

Hierarchical effects of environmental filtering and spatial aggregation on β -diversity in forest communities in northeastern China

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May 5, 2020

Abstract

Species composition of communities are firstly affected by environmental filtering where species are progressively selected from the available species pool, and then by spatial aggregation which result in specific spatial organizations. However, the hierarchical effects of these processes across spatial scales are poorly understood. Using dataset of forest plots in northeastern China, we quantified the effects of environmental filtering at region-zone, zone-area, area-district, district-plot scales, and spatial aggregation at within-plot scale on β -diversity along latitudes. We showed that the patterns of β -diversity was mainly dominated by the processes at the region-zone, district-plot, and within-plot scales. We also showed that environmental filtering at the broader scales had stronger effects at higher latitudes, while at the finer scales only at lower latitudes. The effects of spatial aggregation were more prominent at lower latitudes. We highlight that the scale-dependency of the ecological processes needs to be fully considered in future studies.

INTRODUCTION

Understanding the variation in species composition of ecological communities, commonly known as β -diversity, is a major challenge confronting ecologists (Sepkoski 1988; Tuomisto & Ruokolainen 2006; Anderson et al. 2011). Such researches can help to reduce the constant threat to biodiversity loss by contributing to the question of what factors control the distributions and abundance of organisms (Socolar et al. 2016). However, despite substantial efforts to disentangle the drivers of community assemblages (Legendre et al. 2005; Ferrier et al. 2007; Tuomisto 2010), scientists begin to realize that different ecological processes may result in very similar patterns of species composition (Myers et al. 2013).

The realization that the ecological processes are scale-dependent has assisted in uncovering essential features of the community assembly (McGill 2000; Barton et al. 2013; Chase et al. 2018). Processes of community assemblage are assumed to work as constraints with potentially varying strengths at different scales, which hierarchically determine the local community structures (Whittaker et al. 2001; Ricklefs & He 2016). For example, macroclimate (i.e. the overall climate of a large geographical area) is effective at large scales, while microclimate (i.e. the essentially uniform local climate of a small site or habitat) at small scales, (McGill 2000), and biotic interactions within neighborhoods are important at small scales (Huston 1999). Community structures are thus the result of hierarchical constraints at multiple scales (Scherrer et al. 2019).

Among the various ecological processes, environmental filtering and within-habitat spatial aggregation are considered to be the two major mechanisms invoking the spatial variations in species compositions (Plotkin

et al. 2000; Seidler & Plotkin 2006; Laliberté et al. 2014; Kraft et al. 2015). Environmental filtering processes tend to support the survival of specific species in some habitats in preference to other species. Within-habitat spatial aggregations are clustering processes resulting from dispersal limitations, patchy extinction, or interactions among species within a given type of habitat (Kretzschmar & Adler 1993; Öhman et al. 1998; Cornell et al. 2007; Shen et al. 2009). One hypothesis regarding community assembly suggests that environmental filtering and spatial aggregation limit the survival and organization of potentially coexisting species (Myers et al. 2013; Xu et al. 2015). Specifically, environmental filtering processes progressively select the species which are best adapted to local conditions from the regional pool, first by large-scale environmental factors, and subsequently by fine-scale environmental factors (Diaz & Casanoves 1998; De Bello et al. 2013). Then spatial aggregation processes ultimately determine the spatial organization of the selected species (Cornell et al. 2007; Shen et al. 2009). However, to our knowledge, no research has been done to quantify the effects of environmental filtering and spatial aggregation on variations in species compositions across spatial scales.

According to Cornell et al. (2007), specific null models involving habitat features can effectively separate the effects of environmental filtering and spatial aggregation processes at a given spatial scale. On this basis, we divided the study region into different habitats at different spatial scales i.e. the region-zone, zone-area, area-district, plot-district and within-plot scales, ranging from the broad to fine, to examine the ecological processes. Specific null models were then applied by shuffling individuals among and within the various habitats at each spatial scale. The effects of environmental filtering which progressively select species from the species pool at the region to zone level, zone to area level, area to district level, and district to plot level, as well as the effects of spatial aggregation which ultimately shape the spatial organization of the selected species in the observed communities were hierarchically partitioned, as detailed in Figure 1.

