

LETTER

Environmental filtering explains a U-shape latitudinal pattern in regional β -diversity for eastern North American trees

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Abstract

The underlying drivers of β -diversity along latitudinal gradients have been unclear. Previous studies have focused on β -diversities calculated at a local scale and shed limited light on regional β -diversity. We tested the much-debated effects of range size vs. environmental filtering on the β -gradient using data from the US Forest Inventory Analysis Program. We showed that the drivers of the β -gradient were scale dependent. At the local scale species spatial patterns contributed little to the β -gradient, whereas at the regional scale spatial patterns dominated the gradient and a U-shape latitudinal relationship for the standardised β -diversity deviation was revealed. The relationship can be explained by spatial variation in climate and soil texture, thus supporting the environmental filtering hypothesis. But it is inconsistent with Rapoport's rule about the effect of range size on β -gradient. These results resolve the debate on whether species spatial distributions contribute to β -gradient and attest the importance of environmental filtering in determining regional β -diversity.

Keywords

Beta diversity, community assembly, environmental filtering, metacommunity, range size, species abundance distribution, species aggregation.

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INTRODUCTION

The spatial variation in species composition, or β -diversity, is an important concept in ecology and plays a significant role both in testing ecological theories (Condit *et al.* 2002; Harte 2011) and informing conservation practices (Groves 2003; Ferrier *et al.* 2007). One promising, yet controversial, problem is identifying the causes of β -diversity patterns observed across ecological gradients, such as the global-level latitudinal gradient (Willig *et al.* 2003). While recent studies generally agree that β -diversity is negatively related to absolute latitude (Koleff *et al.* 2003; Qian & Ricklefs 2007; Soininen *et al.* 2007; De Cáceres *et al.* 2012), insignificant relationships have also been observed (e.g. Gaston *et al.* 2007). Moreover, there is little consensus on whether community assembly processes contribute to the latitudinal gradient of β -diversity (Kraft *et al.* 2011; Qian *et al.* 2012, 2013; Tuomisto & Ruokolainen 2012; Myers *et al.* 2013; Xu *et al.* 2015).

Variation in species range size and habitat heterogeneity are considered two major mechanisms invoking gradients of regional scale β -diversity. According to Rapoport's rule, which has seen empirical support across many taxa (Stevens 1989; Brown *et al.* 1996; Morin & Lechowicz 2011), average species range size is positively related with absolute latitude (but see Weiser *et al.* 2007). As a consequence, β -diversity is predicted to be higher at lower latitude (due to smaller range size) than at higher latitude (Rodríguez & Arita 2004; Jankowski *et al.* 2009). Besides this range size variation hypothesis, the environmental filtering hypothesis has also been invoked to explain the latitudinal gradient of β -diversity by hypothesising that there is a negative relationship of habitat heterogeneity with latitude (Pianka 1966) and the higher β -diversity at the lower latitude is caused by stronger

environmental filtering (Ricklefs 1977; Qian & Ricklefs 2007). In contrast to these hypotheses, recent work has found that after correcting for the sampling effect of the regional community species abundance distribution (SAD) using an individual-based null model, standardised β -diversity deviation (β -deviation) for an empirical set of global forest plots shows no latitudinal gradient (Kraft *et al.* 2011). This resulted in rejection of both the range size variation and the environmental filtering hypotheses and led to a suggestion that 'there is no need to invoke differences in the mechanisms of community assembly in temperate vs. tropical systems to explain these global-scale patterns of β -diversity' (Kraft *et al.* 2011), or a more precise conclusion that 'latitudinal differences in SADs, rather than spatial aggregation, explain β -diversity along latitudinal gradients' (Xu *et al.* 2015).

