables of interest (ESR and minimum area) was partitioned into fractions [a]~[h] using the three explanatory variables. The fractions [a]~[c] are explained uniquely by altitude, longitude and latitude, respectively; fractions [d]~[f] are the intersections between two variables, which indicate the amount of variation explained by linear models of the two explanatory variables; and fraction [g] is the intersection among all three variables.

Results

Estimating the minimum area

The SAR curve was fitted to each of the 21 research plots using the logistic model. The ESR and the minimum areas were then calculated from these SAR's. The results show, as expected, an increase of the ESR with increasing minimum areas in all research plots. The ratios of the ESR to the OSR varied between 0.6 and 0.8, which shows that approximately 60-80% of all observed species may be included in the corresponding contiguous minimum areas in the studied forest communities (Table 2).

In each of the research plots, greater sampling areas include increasing numbers of species, which is expressed by the species-area curves. However, the different curve parameters reflect different change rates in the numbers of species in the different forest plots. With increasing sampling area, and with the number of species gradually reaching a maximum, the differences in the curve shapes among the forest types become gradually more pronounced (Fig. 2; Fig. A2 in Appendix).

The relationship between the ESR and the minimum areas (A_{min}) within the 21 research plots and three forest types is shown in Figure 3. This relationship can be described by the following linear model: ESR = 0.0045×A_{min}+ 2.58 (R^2 = 0.74, p < 0.0001). This model may be regarded as a summary model for three forest types of the broadleaf-conifer mixed forest in Northeastern China.
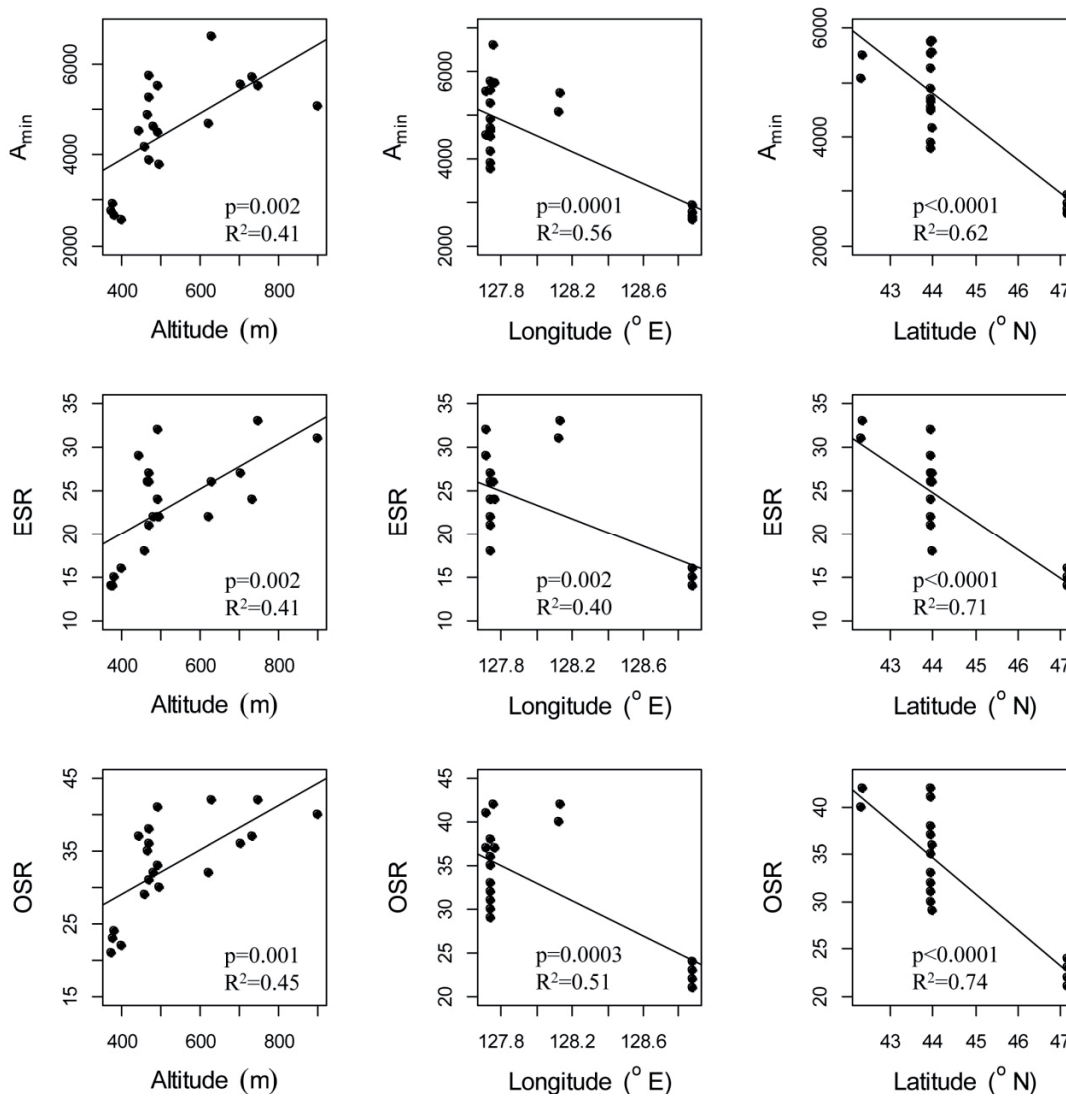
Geographical variations of species richness and minimum area

The species richness (ESR and OSR) and the minimum areas can be successfully described by three geographical variables (altitude, longitude and latitude) for 21 research plots. The geographical variation is similar in all plots, exhibiting a significant increase along altitudinal gradients and decrease with longitudinal and latitudinal gradients (Fig. 4).