With the exception of measuring the magnitudes of the ecological effects at each spatial scale, the focus was on the determination of how the effects of environmental filtering and spatial aggregation on β -diversity had vary along the latitudes. In addition, potential factors related to the environmental filtering processes were explored. According to the division criteria of the vegetation regionalization map of China (Zhang 2007), at the zone level, the species compositions were determined to vary mainly due to the changes in heat patterns from south to north, or along the elevational gradient; at the area level, the causes were mainly the changes in water-heat patterns with the medium geomorphic types; at the district level, local geomorphology was found to be the main reason. We thus related the effects of environmental filtering to a group of climate and plot variables.

Overall, the following hypotheses are formulated: **H₁**, the effects of the environmental filtering processes are stronger at the broader scales due to an increasing environmental heterogeneity with increasing spatial scale (Leboucher et al. 2019). **H₂**, environmental filtering at the broader scales increases with increasing latitudes where fewer species are often observed (Hillebrand 2004), which indicates stronger filtering effects from the regional species pool (Chu et al. 2019). Environmental filtering at the fine scales decreases with increasing latitude since the habitat heterogeneity at the lower latitudes is greater, which supports greater variation in species compositions (Xing & He 2019). **H₃**, the effect of the spatial aggregation at the within-plot scale decreases with increasing latitude. This is due to clustering caused by dispersal limitations and biotic competition which is assumed to be more dominant in species-rich communities when compared with species-poor communities (Myers et al. 2013).

In this study, we first quantified the hierarchical effects of environmental filtering and spatial aggregation on β -diversity patterns across five spatial scales. We also proposed one hypothesis to examine the relative importance of environmental filtering across scales, and two hypotheses to explain the variation of environmental filtering and spatial aggregation along latitudes at each scale. We showed that the pattern of β -diversity was mainly dominated by environmental filtering at the region-zone, district-plot scales, and spatial aggregation at within-plot scale. The environmental filtering at the broader scales had stronger effects at higher latitudes, while at the finer scales only at lower latitudes. The effects of spatial aggregation were more prominent at lower latitudes.

MATERIALS AND METHODS

Study area

The study area is located in northeastern China, in a temperate monsoon climate which is characterized by four distinct seasonal conditions. The annual mean temperature of the area is approximately 2.54°C. The average coldest monthly temperature is -18.42°C (January), and the average hottest monthly temperature is 20.54°C (July). The mean annual precipitation is 622 mm, the rainy season is from June to September.

Forest plot network

During the summer months of 2017 and 2018, an extensive network of forest plots was established. The network includes 397 circular field plots each covering an area of 0.1 ha (radius: 17.85 m; Figure 2). All the natural temperate forest types in the region are included. The plots are located between 40°47.134' to 53deg22.053' N, and 120deg3.546' to 134deg1.008' E. The elevations of the plots range from 79 to 1,255 m. The distances between the individual plots range from 24 to 60 km.

Each circular plot was divided into four subplots in north-south and east-west directions. All trees with DBH [?] 5 cm were assessed. The x/y coordinate, species, DBH, height, and crown width of each tree was recorded. 30,539 individual trees were recorded, belonging to 62 species, 33 genera, and 16 families.

Spatial scales

On the basis of the published vegetation regionalization map of China (Zhang 2007), the region in this study was divided into 3 zones, 9 areas, and 17 districts (Fig. 3). The species compositions and environmental conditions are similar within each habitat, but dissimilar among different habitats. Five different spatial scales were used: zones within the region (region-zone), areas within the zones (area-zone), districts within areas (district-area), plots within the districts (plot-district), and the within-plot scales. These divisions are effective in detecting the signatures of particular ecological processes at each spatial scale.

Beta Diversity Calculation

Following Legendre & De Caceres (2013), the β -diversity was calculated as the total variance of the Hellinger-transformed community matrix, i.e. Y_{Hel} , for each forest plot as follows:

$$BDTotal = Var(Y_{Hel}) = SS\ Total / (n - 1)(1)$$

Where SS_{Total} indicates the sum of the squared deviations from the column means of the entire Y_{Hel} matrix; and n is the number of subplots. Since the Hellinger distance was bounded between 0 and $\sqrt{2}$, the $BDTotal$ had varied between 0 and 1, which indicated that all of the subplots had identical composition and each subplot contained a unique set of species, respectively.

