

Effects of geographical extent on the determinants of woody plant diversity

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Despite a long history of study, the mechanisms underlying the geographical patterns of species richness are still controversial. Patterns and determinants of species richness are well-known to vary with spatial scale. However, most studies on the effects of scale have focused on grain size whereas the quantitative effects of geographical extent are rarely tested. Here, using distribution maps of 11 405 woody species found in China and associated environmental data to the domain, we investigated the influence of geographical extent on the determinants of species richness patterns. Our results revealed consistent extent dependence of all species, narrow- and wide-ranged species: with the expansion of geographical extents, the explanatory power of climate (i.e. environmental energy, water availability and climatic seasonality) increased, while the explanatory power of habitat heterogeneity and human activities decreased. Although the primary determinant of species richness patterns varied significantly at small to meso-geographical extent, we showed that species richness was predominantly determined by environmental energy at large extent. Our findings indicate that differences in geographical extent may have led to the controversies regarding the primary determinants of richness patterns in previous studies, and that a multi-scale perspective not only with regard to grain-size but also extent is likely to shed new light on this old debate of what determines richness patterns.

Broad-scale geographical patterns of species richness are a remarkable feature of nature, and have attracted the attention of ecologists and biogeographers since the time of Darwin (Darwin 1859, see also Huston 1994, Brown and Lomolino 1998). To understand the mechanisms underlying these patterns, previous studies have explored the relationships between species richness and many factors, including environmental energy (Currie 1991, Rahbek and Graves 2001, Hawkins et al. 2003, Wang et al. 2011), water availability (O'Brien 1998, 2006), climatic seasonality (O'Brien 1998), habitat heterogeneity (Kerr and Packer 1997, Rahbek and Graves 2000, 2001) and human activities (Balmford et al. 2001, Gaston 2005, Fang et al. 2006). Based on these relationships, many hypotheses have been proposed in the last three decades. However, the relative roles of different factors in shaping species richness patterns are still controversial, and no consensus has been reached for the primary determinant, probably due to the effects of spatial scale on geographical patterns of species richness in these studies (Rahbek and Graves 2001, Whittaker et al. 2001, Rahbek 2005, Nogués-Bravo et al. 2008).

The effect of spatial scale on geographical patterns of species richness has long been recognized (Shmida and

Wilson 1985, Wiens 1989, Levin 1992, Böhning-Gaese 1997), and has been the focus of analytical exploration (Rahbek and Graves 2000, 2001, Jetz and Rahbek 2001, Wang et al. 2009). Two aspects of spatial scale have been recognized: spatial resolution (i.e. grain size or grid cell size) and geographical extent (i.e. study area) (Rahbek 2005). The former refers to the size of minimum sampling unit or grid cells (pixel), while the latter refers to the total length of the study gradients (one-dimensional studies) or domain of the study area (two-dimensional studies). While the effects of spatial resolutions have been widely studied (Rahbek and Graves 2001, Wang et al. 2009, Qian and Kissling 2010, Belmaker and Jetz 2011), the influence of geographical extent on the determinants of species richness has been poorly elucidated.

Geographical extent used in previous studies of species richness varies considerably, ranging from several hectares (Silvertown et al. 2001, Tilman et al. 2001, Cheng et al. 2012) or km² (Tang and Ohsawa 1997, Swenson et al. 2011) in the studies of local ecological communities, to continents and the entire globe in the studies of large-scale species richness patterns (Currie and Paquin 1987, Adams 1989, Jetz and Rahbek 2001, Francis and Currie

2003, Hawkins et al. 2003, Wang et al. 2011). The magnitude of the difference in geographical extent reaches 10^{10} from local to global studies, which may be one of the reasons for the controversy on the determinants of species richness patterns. For example, meta-analysis of previous studies suggested that the effects of primary productivity and climates on species richness varied substantially from local to global extents (Mittelbach et al. 2001, Field et al. 2009). However, quantitative assessments of the effects of geographical extent on the relationships between species richness and environmental factors are rare (see Nogués-Bravo et al. 2008 for a study along elevational gradient).

