


Latitudinal gradients and ecological drivers of β -diversity vary across spatial scales in a temperate forest region

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Funding information

the the Key Project of National Key Research and Development Plan, Grant/Award Number: 2017YFC0504005; Beijing Forestry University Outstanding Young Talent Cultivation Project, Grant/Award Number: 2019JQ03001; the Program of National Natural Science Foundation of China, Grant/Award Number: 31971650

Editor: Richard Field

Abstract

Aim: Our understanding of the mechanisms driving β -diversity is still rather rudimentary. This study evaluates the influences of environmental filtering versus spatial scale of regional communities on β -diversity across latitudes.

Location: North-eastern China.

Methods: The β -diversity was calculated in each regional community. The spatial extent of these “regional communities”, which included five or 10 plots, was ≤ 140 km. A random assembly null model was used to assess the effects of species abundance distribution on the β -diversity. Moreover, the deviation of observed β -diversity from a null model (called β -deviation) was also assessed. The variations of the β values were partitioned into environmental, latitudinal and their joint effects.

Results: The observed β -diversity declined with increasing latitude, although the β -deviations showed a non-monotonic pattern as the latitude increased at two studied scales. All the regional communities consisting of five or 10 local plots exhibited significantly positive β -deviations. The total amount of variation in β -deviations explained by environmental and latitudinal variables increased dramatically with increasing scale. A significant pure environmental effect was observed at both scales, explaining 30% of the variation in β -deviation for regional communities consisting of five local plots and 58.7% for regional communities consisting of 10 local plots. The spatial variation in precipitation primarily accounted for the β -gradient.

Main conclusions: This is one of the few multiscale analyses to investigate latitudinal patterns and driving mechanisms of tree β -diversity in temperate forests. The β -deviation showed a similar trend of change with latitude, but the variation of β -deviation explained by the environments and latitude was highly dependent on the scale of regional communities studied. Environmental filtering and the spatial scale of regional communities jointly accounted for the β -gradient, with environmental filtering appearing to determine the high variation of species turnover along the latitudinal gradient.

KEYWORDS

environmental filtering, latitudinal gradient, regional community, regional species pools, spatial scale, tree β -diversity

1 | INTRODUCTION

β -Diversity, which describes the change of species composition across space in a given region (Whittaker, 1960), has received much attention in recent years, with a special focus being on the effect of latitudinal change (De Cáceres et al., 2012; Kraft et al., 2011; Xing & He, 2019). Although the latitudinal variation of β -diversity has been reported widely, the explanation of the latitudinal pattern remains controversial. For example, β -diversity has been found to be positively, negatively or not at all correlated with latitude (Bowman, 1996; Kraft et al., 2011; Qian & Ricklefs, 2007; Tang et al., 2012). Koleff, Lennon, and Gaston (2003) reviewed 15 possible relationships between β -diversity and latitude. They documented seven negative, two positive and six non-significant relationships. The variety of relationships may be caused by differences in the taxa (Hao et al., 2019), the latitudinal span, the size of sampling units, the specific geographical region of each study and the use of different β -diversity metrics. In addition to the effect of the geographical region from which local communities are sampled, β -diversity in a local site is also subjected to the effect of local niche- and dispersal-based processes (Myers et al., 2013). To understand how regional β -diversity changes with latitude, it is necessary to quantify the contributions of these local processes to β -diversity.

A species pool is typically defined as a set of species that could persist in, and potentially be dispersed over, a given region (Zobel, van der Maarel, & Dupré, 1998). The divergence of species pools is an important determinant of community assembly (De Cáceres et al., 2012; Mori et al., 2013). β -Diversity is often influenced strongly by the size of a regional species pool through a sampling effect (Burkle, Myers, & Belote, 2016; Chase & Myers, 2011; Grman & Brudvig, 2014; Kraft et al., 2011). This finding suggests that a regional species pool would inevitably confound an observed β -diversity when it comes to quantifying the relative importance of local driving mechanisms. Therefore, it is crucial to control the effect of the size of a regional species pool in such analyses.