Null Models and Partitioning of Ecological Effects

Individual-based randomizations were used to partition the effects of the environmental filtering and spatial aggregation processes on community compositions. At the region-zone scale, all plots were pooled and the individuals were randomly shuffled 1,000 times. This process removed the effects of both the environmental filtering among the zones and the spatial aggregation within each zone. For each shuffling process, the number of individuals in each plot and the number of species, as well as the abundance of each species, were preserved. Then, the β -diversity of each plot was calculated after each shuffle. The mean value of the 1,000 iterations was used to represent the expected β -diversity at the regional level and referred to as β_{exp_region} . In addition, in order to remove the effects of the spatial aggregation, the plots within each

zone were pooled and the individuals were randomly shuffled for 1,000 times. For each shuffling process, the number of individuals within each plot and the number of species, as well as the abundance of each species within each zone, were preserved. The mean value of the β -diversity values calculated after 1,000 iterations was used to represent the expected β -diversity at the zone level, and referred to as $\beta_{\text{exp_zone}}$. Subsequently, the effects of environmental filtering on each plot were calculated as $\beta_{\text{exp_region}} - \beta_{\text{exp_zone}}$. The mean value of $\beta_{\text{exp_region}} - \beta_{\text{exp_zone}}$ for all the plots was used to represent the effects of the environmental filtering processes at the region-zone scale. Similarly, at the zone-area, area-district, and district-plot scales, the plots were pooled within 9 areas and 17 districts, respectively. Individuals were randomly shuffled 1,000 times within each area, district, and plot, respectively, on an independent basis. For each shuffling process, the number of individuals within each plot and the number of species, as well as the abundance of each species within each area, district, and plot, were preserved, respectively. The expected β -diversities at the area, district, and plot levels (i.e. $\beta_{\text{exp_area}}$, $\beta_{\text{exp_district}}$, and $\beta_{\text{exp_plot}}$) were calculated as the mean values of the 1,000 iterations. The effects of the environmental filtering on each plot at the zone-area, area-district, and district-plot scales were calculated as $\beta_{\text{exp_zone}} - \beta_{\text{exp_area}}$, $\beta_{\text{exp_area}} - \beta_{\text{exp_district}}$ and $\beta_{\text{exp_district}} - \beta_{\text{exp_plot}}$. The mean values of $\beta_{\text{exp_zone}} - \beta_{\text{exp_area}}$, $\beta_{\text{exp_area}} - \beta_{\text{exp_district}}$, and $\beta_{\text{exp_district}} - \beta_{\text{exp_plot}}$ of all the plots was used to represent the effects of the environmental filtering effects at the zone-area, area-district, and district-plot scales. We calculated the observed β -diversity of each forest plot. Then, $\beta_{\text{obs}} - \beta_{\text{exp_plot}}$ was used to measure the effects of the spatial aggregation processes on each forest plot. The mean value of $\beta_{\text{obs}} - \beta_{\text{exp_plot}}$ of all the examined plots was calculated to represent the effects of the spatial aggregation processes at the within-plot scale. A summary of the models used to measure the effects of environmental filtering and spatial aggregation are presented in Table 1.

Key environmental factors identification

A multiple stepwise regression method was used to identify the key factors of the environmental filtering processes. The candidate environmental factors included 21 climate variables and 5 plot attributes. The climate data were collected from *WorldClim Version 2* (Fick & Hijmans 2017). The 5 plot attributes were obtained from field observations, including elevation, slope, aspect, soil depth, and litter thickness. The statistical information of these environmental variables is shown in Table S1.1 of Appendix S1. To mitigate the inherent collinearity among the climate variables, the 11 temperature variables and the 8 precipitation variables, respectively, were subjected to principle component analysis (PCA) based on their correlation matrixes. The first two axes were determined to account for over 92% and 95%, respectively, of the variances in the temperature and precipitation variables, as detailed in Tables S1.2 and S1.3 of Appendix S1.

In this study, all of the calculations and statistical analyses were conducted using the statistical program R 3.5.1.

RESULTS

Beta diversity values

As shown in Table 2, the expected β -diversity of each plot at the region, zone, area, district, and plot levels ranged between 0.332 and 0.684, 0.107 and 0.664, 0.046 and 0.694, 0.042 and 0.695, and 0.000 and 0.537, respectively. The mean values of the expected β -diversity decreased as the pooling size decreasing from the regional to the plot level. In addition, the observed β -diversity of each plot ranged between 0.000 and 0.737, and the mean value was found to be higher than the expected β -diversity at the plot level.