Species with different range sizes may respond differently to environmental factors due to the differences in body size and (or) dispersal limitation (Ritchie and Olff 1999, Normand et al. 2011, Wang et al. 2012b). For example, studies indicated that narrow-range plant species in eastern Asia and Europe are more strongly influenced by dispersal limitation than wide-range species, and can hardly reach all environmentally suitable regions due to strong dispersal limitation (Normand et al. 2011, Wang et al. 2012b). Consequently, species with different range sizes show different richness–environment relationships (Jetz and Rahbek 2002, Kreft et al. 2006). However, few studies explored the influence of range size on the extent dependence of species richness–environmental relationships.

Here, using a large database of Chinese woody plants, we quantitatively evaluated the extent dependence of the explanatory power of different environmental factors in explaining large-scale species richness patterns. China spans a huge geographical area, and has broad climate gradients ranging from tropical over subtropical to temperate and boreal regions, and to extremely dry desert. Meanwhile, China harbors > 30 000 vascular plants, of which > 11 000 are woody plants (Fang et al. 2011). Therefore, China provides an ideal template for exploring the effects of geographical extent on the determinants of species richness patterns. In our study, using the distribution maps of 11 405 woody species in China (Fang et al. 2011), we aim to elucidate 1) how geographical extent influences the explanatory power of different environmental factors on species richness, 2) if the relative importance of different environmental factors in explaining species richness varies with extent expansion, and 3) the influence of species range size on extent dependence. We expect that the effects of different environmental factors on species richness respond differently to extent expansion, which leads to a ‘re-shuffle’ of the relative importance of environmental factors at different extent. We also expect different extent dependence for species with different range sizes.

Material and methods

Distributions of China's woody plants

The distributions of woody plants in China are documented in the Database of China's Woody Plants (ver. 2.0; Wang et al. 2009, Fang et al. 2011). The database encompasses 11 405 woody species found in China, including 3165 trees, 7205 shrubs and 1035 lianas. In the database, the species

distributions were compiled from all national and provincial floras in China published before 2009 (including more than 150 and 120 volumes of national and provincial floras, respectively), as well as a great number of local floras and inventory reports across the country. To improve the quality of the database, we invited 21 experts of plant distributions in different regions to check and complement the distribution map of each species in each region. Therefore, the species distributions in the database include both herbarium specimen records and experts' field observations. The taxonomy in the database has been updated according to the newly published Flora of China (revised English version of Flora Republicae Popularis Sinicae, <www.efloras.org>), in which the taxonomy reflects the current understanding of each group, and is therefore comparable with the floras of other regions. For more details of the database, see <www.ecology.pku.edu.cn/plants/woody/index.asp>.

Environmental data

Environmental data used here included the variables of environmental energy, water availability, climatic seasonality, habitat heterogeneity and human activities (see Supplementary material Appendix 1 for a full list and the statistics of the variables). All variables were calculated to a resolution of 50×50 km for final analysis.

Environmental energy

Mean annual temperature (MAT), mean temperature of the coldest and the warmest quarters (MTCQ and MTWQ, respectively), warmth index (WI), and annual potential evapotranspiration (PET). In previous studies, PET is often used to represent ambient energy (Currie 1991) and was calculated using Thornthwaite and Hare's (1955) method. WI, representing the annual accumulation of growing temperature, is widely used in the studies on species and vegetation distributions in eastern Asia (Kira 1991), and was calculated following Fang and Lechowicz (2006):

$$WI = \text{Sum of } (MMT - 5), \text{ where } MMT > 5^{\circ}\text{C}$$

where MMT was the monthly mean temperature.

Water availability

Mean annual precipitation (MAP), annual actual evapotranspiration (AET), precipitation of the driest quarter (PDQ), moisture index (MI) and water deficit (WD). In previous studies of species richness patterns, AET was often used as the surrogate of primary productivity (Hawkins et al. 2003). In China, AET is strongly correlated with MAP (Wang et al. 2011). WD is defined as the difference between PET and AET, measuring the biological aridity of a region (Francis and Currie 2003). MI and AET were calculated following Thornthwaite and Hare (1955).