Niche-based mechanisms of community assembly, such as environmental filtering, are potential drivers of latitudinal variation in β -diversity, because environmental variables may vary geographically. For example, soil texture is found to be correlated closely with tree β -diversity in North America (Xing & He, 2019), and other soil conditions are also found to contribute to the patterns of β -diversity in tropical dry forests (Ayma-Romay & Brown, 2019; López-Martínez, Hernández-Stefanoni, Dupuy, & Meave, 2013). Specific topography-related environmental factors, such as elevation and aspect, could also influence the β -diversity gradient (De Cáceres et al., 2012; Gallardo-Cruz, Pérez-García, & Meave, 2009). Climate is another strong niche process that would contribute to the latitudinal pattern of β -diversity (Tang et al., 2012; Xing & He, 2019).

In addition to the niche-based processes, dispersal-based processes have also been found to affect β -diversity patterns. It has been reported that β -diversity is negatively related to dispersal ability (Qian, 2009). Dispersal limitation at local scales can contribute to β -diversity (Chust et al., 2006), as evidenced by the fact that

intraspecific aggregation leads to high β -diversity (Myers et al., 2013). Although both environmental filtering and dispersal limitation can create species clumping and thus contribute to specific patterns of biodiversity (Chave, Muller-Landau, & Levin, 2002; Ganeshiah, Sanjappa, Rao, Murugan, & Shivaprakash, 2019), the relative importance of these local community assembly mechanisms differs between temperate and tropical regions. Myers et al. (2013) argue that the spatial pattern of β -diversity is affected by environmental filtering in temperate forests and by dispersal limitation in tropical forests.

In this study, we first compare tree β -diversities to examine their possible spatial gradients across latitudes. We then quantify the contribution of environmental filtering versus the size of the regional community to the β -gradient. The aim of our study is to address the following two hypotheses relating to a northern temperate forest region: (a) to test the hypothesis that the β -gradient has a non-monotonic pattern in response to environmental heterogeneity among ecoregions; and (b) to test the effects of environmental filtering and the size of regional communities on the β -gradient. We expect that the effects of environmental determinants on the β -gradient are strongly affected by the spatial scale characterized by the size of regional communities that is sampled.

2 | MATERIALS AND METHODS

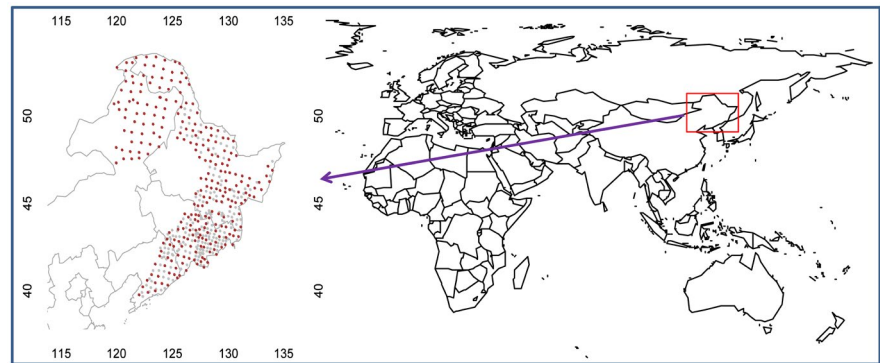
2.1 | Study area and forest plot network

The study covers a large area of natural forests in north-eastern China, including six mountain ranges: the Greater and Lesser Khingan, the Zhangguangcailing, the Changbai, the Laoyeling, the Hadaling and the Longgang Mountain areas. The latitudinal and longitudinal ranges of the study region extend from 39 to 54° N (a range of 15°) and from 119 to 134° E (a range of 15°), respectively. The climate varies from a middle temperate zone to a cool temperate zone. All these zones are characterized by strong seasonality, with four distinctly different seasons. The main precipitation period is between July and September, and there is a harsh dry spring season.

In the summer of 2017 and 2018, a total of 456 0.1 ha circular (radius = 17.84 m) forest plots were established in the region (Figure 1). The standard plot size that is widely used for sampling plant diversity is 0.1 ha (Stohlgren, Falkner, & Schell, 1995; Wu, Zhang, & Wang, 2019). In the temperate forests studied here, it has been shown that a plot size of 500–600 m² is adequate for sampling tree diversity (Fang et al., 2012; Hao, 2000). Therefore, a 0.1 ha plot should be sufficiently large for this study. Data on elevation and slope were recorded for each plot. All trees with a diameter at breast height (d.b.h.) > 5 cm were identified, measured and mapped in each plot.