Effects of the environmental filtering and spatial aggregation processes

As shown in Table 3, the effects of the environmental filtering at the region-zone, zone-area, area-district, and district-plot scales were 0.077, 0.027, 0.019, and 0.189, respectively. The environmental filtering effects at each spatial scale were all observed to be significant. The effect of the spatial aggregation was 0.074 and found to be significant at the within-plot scale. The change in the β -diversity patterns (Figure 4) indicated that the magnitude of ecological effects was the strongest at the district-plot scale, followed by that at the region-zone and within-plot scales. The comparison of ecological effects along the latitudinal gradients (Figure 5) showed that the environmental filtering effects at the region-zone and area-district scales had significantly increased with increasing latitude. In addition, the environmental filtering effects at the district-plot scale, and the spatial aggregation effects at the within-plot scale, decreased significantly with increasing latitudes.

Key factors of the environmental filtering processes

At the region-zone, zone-area, area-district, and district-plot scales, approximately 74%, 22%, 20%, and 33% of the environmental filtering effects, respectively, could be explained by the climate variables and plot attributes (Table 4). At all four scales, both the temperature and precipitation factors significantly contributed to the environmental filtering. Furthermore, the other climate variables and plot attributes had contributed to the environmental filtering effects, including the wind speed, elevation, and soil depth at the region-zone scale; solar radiation, wind speed and litter thickness at the zone-area scale; solar radiation and litter thickness at the area-district scale; and slope, aspect and litter thickness at the district-plot scale.

DISCUSSION

In this study, we compared and analyzed the variations in species composition in the observed and randomized communities at five different spatial scales. Our study is the first to quantitatively partition the hierarchical effects of environmental filtering and spatial aggregation processes on the variations in species compositions of forest communities. The results revealed that the community structure is a result of both the ecological processes of environmental filtering and spatial aggregation at varying strengths depending on the spatial scale. Specifically, three hypotheses regarding the variations in the ecological effects across spatial scales and along latitudinal gradients, as well as the key factors of environmental filtering were examined and discussed in the present study to reveal the mechanisms that determine the origin and maintenance of the studied local community assemblages.

Our study agrees with a growing number of studies which have assumed or verified the hierarchical nature of ecological effects (Whittaker et al. 2001; McGill 2010; De Bello et al. 2013; Chalmandrier et al. 2013; Scherrer et al. 2019). In related investigations, De Bello et al. (2013) tested the relative influences of multiple environmental filters on plant functional trait structures. The results confirmed that the large-scale environmental filters tended to select a pool of species adapted to a specific site, and then the finer-scale filters determined the species abundance and local species coexistence. Scherrer et al. (2019) quantified the relative importance of habitat filtering and limitations of similarity in species traits in grassland environments. It was found that habitat filtering was the dominant assembly process at the plot level, with diminished effects at the subplot level, whereas limiting similarity prevailed at the subplot level, with weaker average effects at the plot level. To be more concrete, our study partitioned the ecological effects layer by layer across the five examined spatial scales, ranging from the region level which covered the entire natural forest areas of northeastern China, to the plot level (0.1 ha) which was on a smaller scale but sufficient for tree community sampling (Kraft et al. 2011). The results indicated that the species compositions of the local communities were controlled by both the up-scale environmental filtering and the down-scale spatial aggregation. The effects of the environmental filtering and spatial aggregation processes on β -diversity at the five examined spatial scales were all significant. However, it was determined that the environmental filtering at the region-zone and district-plot scales, as well as spatial aggregation at the within-plot scale, were the most dominant

effects.

Inconsistent with \mathbf{H}_1 , the effects of the environmental filtering did not vary monotonically with the spatial scales. The results suggest that the degree to which the environmental conditions filtered the species from a large pool to a small pool may vary with the spatial scale. The species compositions of each plot were mainly affected by the environmental filtering at the smaller district-plot scale, less than by that at the broader region-zone scale. These results are not in agreement with those obtained by Cornell & Hughes (2007), who demonstrated that the environmental filtering in coral community assemblages did not change appreciably with spatial scales due to the habitat differences being the same regardless of the scale. We speculate that the variations across the spatial scales in this study are due to the fact that the effects of the environmental filtering at the region-zone scale produced marked effects mainly at the higher latitudes, while the effects at the district-plot scale are conspicuous throughout the study area (Figure 4 and 5). The results highlight the fact that the environmental factors which filtered the species from the regional pool to the zone level as well as from the district to the plot level are crucial for the species compositions in northeastern China.