Climatic seasonality

Mean annual and diurnal ranges of temperature (ART and MDR, respectively), and temperature/precipitation seasonality (TSN and PSN, respectively). ART was calculated as the mean difference between the maximum temperature

of the warmest month and minimum temperature of the coldest month. MDR was defined as the mean difference between monthly maximum and minimum temperature. TSN was defined as the standard deviation (SD) of monthly mean temperature, while PSN was defined as the coefficient of variation (CV) of monthly precipitation.

Climatic data except for PET, AET, WI, MI and WD were obtained from the WorldClim website (<www.worldclim.org>), and their resolutions were all 30×30 arc second (ca 1×1 km²). The value of a 50×50 km² grid cell was calculated as the average of all 1×1 km² grid cells within it.

Habitat heterogeneity

Elevational range (TOPO), number of vegetation formations (VEG), Shannon–Wiener diversity index for vegetation formations (VEGH), and spatial ranges of MAT and MAP (RMAT and RMAP, respectively) within a grid. TOPO is a surrogate of topographic heterogeneity (Rahbek and Graves 2001, Ruggiero and Hawkins 2008), and was estimated as the difference between the highest and lowest elevation in a grid cell using DEM data (1×1 km) obtained from United States Geological Survey (USGS, <http://eros.usgs.gov/>). VEG and VEGH represent the land cover heterogeneity. VEG of a grid cell was extracted from the 1:1 000 000 vegetation map of China (Hou 2001), in which China's vegetation is divided into ca 69 000 polygons belonging to 573 formations. The average vegetation polygon size is 140 km² (ca 12×12 km). VEGH was calculated using the area proportions of vegetation formations in a grid cell. RMAT and RMAP represent climatic heterogeneity, and were estimated as the difference between the highest and lowest MAT and MAP, respectively.

Human activities

We used human population density (HPD), gross domestic product (GDP) and area of cropland in each grid cell (CROP) to evaluate the intensity of economic and agricultural activities. HPD and GDP were obtained from China Statistical Yearbook for Regional Economy (2003–2005), which provides county-level population density and GDP in China. We interpolated the county-level data into rasters with the resolution of 50×50 km. CROP in a grid cell was extracted from the vegetation map of China (Hou 2001).

Geographical extent

To explore how geographical extent influences species richness–environment relationships, we set 17 levels of geographical extent with size of 25, 50, 100, 150, 200, 250, 300, 350, 400, 450, 500, 550, 600, 650, 700, 750 and 875×10^4 km² (corresponding to 100, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, 2000, 2200, 2400, 2600, 2800, 3000 and 3500 grid cells of 50×50 km, respectively). In order to generate a random geographical extent with given size, a spreading-dye algorithm (Jetz and Rahbek 2001) was used. The process is analogical to the expansion of a drop of dye on paper, and can produce random,

continuous, and cohesive geographical regions with given size. Specifically, to generate a random extent, a grid cell was first randomly chosen from all of the 50×50 km grid cells in China as the starting point, from which the region was to be expanded. Then the region was expanded by repeated random selection from the neighbors of chosen grid cells, until the given area of the extent is reached. In the expansion process, the probability of an empty grid cell to be chosen is a linear function of the number of its chosen neighbors. For each level of extent area, 1000 random geographical extents were generated.

Statistical analyses

Multiple regressions were used to explore the species richness–environment relationships in each random geographical extent. In China, most environmental (especially climatic) variables are significantly correlated with each other (Wang et al. 2011), which may reduce the model performance due to multiple collinearity (Faraway 2006). Therefore, we did not use the original environmental variables as predictors in regressions. Instead, we conducted principal component analysis (PCA) for each of the five environmental groups respectively (i.e. environmental energy, water availability, climatic seasonality, habitat heterogeneity and human activities) (Supplementary material Appendix 2). The first three PC axes of each group captured >90% of the variance in the original variables, and were used in regression models to evaluate the effects of each group on species richness. For comparison, we also conducted simple linear regressions using each of the original variables.