It is clear from Figure 1 that the 456 plots were not even distributed across the study region. This uneven sampling coverage could potentially bias the β -gradient analysis in this study. For example, the spatial extent of the five-plot (or 10-plot) regional community in the intensively sampled area should be much smaller than the regional community in the sparsely sampled area. To minimize this problem, we

FIGURE 1 Location of the studied forest plots in north-eastern China. A total of 262 (brown points) out of 465 forest plots (brown and grey points) were included in the analysis to ensure an even sampling coverage across the region [Colour figure can be viewed at wileyonlinelibrary.com]



sampled a subset of plots to ensure even sampling coverage, leading to 262 plots. The distance between neighbouring plots was approximately constant across latitude (Supporting Information Appendix S1). In these forest plots, a total of 20,012 individual trees and 66 tree species were recorded. The number of tree species among the plots varied from one to 20 (Supporting Information Appendix S2).

2.2 | Defining the spatial scales of regional communities

The delineation of regional communities for the quantification of β -diversity is crucially important to ensure an unbiased comparison of diversity across sites (Bennett & Gilbert, 2016; Kraft et al., 2011), but they are often defined arbitrarily (Kraft et al., 2011). Following Xing & He (2019), we used each of the forest plots and its nearest n neighbouring plots to define a particular regional community as a basis for calculating a species pool. This approach allowed us to assess the possible effect of regional species pools on β -diversity. In this study, the β -diversity was calculated in each regional community consisting of five or 10 local plots ($n = 4$ or 9, plus the focal plot in each case), respectively. Therefore, $n + 1$ (i.e., five or 10) was the size of a regional community and defined the spatial scale of each community (there were two scales: five and 10 plots). The spatial extent of these regional communities including five or 10 plots usually covered a distance of < 140 km.

A Mantel correlogram (Legendre & Legendre, 2012) was used to assess the spatial correlation of the community composition as a function of the geographical distance classes among the studied plots. The calculation was performed using the `mantel.correlog` function in the R software package `vegan` (<https://www.r-project.org/>). The result presented in the Supporting Information (Appendix S3) shows that adjacent plots tend to exhibit a similar community composition, whereas plots ≥ 178 km apart are more dissimilar in tree communities. This observation indicates that the two studied scales are suitable for defining regional communities.

2.3 | Tree β -diversity and β -deviation

The total variation of the community data table Y in each regional community consisting of five or 10 local plots can be used to

estimate β -diversity (Legendre & De Cáceres, 2013). We defined $Y = [y_{ij}]$ as a plot-by-species matrix containing the abundance values of p species (column vectors y_1, y_2, \dots, y_p) observed in n plots (row vectors x_1, x_2, \dots, x_n). The index i was used for forest plots, j for species and y_{ij} for individual entries in Y . β -Diversity (BD) was then computed as the total variance of the Hellinger-transformed Y as follows: $BD = \text{Var}(Y) = \sum_{i=1}^n \sum_{j=1}^p (y_{ij} - \bar{y}_i)^2 / (n-1)$. The Hellinger distance is bounded between zero and 1.414, and the observed value of BD varies between zero and one.

We compared the observed values of β -diversity with the expected values from a random sample of the regional communities. Following previous studies (Crist, Veech, Gering, & Summerville, 2003; Kraft et al., 2011), a random species assemblage from the observed species pools was used to generate the random spatial patterns of β -diversity. The individuals were randomly shuffled among local plots while preserving the total number of species, the relative abundance of each species in the regional community and the total number of individuals in each plot. This type of null model is thus determined solely by species abundance distribution (Xu, Chen, Liu, & Ma, 2015). The β -deviation, which quantifies the degree of deviation of the observed β -diversity from the expected β -diversity, was calculated as the difference between the observed and expected value divided by the standard deviation of randomly simulated β -diversity values (Kraft et al., 2011).

The null model may be affected by a sampling effect (Bennett & Gilbert, 2016; Ulrich et al., 2017). Therefore, we generated 1,000 iterations to calculate the mean of randomly simulated β -diversity values as the expected β -diversity. Then the 95% confidence intervals were calculated by the 0.025 and 0.975 quantiles of 1,000 simulated β -diversity values. When an observed β -diversity value was outside of the 95% confidence intervals, the observed pattern was strongly regulated by either environmental filtering, dispersal limitation or both. Positive β -deviations were assumed to indicate higher β -diversity than expected by chance and to reflect an intraspecific aggregation (Myers et al., 2013). The β -deviation is thus informative in suggesting potential driving mechanisms (Kraft et al., 2011).