A major problem with these studies is that the spatial extent (at < 500 m in distance) that was used to define 'regional' species pool was too local and small to be relevant, as criticised by Qian *et al.* (2012) and Tuomisto & Ruokolainen (2012). With few exceptions, species' distribution ranges are typically much larger than the 'region' as defined in Kraft *et al.* (2011). More importantly, species spatial patterns and the processes that generate the patterns are scale dependent. Species interactions, local habitat heterogeneity and demographic stochasticity have often been shown to be more important at finer scales, whereas long-range environmental gradients and dispersal limitation are more prevailing at broader scales (Wiens 1989; Shipley *et al.* 2012; Xing *et al.* 2014). Although analyses using local community data could capture fine-scale species aggregation, such analyses are unlikely able to reveal latitudinal patterns of regional β -diversity, nor relevant to testing their underlying hypotheses. Therefore, it remains an unanswered question how local community assembly mechanisms

may contribute to latitudinal gradient of regional β -diversity (Tuomisto & Ruokolainen 2012).

Here we test the range size variation and the environmental filtering hypotheses for regional β -diversity using the comprehensive data set of forest tree diversity from the United State Forest Inventory and Analysis Program. The effects of both range size and habitat heterogeneity on β -diversity are acting through species spatial patterns with higher degree of spatial aggregation associated with smaller range size and greater habitat heterogeneity. β -deviation was defined as a standardised effect size to measure departure of observed β -diversity from expected β -diversity under the random spatial distribution (Crist *et al.* 2003; Kraft *et al.* 2011; Myers *et al.* 2013). Thus, β -deviation should be inversely related with mean range size and positively related with habitat heterogeneity. Under the range size variation hypothesis, β -deviation should show a negative relation with absolute latitude due to Rapoport's rule (Fig. 1). Under the environmental filtering hypothesis, the gradient of β -deviation should also decrease with latitude if the hypothesized negative relationship of environmental complexity with latitude is true. However, recent work has shown that there is no simple linear pattern in global habitat heterogeneity (Tuanmu & Jetz 2015). Particularly, transition zones between biogeographical regions have often been shown to have greater habitat variability coinciding with higher species turnover (Williams 1996; Smith *et al.* 2001; Williams *et al.* 2002; Speziale *et al.* 2010). Accordingly, a non-monotonic relation of β -deviation with latitude should be expected under the environmental filtering hypothesis when such a transition zone is involved in the study region (Fig. 1). For instance under the environmental filtering hypothesis, β -deviation should decrease from the tropical-temperate transition zone to the temperate zone, because of the decrease in habitat heterogeneity. When moving from the temperate area to the temperate-boreal transition zone, β -deviation will increase because of the increasing habitat heterogeneity (Fig. 1D).

In this study, we first evaluated the latitudinal gradient of regional β -deviation. We then tested the two hypotheses proposed above for their ability to explain the latitudinal patterns in β -deviation. We showed a U-shape latitudinal relationship of the standardised β -deviation for eastern US tree species. The relationship can be explained by a species aggregation index, which in turn was determined by spatial variation in soil texture and climate seasonality. Our analyses thus show support for environmental filtering as a dominant factor for the regional latitudinal β -gradient.

MATERIALS AND METHODS

Data

We used plot-level data from the US Forest Service Forest Inventory and Analysis Program (FIA; <http://fia.fs.fed.us/>) in this study. Each FIA plot is composed of four circular sub-plots of area 0.017 ha, where all free-standing woody stems with diameter at breast height ≥ 12.7 cm were inventoried. We used the most recent inventories (from 2005 to 2014) of 32 695 FIA plots that located in natural stands in eastern US (east of 97° W longitude) to create samples of regional

communities following a standardised sampling procedure (see Fig. S1.1 in Appendix S1). The whole eastern US was divided into $1^\circ \times 1^\circ$ grid cells and one FIA plot, if present, was randomly chosen in each of the cells as focal plot. The nearest n neighbouring plots for each of the focal plots were then selected to form a regional community together with the focal plot. Consequently, each regional community consists of $n + 1$ local plots, from which the β -diversities are calculated (see below). Different n {1, 4, 9, 19, 49, 99}, which corresponds to the size (i.e. extent) of regional communities (Fig. S1.2) and thus is used as a measure of scale in this study, was used to investigate the effect of the size of regional species pool on β -deviation. The spatial extent of a regional community increased from roughly 7 km for $n = 1$ to about 140 km for $n = 99$. For each of the six scales, the above method generated 414 regional communities distributing across eastern US (Fig. S1.1).