Species richness data are significantly right skewed, and are usually Poissonian rather than normal distribution. Therefore, generalized linear models (GLM) with Poissonian residuals were used for all regressions (Faraway 2006). To eliminate the effects of different degrees of freedom when comparing models with different numbers of predictors, adjusted R^2 (R^2_{adj}) was used in our analysis:

$$R^2_{\text{adj}} = 100 - 100 \times (\text{residual deviance/residual DF}) / (\text{null deviance/null DF})$$

where null DF and residual DF are the degrees of freedom of the model and residuals respectively, while null and residual deviance are the deviance in species richness and residuals respectively.

Regressions between the richness of all woody plants and the five environmental groups were conducted within each random extent. The average R^2_{adj} of the 1000 models at each level of extent size was determined, and then was plotted against extent area to assess the extent dependence of species richness–environment relationships. To explore if species with different range sizes show different extent dependence, we repeated all analyses for the 50% of the most wide- and narrow-range species.

Studies suggested that the changes in predictor variance with extent expansion might account for the extent dependence of richness–environment relationships (Whittaker and Heegaard 2003). To evaluate how much the environmental variance at different extents can account for the extent dependence of different environmental groups,

we estimated the proportions of the environmental variance captured by a random extent to the total environmental variance (VAR%), and then plotted them against extent area. In particular, VAR% was calculated as: $VAR\% = \sum \text{var}(PC_i) / \sum \text{var}(PC_j)$, ($i = 1, 2, 3, j = 1, \dots, N$), where PC is the scores of a PC axis, and PC' is the subset of a PC axis in a random extent; N is the total number of PC axes of each environmental group (Supplementary material Appendix 2). Furthermore, regression analysis was conducted, using the R^2_{adj} of environmental models at each extent size as the response variable, and VAR% as the predictors.

Stepwise regression analyses were conducted to further evaluate the influence of geographical extent on the relative roles of the five environmental groups in shaping species richness patterns. In contrast with normal stepwise regression methods, we treated each group as an 'individual variable'. The stepwise regression included the following steps (Wang et al. 2012a): 1) multiple regression models were conducted for each group separately, and the model with the highest R^2_{adj} was selected. 2) For the remaining groups, the one that returned the largest increase in R^2_{adj} was added into the model. 3) Step 2) was repeated until all groups had been included in the model. For each geographical extent, stepwise regressions were conducted for each of the 1000 randomly re-sampled regions. Then, the frequency of environmental factors to enter the regression models as the i th ($i = 1$ to 5) group was calculated. In our analysis, we did not use the model averaging method based on Akaike weights (Burnham and Anderson 2002) to evaluate the relative importance of different environmental factors, because AIC estimates are influenced by the sample size and the spatial autocorrelation structures of the data (Burnham and Anderson 2002, Hoeting et al. 2006).

Data of gridded species richness usually show strong spatial autocorrelation, which will inflate type I error in statistical tests, and lead to more significant results than data actually support (Lennon 2000). Spatial correlograms (expressed by Moran's I) indicated significant spatial autocorrelation in species richness patterns (Supplementary material Appendix 3). Therefore, significance levels (i.e. p values) for regression models were not presented in this study. Instead, we used R^2_{adj} to assess the fitness of regression models.

All statistical analyses were conducted in R (R Development Core Team).

Results

Our results indicated that geographical extent substantially affected the explanatory power (R^2_{adj}) of environmental factors on species richness (Fig. 1). However, different environmental factors responded differently to extent expansion. In particular, the R^2_{adj} of environmental energy, water availability and climatic seasonality rapidly increased with extent expansion at extent $< 600 \times 10^4 \text{ km}^2$ (i.e. 2400 grid cells), maintaining a constant R^2_{adj} at larger extent. In contrast, the R^2_{adj} of habitat heterogeneity and human activities decreased with extent expansion. Specifically, the R^2_{adj} of habitat heterogeneity maintained at 42–44% at