Consistent with \mathbf{H}_2 , it was found the environmental filtering at the broad scales had positive correlations with latitude, but negative correlations at the finer scales. The positive correlations at the broad scales indicates that fewer species had adapted to the environments at the higher latitudes (Qiao et al. 2015), which was linked to the theory of the conservation of cold tolerance across the species (Algar et al. 2009). This was found to be in line with the results presented by Freestone & Osman (2011), who found that the proportion of species from the regional species pool that were present at the local scale had increased from the tropics to the temperate zone, thereby demonstrating that higher-latitude communities may experience greater influencing effects of species filtering from the regional pool than communities at lower latitudes. At the fine scales, the negative relationships between the environmental filtering effects and the latitudes reveal that more pronounced environmental filtering had resulted from greater habitat heterogeneity (Pianka 1966), which subsequently contributed to higher β -diversity values at the lower latitudes (Xing & He 2019). Myers et al. (2013) found that among forest plots spanning local scales, environmental filtering explained a larger proportion of the variations in β -diversity (after correcting for sampling effects) in temperate forests when compared with those of tropical forests. Our results emphasized the fact that the β -diversity values along the latitudinal gradients had responded differently to environmental filtering at the different spatial scales. Therefore, hierarchical analyses are necessary in view of possible confounding effects across multiple scales.

Our study confirmed that environmental filtering effects are related to different variables at each spatial scale. Part of the results are consistent with the priori criteria of the vegetation regionalization map of China, in which temperature and precipitation factors are always significant variables that may have resulted from different regulators. For example, at the broad scale (e.g. the region-zone scale) the effects are mainly mediated by latitude and elevation regulating factors (Table 4). However, at the fine scale (e.g. the district-plot scale), the local topographical environmental conditions, such as slope and aspect, are the dominant regulators (Table 4). In addition, some further clarifying details were obtained, including that wind speed and solar radiation were important filtering factors at the broad scales. They may have influenced the abundance and distributions of species by altering species dispersal potentials (Tackenberg et al. 2003) and creating heterogeneous light environments (Parks & Mulligan 2010). We also found that soil depth was a significant variable at the region-zone scale, and litter thickness was a significant variable at both the zone-area and district-plot scales. These findings reveal that soil attributes also contributed to the environmental filtering processes. Overall, the identified variables were sufficient to explain the environmental filtering effects at the region-zone scale (approximately 70% of the variation). Additional variations could probably be explained if more soil variables would have been available (John et al. 2007; Jones et al. 2008), particularly at the zone-area, area-district, and district-plot scales where the explained variances (approximately 20 to 30%) were much lower than those at the region-zone scale.

Spatial aggregation can reflect interactions between individuals and their close neighbors, which emphasizes the fundamental importance of the local distributions of trees within communities. We found that the effects

of spatial aggregation in this study were significant and remarkable, which provided support for the theory that spatial aggregation is one of the dominant factors underlying the variations in species compositions (Cornell et al. 2007; Flinn et al. 2010).

Consistent with H_3 , our study showed that the effects of spatial aggregation decreases with increasing latitude, indicating that the spatial aggregation was more dominant in the high-diversity communities. These results are causing the negative gradients in the observed β -diversity values along latitudes (Figure 4 and 5). In previous studies, the index of beta-deviation was considered to be closely related to spatial aggregation (Kraft et al. 2011; Qian et al. 2013; Xu et al. 2015; Xing & He 2019). Kraft et al. (2011) showed no global latitudinal gradient of beta deviation in global extent; Qian et al. (2013) showed a negative gradient in New World North and China, but no relation in New World South; Xu et al. (2015) observed a positive gradient in New World South, but no relation in a global extent and New World North. Xing & He (2019) found a strong unimodal latitudinal gradient in North America. The reasons for the various relationships may have been due to the different spatial extents among the studies (Patrick & Yuan 2019). Therefore, considering that spatial aggregation effects along geographical gradients could be various (positive, negative, unimodal, or non-relationship), specific spatial extents should be noted in future studies.