2.4 | Variation partitioning of β -diversity

A total of 17 variables grouped into three environmental types (i.e., climate, soil and topography; Supporting Information Appendix S4)

were used to explain the variability of β -diversity. Ten of these variables were bioclimatic variables (BIO1–BIO10) downloaded from the WorldClim database v.1 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005); five variables (BIO11–BIO15) were calculated from WISE30sec v.1 (Batjes, 2015); and two variables (BIO16–BIO17) were assessed by our own field observations. The mean values of these 17 environmental variables were calculated for each of the regional communities composed of the aforementioned local 0.1 ha forest plots at two different spatial scales (five and 10 plots, respectively).

These environmental variables together with latitude were used to partition the total variation in the β -deviations into individual components accounted for by environmental variables alone (fraction [a]), environment and latitude jointly (fraction [b]) and latitude alone (fraction [c]) (Borcard, Legendre, & Drapeau, 1992). The adjusted R^2 was used to assess the partitions explained by the explanatory variables (Peres-Neto, Legendre, Dray, & Borcard, 2006). Fractions [a] and [c] were tested for significance using 999 random permutations, whereas fraction [b] could not be tested independently. We carried out the analysis using the “varpart” function in the R package vegan. It was not necessary to remove collinearity in the explanatory variables before partitioning (Legendre & Legendre, 2012). The latitudinal gradient of each environmental variable, the adjusted R^2 values in the linear relationships between such variables and the β -deviations were used to evaluate the association of β -deviation with those environmental variables.

3 | RESULTS

3.1 | Latitudinal gradients of tree β -diversity

The observed β -diversity showed a strong decline with increasing latitude, irrespective of the size of the regional communities

(Figure 2a,c). However, the β -deviation showed a non-monotonic pattern along the latitude and seemed to peak at c. 50° N (Figure 2b,d). This pattern became stronger for the 10-plot regional communities compared with the five-plot communities, showing a regional scale-dependent latitudinal gradient of β -deviations.

3.2 | The ecological drivers of tree β -diversity

All the observed β -diversity values fell outside the upper limits of the 95% confidence intervals, indicating that the β -deviations were significantly positive for both regional community scales. The variation partitioning in Figure 3 shows that the total amounts of variation in β -deviations explained by environmental heterogeneity and latitude increased dramatically from the five-plot regional communities to the 10-plot regional communities. Environmental factors, after accounting for the effect of latitude, explained a larger fraction of β -deviations (bootstrap test of environmental fractions, $p < .001$). Measured environmental variables alone explained 30% of the variation in β -deviations for the five-plot regional communities and 58.7% for the 10-plot regional communities.

The environmental variables that might be responsible for the increase in latitudinal β -deviations are shown in Figure 4. We identified three precipitation-related climate variables that showed a non-monotonic increase or decrease with increasing latitude and strong correlations with the β -deviations. These correlations were much more pronounced for the 10-plot than for the five-plot regional communities.

4 | DISCUSSION

β -Diversity has been reported widely to change with latitude, but the mechanisms behind the latitudinal gradient are not well understood.