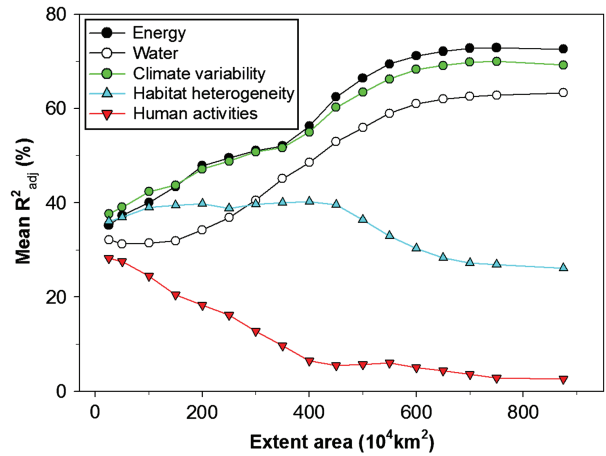


Figure 1. Changes in the explanatory power (R^2_{adj}) of the five groups of environmental factors with geographical extent. Each R^2_{adj} at an extent is the average of R^2_{adj} from 1000 repeated regression models performed in randomly-generated continuous regions using a dye-spread algorithm. For details, see the text.

extent $< 400 \times 10^4 \text{ km}^2$ (1600 grid cells), and decreased with extent expansion at larger extent. The R^2_{adj} of human activities decreased from approximately 30% at the smallest extent ($25 \times 10^4 \text{ km}^2$, 100 grid cells) to about 5% at an extent of $400 \times 10^4 \text{ km}^2$, and then remained at about 3–4% with a further expansion of extents. Simple linear regressions indicated that the individual variables showed consistent extent dependence within each environmental group, and further confirmed the extent dependence observed for each group (Supplementary material Appendix 4).

The relative importance of different environmental factors in explaining species richness also varied with extent (Fig. 1). At extent $< 150 \times 10^4 \text{ km}^2$ (600 grid cells), climatic seasonality had higher R^2_{adj} than other groups, and was the best predictor of species richness, while at bigger extent environmental energy became the best predictor among the five groups (Fig. 1). The R^2_{adj} of habitat heterogeneity was similar to that of climate variables (energy, water and climatic variability) at extent $< 300 \times 10^4 \text{ km}^2$ (1200 grid cells), but became smaller at larger extent (Fig. 1). The R^2_{adj} of human activities was the lowest among the five environmental groups, but was comparable with that of other groups at extent $< 100 \times 10^4 \text{ km}^2$ (Fig. 1).

Compared with all species, the wide- and narrow-range species showed highly consistent extent dependence (Supplementary material Appendix 5): the R^2_{adj} of climatic groups increased with extent, while that of habitat heterogeneity and human activities decreased. For narrow-ranged species richness, environmental energy was not the best predictor any more, as the R^2_{adj} of climatic seasonality was very close to that of environmental energy at all extents (Supplementary material Appendix 5).

For all of the five environmental groups, the average proportions of variance captured in the random extents increased with extent area (Fig. 2). However, compared with the three groups of climate variables, habitat heterogeneity and human activities reached a much higher proportion of their total variance at small to medium extent.

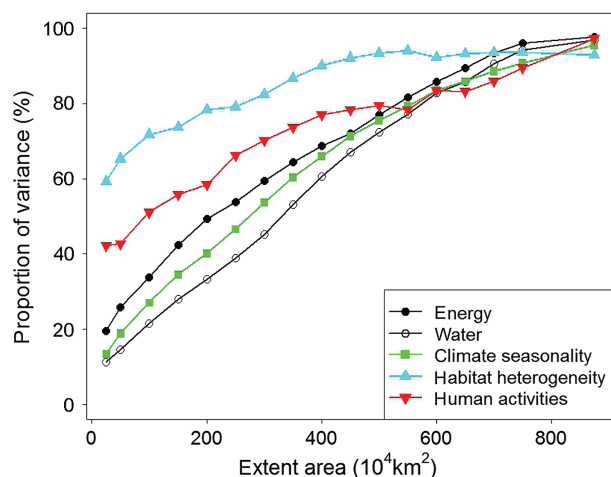


Figure 2. Changes in the mean proportions of environmental variance captured by random extents.

Regression analysis indicated that for climatic groups, the proportion of predictor variance captured in random extents explained 40–57% of the R^2_{adj} variance cross extent (energy: 39.8%; water: 57.4%; climatic seasonality: 47.4%), while only 13 and 7% of the R^2_{adj} variance could be explained for habitat heterogeneity and human activities, respectively.