In conclusion, the stepwise partitioning of the environmental filtering and spatial aggregation processes used in this study highlighted the scale dependencies of the ecological effects on community structures. Accordingly, we recommend that greater emphasis should be placed on the scale effects of ecological processes (McGill 2010). Our study also emphasized that the divisions of spatial scales should be optimized to match the environmental patches which maximize environmental heterogeneity (Viana & Chase 2019). This will be particularly important due to the fact that the specific patterns and definitions of spatial scales will affect the variations in the data, and thereby the conclusions (Jelinski & Wu 1996).

ACKNOWLEDGEMENTS

This study is supported by the Key Project of National Key Research and Development Plan (2017YFC0504005), the Program of National Natural Science Foundation of China (31971650), and Beijing Forestry University Outstanding Young Talent Cultivation Project (2019JQ03001).

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Tables

Table 1 Summary of the models and ecological definitions

Models	Ecological Interpretation
$\beta_{\text{exp_region}} - \beta_{\text{exp_zone}}$	Environmental filtering at region-zone scale
$\beta_{\text{exp_zone}} - \beta_{\text{exp_area}}$	Environmental filtering at zone-area scale
$\beta_{\text{exp_area}} - \beta_{\text{exp_district}}$	Environmental filtering at area-district scale
$\beta_{\text{exp_district}} - \beta_{\text{exp_plot}}$	Environmental filtering at district-plot scale
$\beta_{\text{obs}} - \beta_{\text{exp_plot}}$	Spatial aggregation at within-plot scale

Table 2 Statistical information of the expected β -diversity values of each plot at the region, zone, area, district, and plot levels, and the observed β -diversity values at the plot level

Values	Range	Mean	SD
$\beta_{\text{exp_region}}$	0.332 - 0.684	0.453	0.058
$\beta_{\text{exp_zone}}$	0.107 - 0.664	0.376	0.121
$\beta_{\text{exp_area}}$	0.046 - 0.694	0.349	0.125
$\beta_{\text{exp_district}}$	0.042 - 0.695	0.330	0.152
$\beta_{\text{exp_plot}}$	0.000 - 0.537	0.140	0.118
β_{obs}	0.000 - 0.737	0.214	0.168

Table 3 Magnitudes of the environmental filtering effects at the region-zone, zone-area, area-district, and district-plot scales and of spatial aggregation effects at the within-plot scale

Scale	Effects	SE	t	p
Region-Zone	0.077	0.005	15.148	<0.001***
Zone-Area	0.027	0.002	17.686	<0.001***
Area-District	0.019	0.004	4.960	<0.001***
District-Plot	0.189	0.006	30.308	<0.001***
Within-Plot	0.074	0.004	17.214	<0.001***

Note: Two samples, paired t test; ***indicates $p < 0.001$; ** indicates $p < 0.01$; *indicates $p < 0.05$

Table 4 Significant factors explaining the environmental filtering effects at the region-zone scale, zone-area, area-district, and district-plot scale, respectively

Scale	Variables	Estimate	SE
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Region-zone	(Intercept)	0.205	0.020
	Comp1_temperature	-0.034	0.001
	Comp2_temperature	-0.011	0.003
	Comp2_precipitation	0.006	0.002
	Wind Speed	-0.019	0.005
	Elevation	-1.456×10^{-4}	2.285×10^{-5}
	Soil Depth	-2.201×10^{-4}	6.525×10^{-5}
Zone-area	AIC=-1209.134 Adjusted R ² =0.737	AIC=-1209.134 Adjusted R ² =0.737	AIC=-1209.134 Adjusted R ² =0.737
	(Intercept)	-0.248	0.084
	Comp1_temperature	-0.003	0.001
	Comp2_temperature	0.007	0.001
	Comp2_precipitation	-0.006	0.001
	Solar Radiation	2.276×10^{-5}	6.357×10^{-6}
	Wind Speed	-0.015	0.003
Area-district	Litter Thickness	0.002	7.608×10^{-4}
	AIC=-1730.25 Adjusted R ² = 0.217	AIC=-1730.25 Adjusted R ² = 0.217	AIC=-1730.25 Adjusted R ² = 0.217
	(Intercept)	-0.548	0.201
	Comp1_temperature	-0.008	0.003
	Comp1_precipitation	-0.006	0.002
	Comp2_precipitation	-0.025	0.003
	Solar Radiation	3.868×10^{-5}	1.544×10^{-5}
District-plot	Wind Speed	0.018	0.007
	AIC=-998.816 Adjusted R ² = 0.203	AIC=-998.816 Adjusted R ² = 0.203	AIC=-998.816 Adjusted R ² = 0.203
	(Intercept)	0.213	0.013
	Comp1_temperature	0.019	0.002
	Comp2_precipitation	0.024	0.004
	Slope	0.001	0.001
	Aspect	0.018	0.008
	Litter Thickness	-0.011	0.003
	AIC=-677.707 Adjusted R ² = 0.327	AIC=-677.707 Adjusted R ² = 0.327	AIC=-677.707 Adjusted R ² = 0.327