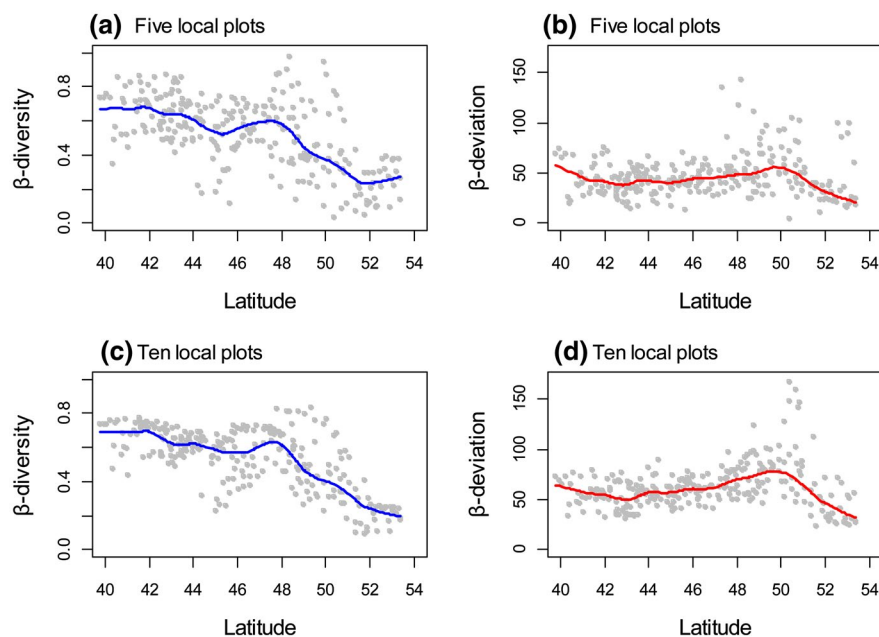


FIGURE 2 Latitudinal gradients of β -diversity and β -deviation for regional communities constituting five and 10 local plots, respectively. The smooth curves are the fit of the locally weighted polynomial regression to each panel [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Venn diagrams showing the variation partitioning of the change in β -diversity. The numbers in the diagrams are adjusted R^2 values ($\times 100$), which are used to assess the partitions explained by the explanatory variables and their combinations (Peres-Neto et al., 2006). Fraction [a] estimates the variation explained by environmental heterogeneity alone; fraction [b] measures the variation jointly explained by environmental heterogeneity and latitude; and fraction [c] measures the variation explained by latitude alone. The bar-plots on the right show the total variation explained by environmental variables and latitude together [Colour figure can be viewed at wileyonlinelibrary.com]

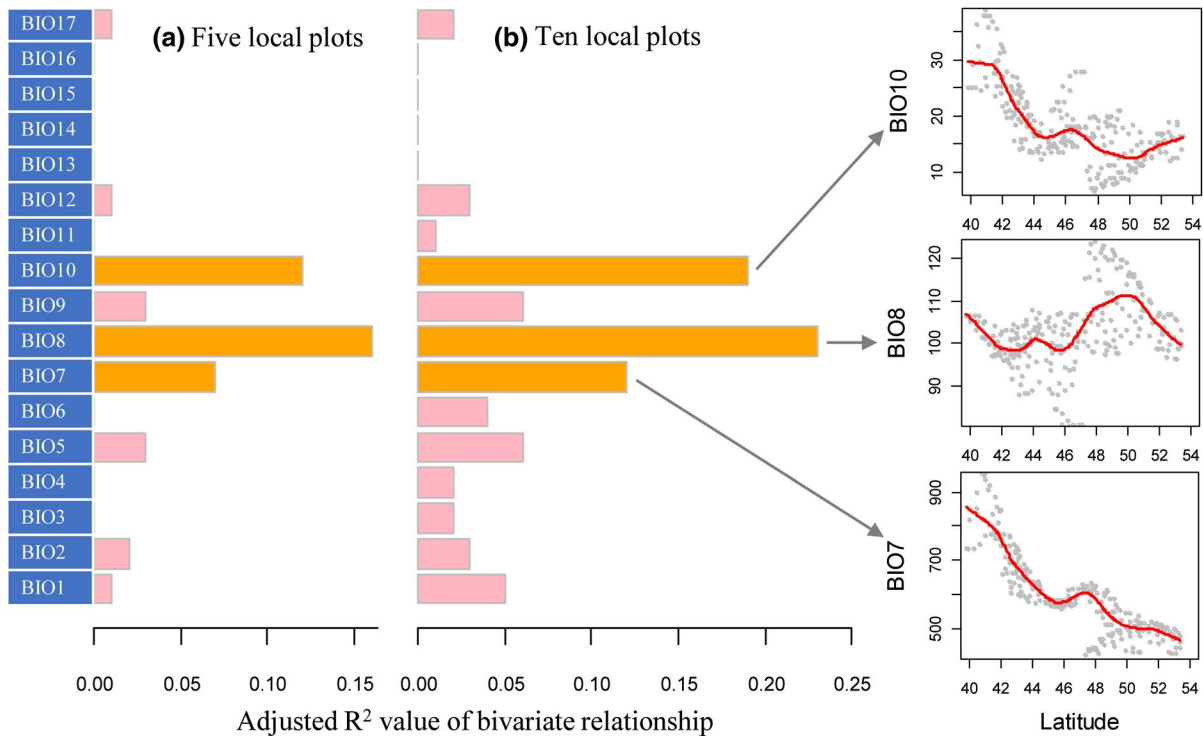
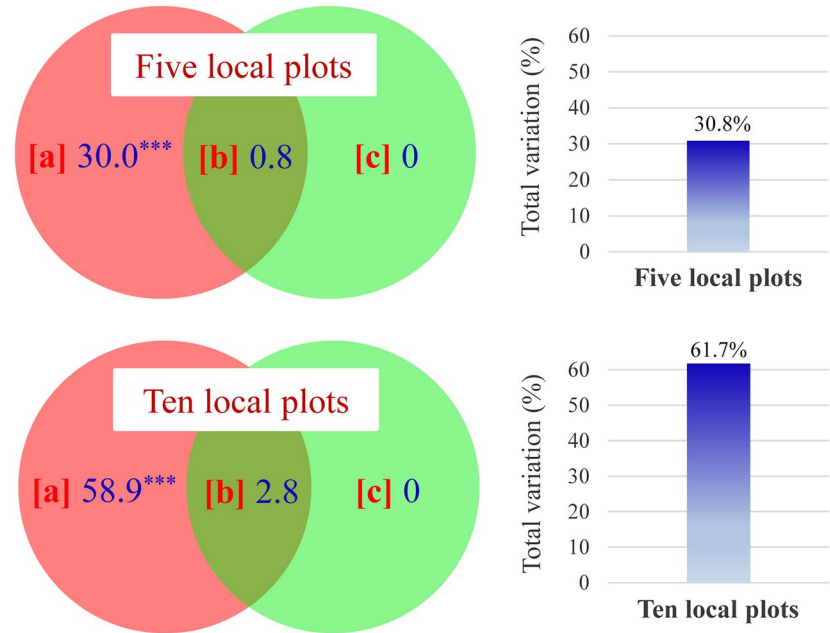