Regional communities generated by aggregating the n nearest plots could represent different area at different location, especially when n is large. If there is a spatial bias in the distribution of plots with latitude, the regional communities so defined could suffer a regional bias in latitudinal β -gradients. We tested this problem by examining the mean distance among the FIA plots that defined a regional community along latitude for each of the six regional scales used in this study and found no systematic trend in this relation (Fig. S1.3). This is not surprising because of the standard sampling protocol used in the FIA. Results from a more complicated method that explicitly controlled the sampling area and the sampling intensity for each regional community also show the robustness of our findings (Fig. S1.4). In the main text we will only report results using the n -nearest neighbour method because of its simplicity and intuitiveness.

We extracted range size data for 134 eastern US tree species from the digitised version of Elbert Little's range maps (Prasad & Iverson 2003). A mean range size value was calculated for each of the regional communities created above from the constituent species. The latitudinal gradient of this mean range size and the relationship between this mean range size and the β -deviation calculated below were assessed for the range size variation hypothesis.

For each of the FIA plots, we downloaded 19 contemporary bioclimatic variables from the WorldClim website (<http://www.worldclim.org/bioclim>) (Hijmans *et al.* 2005) and 17 soil properties from the Unified North American Soil Map Dataset (Liu *et al.* 2013). For each of these variables, a standard deviation (SD) value was calculated for each of the regional communities created above from the constituent plots. The latitudinal gradient of the environmental variables and the bivariate relationships between the response variable (i.e. the β -deviation defined below) and the environmental variables were assessed to test the environmental filtering hypothesis and identify the major factors that contribute to β -deviation.

Measures of β -diversity

Although there are many measures of β -diversity, a consensus of using Hill's number or the effect number of species as a proper diversity measure to partition γ -diversity into α and β