Stepwise regressions further confirmed that the relative explanatory power of different factors varied with geographical extent (Fig. 3). At extent $< 100 \times 10^4 \text{ km}^2$, all five environmental groups had comparable frequencies to be the primary determinant (i.e. the group first selected by stepwise regression). With extent expansion, environmental energy gradually predominated as the primary determinant at large extent, with habitat heterogeneity as the second selected determinant. In contrast, climatic seasonality was the third selected determinant at medium extent, and was gradually replaced by water availability with extent expansion.

Discussion

Using an assembly of random extents ranging from $25 \times 10^4 \text{ km}^2$ to $875 \times 10^4 \text{ km}^2$, our study quantitatively explored the extent dependence of environmental factors in determining the species richness patterns of woody plants. In our analysis, random extent was generated using a dyespread algorithm (Jetz and Rahbek 2002), which eliminated the effects of the shape of study areas, and the resolution of species distributions and environmental variables. Therefore, our analysis reflected only the effects of extents per se.

As expected, different factors had very different extent dependence: with extent expansion, the explanatory power of different factors varied differently, and more interestingly, their relative roles also changed. At large extent, the effects of climate (i.e. environmental energy, water availability, and climatic seasonality) were much stronger than those of habitat heterogeneity and human disturbance, while at small extent, their effects were similar. These findings quantitatively confirmed literature meta-analysis.

For example, Field et al. (2009) analyzed 393 case studies and found that climate/primary productivity had a much higher primacy than environmental heterogeneity in explaining species richness at extent $> 1000 \text{ km}$, while their primacy was very similar at extent $< 100 \text{ km}$. Our results suggest that the proportion of climatic variance captured in random extent might be one of the major reasons for the extent dependence of richness–climate relationships. This finding confirms previous arguments about the mechanism underlying extent effects (Whittaker and Heegaard 2003). However, the predictor variance captured by random extent may not be the major reason for the extent dependence of habitat heterogeneity and human activities, and further studies are needed to disentangle the mechanism underlying their extent dependence. Moreover, different evolutionary and geological histories in North America, Europe and eastern Asia have been shown to influence the species richness patterns in these continents (Latham and Ricklefs 1993, Svenning and Skov 2007), and may alter scale dependence of richness–environment relationships. Therefore, comparing the extent effects between different continents may shed lights on the generality and mechanisms of the extent dependence of different environmental factors (see Wang et al. 2009 for a study on resolution effects).

It is noteworthy that with the increase of extent size, the overlap between random extents increased, which reduced the variation in model R^2_{adj} (Supplementary material Appendix 6). However, the decline in R^2_{adj} variation with extent expansion should not bias the trends of R^2_{adj} values. A comparison between model R^2_{adj} at the smallest and the largest extent levels indicated that only 2.8–6.9% of the smallest extents yielded R^2_{adj} that was bigger than the mean R^2_{adj} at the largest extent for the three climatic groups, while the proportions were 66.2 and 92.8% for habitat heterogeneity and human activities, respectively.

The distributions of species with different range sizes tend to be determined by different environmental processes due to their different body size and dispersal ability (Jetz and Rahbek 2002, Normand et al. 2011, Wang et al. 2012b), and hence different scale dependence was expected for narrow- and wide-ranged species. Indeed, a recent study indicated that species with different range sizes were associated with environmental processes at different grain size, with narrow-ranged species being more sensitive to fine-grain processes than wide-ranged species (Belmaker and Jetz 2011). However, the difference in their association with environment vanished with increasing grain size. In contrast to their findings and our expectation, we did not find different extent dependence between narrow- and wide-ranged species. This may be partly because of the bigger grain size in our analysis compared with the local grain size used by Belmaker and Jetz ($2500 \text{ vs } 488 \text{ km}^2$) (2011).