The variation partitioning analysis shows that the three geographical variables jointly explained a relatively large proportion of the total variation in the ESR and the minimum
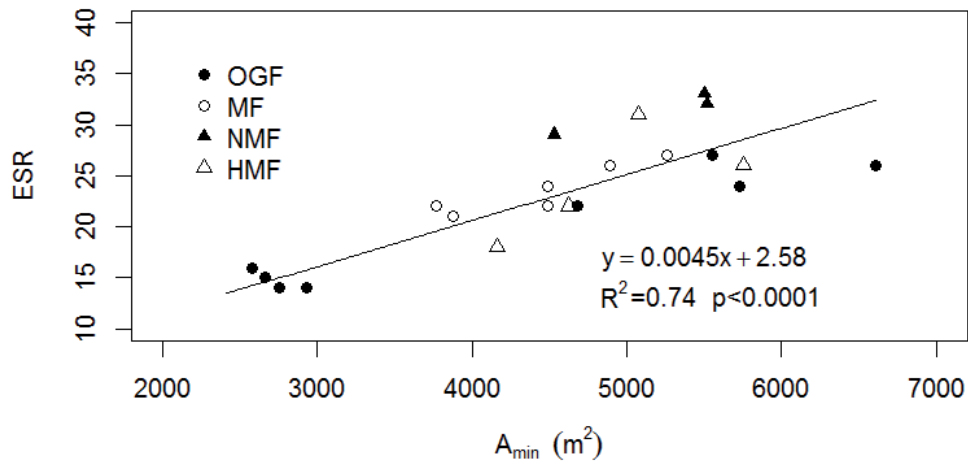
Figure 3. The relationships between estimated species richness (ESR) and minimum area (A_{min}) for 21 research plots in four forest types. OGF indicates old-growth forest; MF indicates mature forest; NMF indicates near-mature forest; HMF indicates half-mature forest.

Figue 4. Geographical variations of species richness (ESR and OSR) and minimum area (A_{min}). The results of the linear regression are also shown.

(a) Diagram explaining partitions   **(b) Estimated species richness**   **(c) Minimum area**
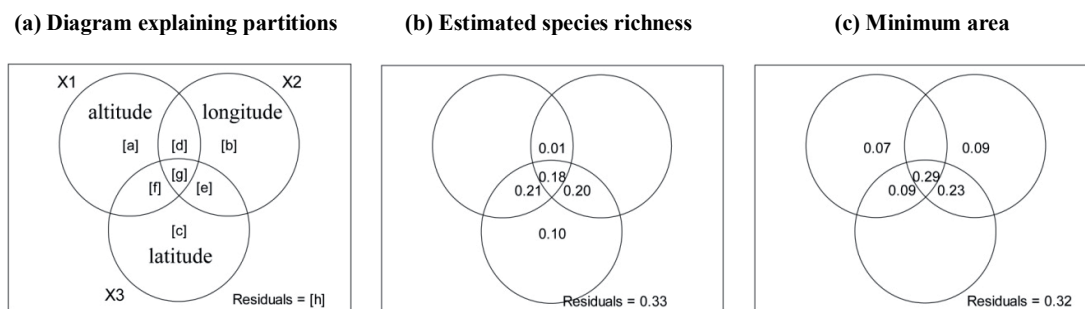
Figure 5. Results of variation partitioning with respect to components accounted for by three explanatory variables and their combined effects. The fractions explained uniquely by each of the three variables are [a] to [c], joint fractions between two variables are [d] to [f], and the joint fraction between all three variables is [g]. Values less than zero are not shown.

area (Fig. 5). The fraction [a+d+f+g] estimates the amount of the variation explained by the altitudinal gradient. It accounted for 40% and 45% of the total variation in the ESR and the minimum area, respectively. Fraction [b+d+e+g] explained by the longitudinal gradient accounted for 39% and 61% of the variation in the ESR and the minimum area, respectively. The fraction [c+e+f+g] shows a high explanatory power for the ESR and the minimum area, mostly explained by the latitudinal gradient which accounts for 69% and 61% of the variation in the ESR and the minimum area, respectively.

Discussion

Plant species richness strongly affects animal species richness (Qian 2007) as well as overall catabolic activity and catabolic diversity of bacterial communities in the soil (Stephan et al. 2000). It has been shown that species richness also exerts a positive influence on ecosystem functioning in forests (Chisholm et al. 2013, Šímová et al. 2013). Thus, species richness has been used widely as a basis for determining conservation and ecosystem management strategies. However, suitable inventory data of species richness are rare, and data acquisition is costly. Species richness in a plant community can be estimated from the number of higher order taxonomic units present (Mazaris et al. 2010). Furthermore, the species-area relationship (Gerstner et al. 2014), rarefaction curves and species-accumulation curves (Williams et al. 2007) were also used to estimate species richness. But it is still difficult to predict species richness at larger regional scales.