FIGURE 4 Adjusted R^2 values of linear regression models between the β -diversities and 17 environmental variables for regional communities consisting of (a) five and (b) 10 local plots. Latitudinal gradients of the three variables (BIO7, BIO8 and BIO10) with the highest adjusted R^2 are presented on the right panels. A local regression smoothing line was fitted to each panel. Abbreviations: BIO1 = annual mean temperature; BIO2 = mean diurnal range; BIO3 = temperature seasonality; BIO4 = temperature annual range; BIO5 = mean temperature of warmest quarter; BIO6 = mean temperature of coldest quarter; BIO7 = annual precipitation; BIO8 = precipitation seasonality; BIO9 = precipitation of wettest quarter; BIO10 = precipitation of driest quarter; BIO11 = cation exchange capacity; BIO12 = clay content; BIO13 = C/N ratio; BIO14 = soil organic carbon; BIO15 = soil total nitrogen; BIO16 = slope; BIO17 = elevation [Colour figure can be viewed at wileyonlinelibrary.com]

Almost all previous studies found that β -diversity decreases with latitude (De Cáceres et al., 2012; Kraft et al., 2011; Qian, 2009; Qian & Ricklefs, 2007; Qian, Ricklefs, & White, 2005). Consistent with these

studies, we also observed that β -diversity decreased significantly with increasing latitude. However, we found that β -diversities exhibited a non-monotonic relationship with latitude, a finding which

is inconsistent with Kraft et al. (2011). Ecological transition zones between biogeographical regions usually have larger environmental variability, leading to higher species turnover (Speziale, Ruggiero, & Ezcurra, 2010; Williams, Klerk, & Crowe, 2002). In our study, the latitudinal gradient of β -deviation reaches a peak at c. 50° N, which presumably corresponds to the transition from the middle to the cold temperate zone in the study region; thereafter, it declines rapidly towards the cold temperate zone because of decreasing environmental heterogeneity, corroborating the study by Williams (1996). This finding supports the recent conceptual model proposed by Xing & He (2019), which proposes that β -diversity decreases with increasing latitude, whereas β -deviation does not show a monotonic relationship with latitude, but depends on underlying environmental conditions.