Note: In the table *** indicates $p < 0.001$; ** indicates $p < 0.01$; * indicates $p < 0.05$

Figure Legend

Figure 1 Framework of the hierarchical effects of environmental filtering and spatial aggregation processes on the structures of community compositions.

Figure 2 Map showing the location of the 397 circular field plots.

Figure 3 Description of the 3 zones, 9 forest types, and 17 districts.

Φιγυρε 4 Τηε ζηανγες ιν τηε β-διερσιτψ παττερνς· τηε μαγνιτυδε οφ εςολογιςαλ εφφερςτς (ι.ε. τηε διωφερενςε βετωεεν τηε ρεδ ανδ βλαςκ δοτς) ωας στρονγεςτ ατ τηε διςτριςτ-πλοτ ςςαλε, φολλωεδ βψ τηατ ατ τηε ρεγιον-ζονε ανδ ωιτηιν-πλοτ ςςαλες. Ηωεερ, τηε μαγνιτυδε ωας ωεακερ ατ τηε ζονε-αρεα ανδ αρεα-διςτριςτ ςςαλες.

Figure 5 Effects of the environmental filtering (a to d) and spatial aggregation (e) processes along latitudes.

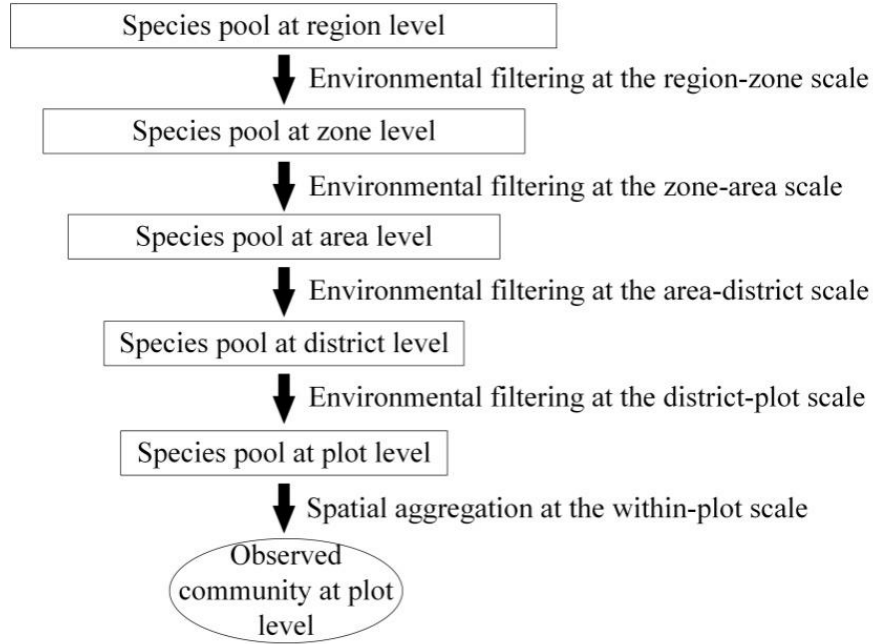


Figure 1

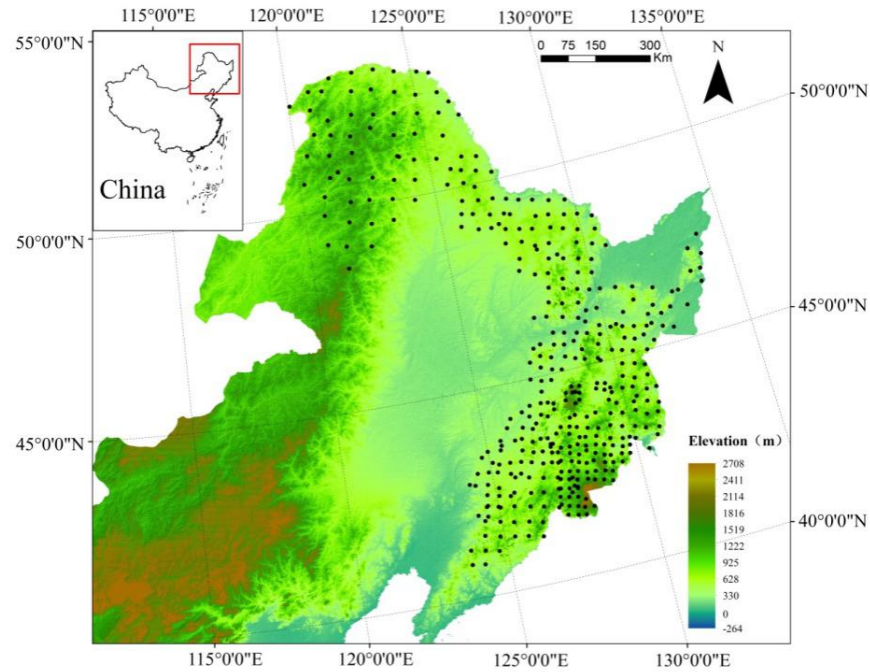


Figure 2



Figure 3

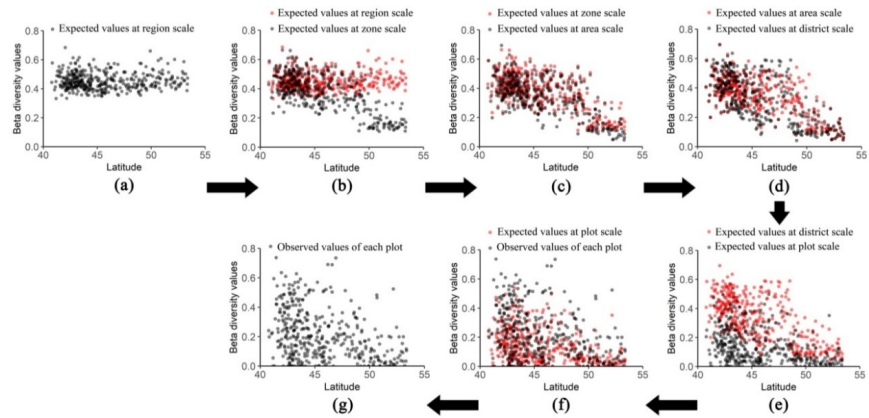


Figure 4

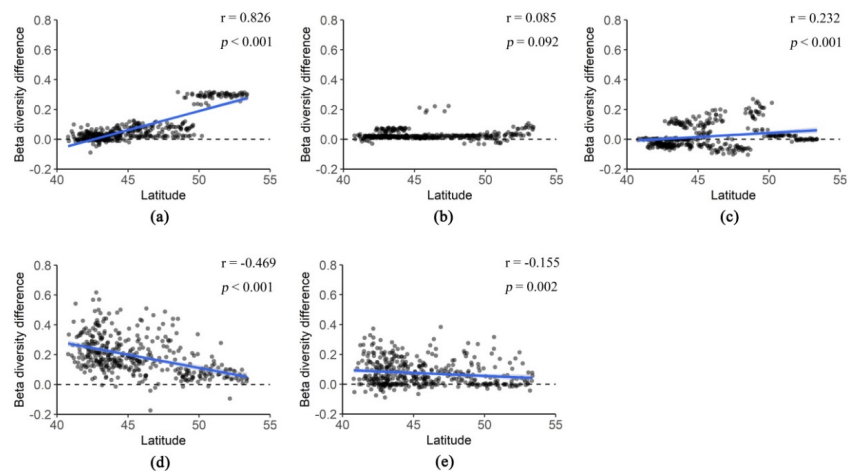


Figure 5