In our approach, the minimum area is the area at which the addition of one increment of ΔA results in the addition (statistically speaking) of one new species. At the minimum area, the value of ESR is 60-80% of the OSR in research plots. Therefore, it is a variable percentage of the observed richness because the maximum plot size is arbitrary relative to the unknown total number of species. Furthermore, it is impossible to standardize the area by asking "at what area can I have 80% (or some other arbitrary percentage) of the total" because the total number of species is often unknown. From a sampling point of view, however, that number is as interesting as the minimum area. The SAR cannot be directly used to calculate the "minimum area" with the estimated asymptote.

This is because we have no guarantee, a priori, that there is an asymptote and therefore we have no way of guessing at what point 80% of the asymptote is reached.

The local patterns of species richness are regulated by environmental filtering, interspecific competition and propagation (Shurin and Allen 2001, Myers and Harms 2009). In contrast, geographical variations in forest communities are very common, but complex and often difficult to interpret (Gaston 2000). Altitude represents a complex combination of related climates closely correlated with other environmental factors (Ramsay and Oxley 1997). A number of recent studies suggest that species richness exhibits obvious altitudinal changes (Rahbek 2005, Grytnes 2003, McCain 2005, Wang and Fang 2012) due to the suitable humidity and moderate temperature in the middle range zones. Our results provide evidence that altitude, which accounts for 40% of the variation of the ESR, plays an important role in regulating species richness in our temperate forests.

Fraction [f]+[g] indicates the joint effect explained by linear model of the altitude and latitude; and fraction [e]+[g] indicates the joint effect by longitude and latitude. They largely account for the variations in the ESR and the minimum area when compared with fraction [d], which is the joint effect explained by altitude and longitude but not explained by latitude. This indicates that the effects of altitude and longitude on both the ESR and the minimum area closely depend on the latitudinal variation. In addition, the change of longitude is less than 1.2 degrees among the 21 research plots. Thus, latitude had a dominant effect on both, the ESR and the minimum area, among the three geographical variables. This merely reflects the fact that altitudes are decreasing from south to north. Consequently, we conclude that richness patterns mainly result from the latitudinal variation. Compared with longitudinal variations (Atkinson et al. 2007), the latitudinal variations of species richness have been well documented for other forest communities (Turner 2004, Dunn et al. 2007, Iwasa et al. 1995).

The potential mechanisms controlling species richness patterns are among the important issues studied by ecologists (Francis and Currie 2003) and attempts to explain richness patterns include contributions based on the "geographical area hypothesis" (Turner 2004, Gaston and Blackburn 2000,

Hawkins and Porter 2001), the "metabolic hypothesis" (Allen and Gillooly 2007), the "productivity hypothesis" (Šímová et al. 2013), the «mid-domain effect hypothesis» (Colwell et al. 2004) and the «water-energy dynamics hypothesis» (Li et al. 2013). Previous research has shown that the main driving force controlling richness patterns are climatic gradients. Moderate climates may contribute to dicopatric speciation, the evolutionary formation of new species, and higher species richness values (Kessler 2001, Bhattarai et al. 2004, Santamaría et al. 2003). Temperature has shaped the geographical patterns of species richness in both eastern Asia and North America as proposed by the metabolic theory of ecology (Wang et al. 2009). We focused on the response of the ESR and the minimum areas to geographical variability. Thus, a new statistical framework was needed which provides better ways of evaluating these hypotheses. Three geographical variables are strongly associated with temperature and precipitation (Appendix: Table A1). However, potential driving mechanisms of climate have not been studied in this study but should be investigated in the future.

Community composition is generally sensitive to local environmental conditions, such as soil chemistry, topography, sunlight and atmospheric humidity (Zhang et al. 2010). The variation of environmental conditions inevitably affects the minimum area derived from local species-area curves. In our study, minimum areas varied from 2577 to 6613 m^2 involving 21 large research plots in a variety of locations. We developed a quantitative approach that allowed 60-80% of observed species to be detected for the corresponding minimum areas. These minimum areas show significant geographical variations.

As far as we know, this study is the first to report minimum areas for forest communities on geographical gradients. Previous studies documented minimum areas between 514 and 600 m^2 in Northeastern China (Hao 2000, Fang et al. 2012). The minimum areas in the above-mentioned studies were calculated using different methods, resulting in smaller areas than those in our study, which may also be attributed to smaller plot sizes. When sample plots are small, some species are not captured. As the area of the sample plots increases, the species-area curve will change until a new balance is reached. Consequently, large observational research plots, as used in our study, are essential for investigating species-area relationships.

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Electronic Appendix

Figure A1. An example showing the relationships between ΔS and A_0.

Figure A2. Calculating the minimum area from differential curve and logistic model.

Table A1. Correlation coefficients between climatic variables and geography.

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