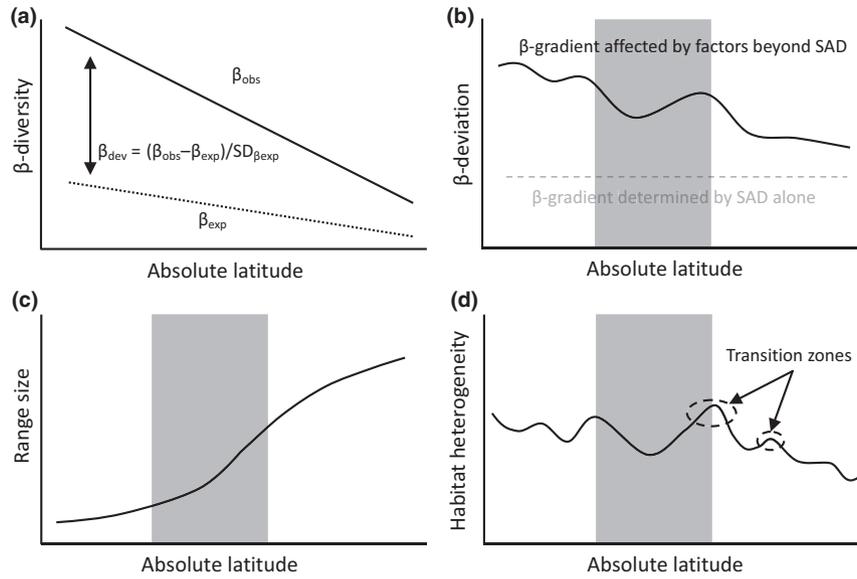


Figure 1 Conceptual graphs showing latitudinal patterns of both the raw β -diversity (A) and the β -deviation (B). The β -deviation is defined following Kraft *et al.* (2011): $\beta_{\text{dev}} = (\beta_{\text{obs}} - \beta_{\text{exp}})/SD_{\beta_{\text{exp}}}$, where β_{obs} (solid line in A) is the observed β -diversity, β_{exp} (dotted line in A) and $SD_{\beta_{\text{exp}}}$ are the expectation and standard deviation of β -diversity under an individual-based null model respectively. The dashed line in (B) shows the expectation under the hypothesis that patterns of β -diversity are fully determined by species abundance distribution (SAD), whereas the solid line shows that β -gradient is affected by factors beyond SAD. β -deviation should decrease monotonically with increasing absolute latitude if range size is the dominant factor (i.e. the Rapoport's rule as shown in C). However, a non-monotonic relationship is expected if environmental filtering is the factor dominating β -diversity because the latitudinal gradients of habitat heterogeneity are not monotonic (D). The shaded area indicates the latitudinal range covered by this study.

components was recently reached (Ellison 2010). Most other β -diversity measures could be unified under a q -th order diversity framework where the order q (≥ 0) represents sensitivity to species abundance (Jost 2007; Chao & Chiu 2016). We employed this framework and calculated α -, β - and γ -diversity of different orders for each regional community. Specifically, we used the following formulae (Chao & Chiu 2016):

$${}^q D_{\gamma} = \begin{cases} \left(\sum_{i=1}^S \left(\frac{z_{i+}}{z_{++}} \right)^q \right)^{1/(1-q)}, & q \geq 0, q \neq 1, \\ \exp \left(- \sum_{i=1}^S \left(\frac{z_{i+}}{z_{++}} \right) \log \left(\frac{z_{i+}}{z_{++}} \right) \right), & q = 1; \end{cases} \quad (1)$$

$${}^q D_{\alpha} = \begin{cases} \frac{1}{N} \left(\sum_{i=1}^S \sum_{k=1}^N \left(\frac{z_{ik}}{z_{++}} \right)^q \right)^{1/(1-q)}, & q \geq 0, q \neq 1, \\ \exp \left(- \sum_{i=1}^S \sum_{k=1}^N \left(\frac{z_{ik}}{z_{++}} \right) \log \left(\frac{z_{ik}}{z_{++}} \right) - \log N \right), & q = 1; \end{cases} \quad (2)$$

$${}^q D_{\beta} = {}^q D_{\gamma} / {}^q D_{\alpha} \quad (3)$$

where ${}^q D_{\alpha}$, ${}^q D_{\beta}$ and ${}^q D_{\gamma}$ are the q -th order α , β and γ diversity respectively; z_{ik} is the abundance of the i -th species in the k -th local community; z_{i+} and z_{++} are the total abundance of the i -th species and all species, respectively, in the regional community; S and N are the number of species and local communities (or plots), respectively, in the regional community.

In this framework, ${}^q D_{\beta}$ measures 'the effective number of equally large and completely distinct communities', ranges from 1 to N , the number of local communities, and is related to neither α nor γ diversity (Chao & Chiu 2016). ${}^0 D_{\beta}$ is Whittaker's multiplicative beta and can be simply transformed to

the proportional species turnover ($\beta_P = 1 - 1/{}^0 D_{\beta}$) used by Kraft *et al.* (2011). In addition to β_P , we also calculated two monotonic nonlinear transformations of ${}^q D_{\beta}$ that normalise the dependence of β -diversity on N and facilitate comparison across regional communities containing different numbers of local communities (Chao & Chiu 2016). The first one gives a class of local (Sørensen-type) differentiation measures that quantify the effective average proportion of non-shared species in a local community: $\frac{1 - (1/{}^q D_{\beta})^{q-1}}{1 - (1/N)^{q-1}}$. The second gives a class of regional (Jaccard-type) differentiation measures that quantify the effective proportion of non-shared species in the regional community: $\frac{1 - (1/{}^q D_{\beta})^{1-q}}{1 - (1/N)^{1-q}}$. Beyond results for β_P for direct comparison with previous studies, we also present results for these differentiation measures for orders $q = 0, 1$ and 2 . To avoid confusion with our focus on local- vs. regional-scale species aggregation, in the rest of the paper these two measures are called Sørensen and Jaccard differentiations.