The extent dependence of the relative roles of environmental factors provided an explanation for the lasting controversies in previous studies about the primary determinants of species richness patterns. Our analysis confirms that studies performed at continental or global extent tend to reach consistent conclusions, i.e. identifying climate, such as environmental energy, as the primary determinants of richness patterns (Currie and Paquin 1987, Adams 1989,

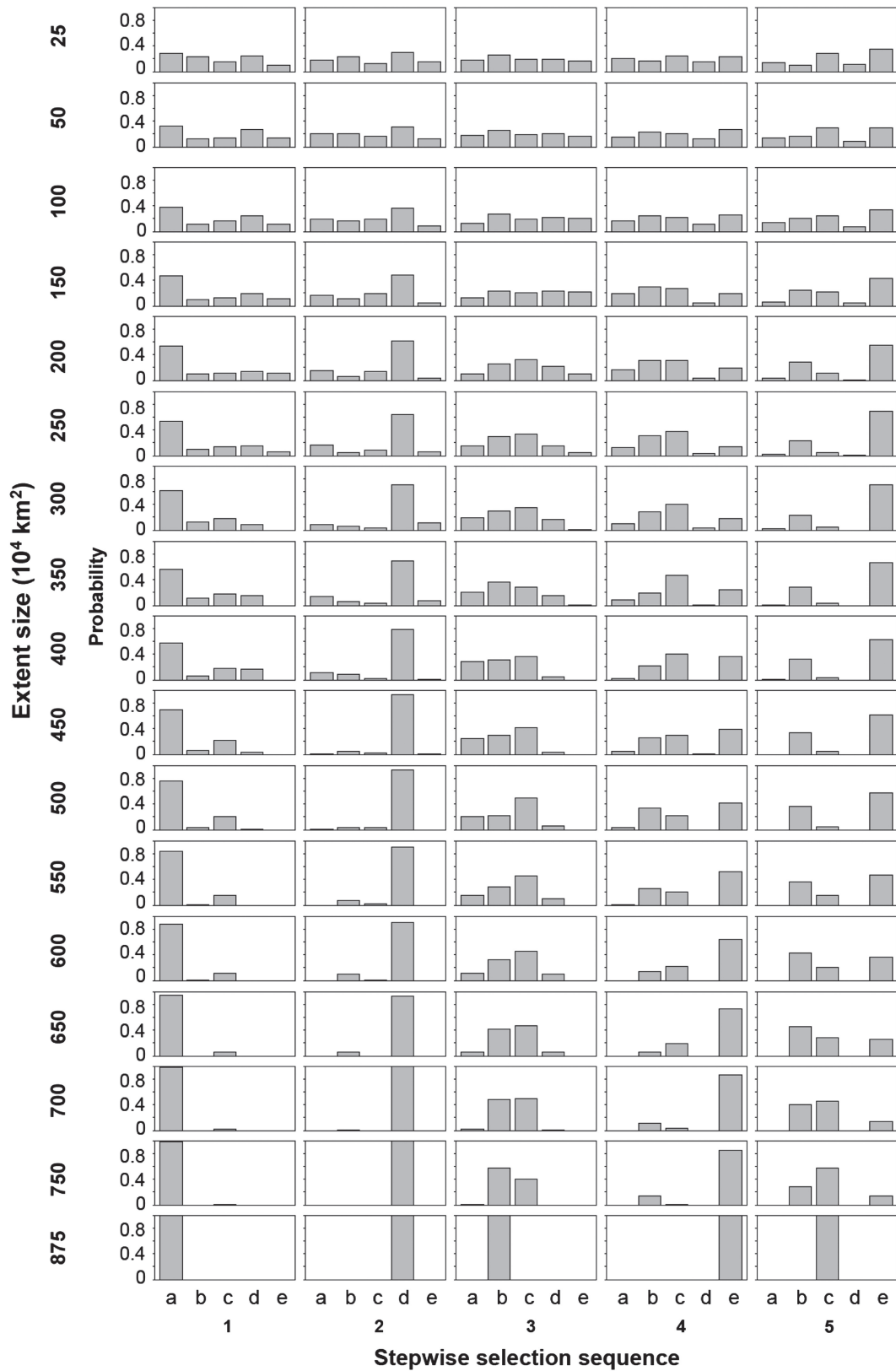


Figure 3. The influence of geographical extent on the roles of environmental factors in shaping species richness patterns. Each row represents the extent with size given by the values on the left side, and the extent size increases from top to bottom. From left to right, each column represents a rank ($i = 1 \sim 5$) at which the environmental variables enter the stepwise regression models. For example, the first column demonstrates the frequencies of the five factors first entering the models at different geographical extent. a – environmental energy; b – water availability; c – climatic seasonality; d – habitat heterogeneity; e – human activities.