The spatially divergent species pools can strongly affect the observed β -diversity through sampling effects (Myers et al., 2013), and we also found a positive relationship between β -diversity and γ -diversity (Supporting Information Appendix S5). Kraft et al. (2011) showed that the widely documented decreasing latitudinal β -diversity pattern becomes independent of latitude after correcting for the variation in pooled species richness. A number of studies have shown that β -diversity was subject to the scale that delineates either local or regional communities (Arita & Rodríguez, 2002; Lennon, Koleff, Greenwood, & Gaston, 2001; Qian, 2009). Our study revealed that the latitudinal gradients of both β -diversity and β -deviation showed similar patterns between the five- and 10-plot scales of regional community (Figure 2). This is because, in our analysis, both the sampling intensity of forest plots (Figure 1) and the size of regional communities (five-plot or 10-plot) were controlled. Our result is different from but supports the study by Bennett and Gilbert (2016), which concluded that β -deviations are not comparable if the size of species pools is different.

A recent study has shown that latitudinal differences in species abundance distributions, rather than spatial aggregation, explain β -diversity along latitudinal gradients (Xu et al., 2015). In contrast, our study highlights the role of spatial aggregation in temperate forest regions. Our results indicate that all regional communities show significantly positive deviations of the observed from the expected β -diversity. These positive β -deviations indicate higher β -diversity than expected by chance and reflect the effect of intraspecific aggregation (Myers et al., 2013). Therefore, intraspecific aggregation tends to shape the patterns of the β -gradient for regional communities. However, dispersal limitation was found to be associated significantly with spatial community dissimilarity in eight fully mapped temperate forest plots (20–35 ha; Wang et al., 2018). Most studies show that the regional-scale β -gradient in temperate forests is affected more by environmental filtering than by dispersal limitation (Gilbert & Lechowicz, 2004; Gilbert et al., 2010; Hubbell, 2001; Myers et al., 2013; Qian & Ricklefs, 2007).

We showed that environmental variables explained a major portion of the β -deviations for the studied forests and that the extent of variation explained by the environmental variables was much higher

for the 10-plot scale than for five-plot scale (Figure 3). This result implies that the latitudinal gradients of β -diversity are mostly likely to be driven by regional environmental filtering, which is responsible for aggregation of many empirical species (Condit et al., 2002; Qian & Ricklefs, 2012; Shen et al., 2009), and spatial aggregation becomes more pronounced at a larger scale. The findings reported here are consistent with those in North American temperate forests (Myers et al., 2013; Xing & He, 2019), in which environmental variables explained a large fraction of the β -deviations. Furthermore, environmental influences on the β -deviations increased greatly with increasing spatial scale, indicating a pronounced scale dependence of environmental effects.

A collection of climatic variables, including annual precipitation, precipitation seasonality and the precipitation of the driest quarter, were identified as determining factors of β -deviations (Figure 4). This reflects the fact that the non-monotonic latitudinal gradients of precipitation variables strongly influence the β -deviations. Annual precipitation values have been identified to influence the global distribution of tree diversity (Liang et al., 2016). Several recent studies found that the latitudinal gradient of precipitation was highly correlated with the spatial turnover of β -diversity (Duivenvoorden, Svenning, & Wright, 2002; Tang et al., 2012; Xing & He, 2019). Our result indicates that β -diversity was controlled mainly by precipitation in north-eastern China, which is consistent with those previous studies showing that environmental filtering is an important driver for the latitudinal gradient of β -deviations.

In conclusion, we found that the non-monotonic pattern in the latitudinal gradients of β -deviation in our study area and the extent of variation of the β -gradient are highly dependent on the spatial scale, that is, the size of the regional community, and the importance of each explanatory variable could be similar. Precipitation variables showed highly significant correlations with the β -deviations. These findings support the environmental filtering hypothesis in temperate forest regions proposed by Xing & He (2019).

ACKNOWLEDGMENTS

This research was 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).

DATA ACCESSIBILITY

The data that support the findings of this study can be accessed on Figshare: <https://doi.org/10.6084/m9.figshare.11923647>

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Zhang C, He F, Zhang Z, Zhao X, von Gadov K. Latitudinal gradients and ecological drivers of β -diversity vary across spatial scales in a temperate forest region. *Global Ecol Biogeogr.* 2020;29:1257–1264.
<https://doi.org/10.1111/geb.13101>