Null model and standardised β -diversity deviation

We used the same individual-level null model as Kraft *et al.* (2011) to calculate the standardised β -diversity deviation (hereafter abbreviated as β -deviation). Specifically, for each regional community all individual plants were randomly shuffled across the constituting local plots while the abundance of each species in the regional community and the number of individuals in each local plot were preserved. This randomisation was repeated 999 times to obtain a mean and standard deviation (SD) for β_P and each order ($q = 0, 1$ and 2) of both

Sørensen and Jaccard differentiations. The β -deviation was then calculated as (observed – mean)/SD for all corresponding indices. The latitudinal gradient of this β -deviation and its drivers were further studied using variation partitioning (see below).

This null model has been criticised that it confounds γ diversity with SADs (Qian *et al.* 2013). The resulting β -deviation is also found to depend on both sample size (i.e. the number of local communities sampled for a regional community) and γ -diversity (Bennett & Gilbert 2016; Ulrich *et al.* 2017). However, under the condition that sampling effort is constant across communities as argued by Bennett & Gilbert (2016) (see also Appendix S2), β -deviation can effectively identify and validly compare non-random β patterns across assemblages. Thus, if we associate the β -deviation explicitly with species spatial pattern rather than the general ‘mechanisms of community assembly’ suggested by Kraft *et al.* (2011), the null model is valid and patterns observed in the β -deviation are useful for inferring processes underlying diversity patterns (Crist *et al.* 2003). In this study, β -deviation was used so that to make our work comparable to others in the debate (Kraft *et al.* 2011; Qian *et al.* 2012, 2013; Tuomisto & Ruokolainen 2012; Myers *et al.* 2013; Xu *et al.* 2015), but to minimise the possible sensitivity of β -deviation to sampling effort we kept sampling effort constant across each calculation of β -deviation.

Intraspecific aggregation

We used the Morisita index as the measure of intraspecific aggregation following Crist *et al.* (2003). For each regional community, we first calculated the mean of the Morisita index across the common species that have more individuals than the number of constituting local communities. These mean Morisita values (x) were then standardised by using the 999 runs of the null model described above. These standardised effect sizes were used to represent the departure from randomness for each regional community (i.e. the regional-community level degree of intraspecific aggregation) and to explain the β -deviation. We also tried some other methods to represent the regional-community level degree of aggregation, including the mean of the Morisita index across all non-singleton species, the mean of the Morisita index across the dominant species that accumulate the first 50% of total abundance and the Morisita index for the most abundant species. The mean across the common species performed the best, whereas the mean across the dominant species and the index for the most abundant species showed qualitatively similar results. The mean across all non-singleton species did not capture patterns reported here for the FIA data, suggesting that latitudinal patterns of β -diversity are mainly shaped by spatial patterns of common species. In the following we only report results using the mean Morisita index across the common species.

Variation partitioning

We used a series of partial regressions to partition the variation in β -deviation into four components (Legendre & Legendre 2012): (1) uniquely explained by species aggregation, (2)

uniquely explained by latitude, (3) jointly explained by species aggregation and latitude and (4) the unexplained portion. By replacing the species aggregation index with the variation in environmental variables, we also performed a second variation partitioning procedure to partition the variation in β -deviation into: (1) uniquely explained by habitat heterogeneity, (2) uniquely explained by latitude, (3) jointly explained by habitat heterogeneity and latitude and (4) the unexplained portion. A forward selection was performed on the environmental variables (i.e. the aforementioned 19 bioclimatic and 17 soil variables) and only those selected variables were used in the variation partitioning.

All analyses were conducted in the statistical program R (<https://www.r-project.org/>). Code and data are available from figshare (<https://doi.org/10.6084/m9.figshare.7264670>) to reproduce our results.

RESULTS

Results for different measures of β -diversity (β_p and the Sørensen and Jaccard differentiation of different orders $q = 0, 1$ and 2) are qualitatively the same. Thus in the main text we only present results for β_p . Full results for the Sørensen and Jaccard differentiation can be found in Appendix S1.