Hawkins et al. 2003). In contrast, studies at local to meso- extent are more variable (Takyu et al. 2002, Ferrer-Castan and Vetaas 2005, Ruggiero and Hawkins 2008), and can reach different conclusions in different regions. Furthermore, according to our results and similar findings in previous studies (Sarr 2005), we can expect that with the decrease of geographical extent to local scale ranging from several to thousands of hectares, the explanatory power of climate will decline, while the explanatory power of habitat heterogeneity and human disturbance will increase and is likely to become stronger than the explanatory power of climate in some regions. However, to further explore the extent dependency of different factors at small extents, data that are more precise are needed.

Shmida and Wilson (1985) suggested that increases in species richness within small extents could be ascribed to an increase in habitat diversity. This conclusion has been supported by several previous studies, including a study of geographical patterns of vertebrate species richness in Wyoming (ca $24 \times 10^4 \text{ km}^2$), where Fraser (1998) discovered that habitat heterogeneity was the most important determinant of richness patterns at meso-extents, and accounted for more variance than energy. Similarly, Kerr and Packer (1997) found that habitat heterogeneity (measured by topographic variation) accounted for most variance within mammalian species richness in the southern part of North America, even though PET is the strongest correlate at the extent of North America in its entirety. Our results also suggested that even though environmental energy was the primary determinant of woody plant species richness at the extent of the entire country (Wang et al. 2011), habitat heterogeneity can greatly alter species richness patterns at smaller extents ($< 400 \times 10^4 \text{ km}^2$), and can become the primary determinant of species richness in some regions. Effects of habitat heterogeneity may also change with spatial resolution. Previous studies showed that the effects of habitat heterogeneity on bird species richness patterns significantly increase from finer to coarser resolution (Rahbek and Graves 2001). Future research addressing the interaction between the effects of geographical extent and resolution is needed.

Over the last two centuries, the intensity of human activities has increased dramatically. Human disturbance can change global land cover, resulting in ecosystem fragmentation, habitat loss and consequently local or global extinction of species (Gaston 2005, Fang et al. 2006). Human activities are also a potential driver of species distributions, and have attracted the attention of ecologists, especially in the background of global change in climate and land-use (White and Kerr 2007). For example, recent study showed that human disturbance is likely to bias the altitudinal gradient of plant species richness towards a humped shape (Nogués-Bravo et al. 2008). A meta-analysis (Pautasso 2006) indicated that correlation coefficients between species richness and human disturbance increase with increasing geographical extent, suggesting that the effects of human activities are greater at larger than at smaller extent. In contrast, our analysis found that the effects of human activities decreased with an expansion of geographical extent (Fig. 3). This apparent controversy demonstrates that more studies are needed to elucidate

the extent dependency of human activities. Our findings provide new insights into the effects of human activities on plant species richness patterns in China. Despite a large population and a long history of agricultural exploitation, significant human effects on woody plant distributions in China are restricted to local- to meso-extent regions. At the extent of the entire country, however, the influence of human disturbance on woody plant species richness is negligible ($R^2 = 3\%$). For example, the R^2 of human activities for species richness in the major plains/basins of China was much higher than that at the extent of the entire country. Particularly, in the Northeast Plain, the Middle and Lower Reaches of Yangtze River and the Pearl River Delta, 39–43% of variance in species richness is accounted for by human activities (Supplementary material Appendix 7).

In summary, our study revealed that effects of geographical extent on species richness vary substantially, and can gradually alter the relationships between species richness and environmental factors. These findings suggest that no single geographical extent is ‘universally applicable’ to all studies on patterns of species richness. Comparisons between studies performed at different spatial scales should take these findings into consideration.

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Supplementary material (Appendix E7786 at <www.oikosoffice.lu.se/appendix>). Appendix 1–7.