Raw β -diversity showed a significant negative relationship with latitude (Fig. 2A) as consistent with other studies (Koleff *et al.* 2003; Qian & Ricklefs 2007; Soinen *et al.* 2007; De Cáceres *et al.* 2012). After correcting for the sampling effect of the regional community SAD, β -deviation showed a U-shaped pattern with latitude with β -deviation decreased first until $\sim 39^\circ$ N, then it began increasing towards the temperate-boreal transition zones of north-eastern US (Fig. 2B). These relationships were significant at all studied scales (i.e. different sizes of regional communities) and became stronger at larger scales (Fig. S1.5). The β -deviations were strongly positively correlated with the regional-community level aggregation index across all scales ($r = 0.54\text{--}0.85$, $P < 0.001$), which itself showed a significant unimodal relationship with latitude (Fig. S1.6).

Latitude and the aggregation index together explained roughly 50–80% of variation in the β -deviation across all studied scales (Fig. 3 and Fig. S1.7). The proportion accounted for by aggregation was relatively stable across both the scale of regional communities and different measures of β -diversity, whereas the proportion accounted for by latitude only increased with the scale. However, a large proportion (over 2/3) of the explained variation associated with latitude was confounded by the effect of species spatial aggregation, regardless of the measure or the indices used to calculate β -diversity. The variation in β -deviations explained by the latitudinal gradients of spatial aggregation (i.e. jointly explained by latitude and the aggregation index) also increased with increasing spatial scale of regional communities, from less than 5% for regional communities constituting of only two local plots to > 20% for regional communities constituting of 100 local plots (see the [b] component in Fig. 3).

Mean range size showed a monotonic positive correlation with latitude (Fig. 4A), unresponsive of the U-shape pattern observed for β -deviation. In contrast, the variation (or

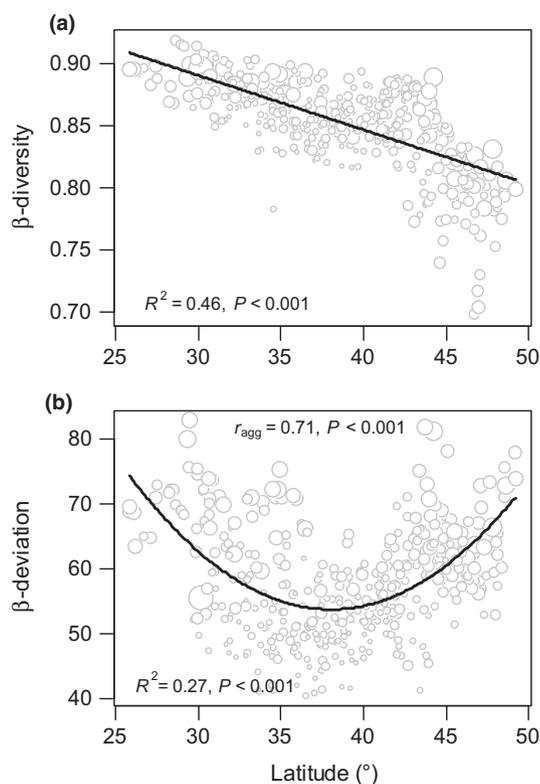


Figure 2 Relationships of β -diversity (A) and β -deviation (B) with latitude for the FIA data. Shown are results for the proportional species turnover (β_p) and $n = 99$ (i.e. each regional community consists of 100 FIA plots). Results for other measures of β -diversity and other scales can be found in Figure S1.5. Sizes of the circles are proportional to the regional-community level species spatial aggregation with larger circles indicating higher aggregation. The best fit linear (A) or quadratic (B) regression lines with R^2 are also shown. The Pearson correlation coefficients (r_{agg}) between β -deviation and the aggregation index (i.e. sizes of the circles) are shown on top of panel B.

heterogeneity) of several climatic and soil variables showed close U-shape relationship with latitude, in consistent with the pattern of β -deviation (Fig. 4B–C). Two groups of variables were identified to significantly contribute to β -deviation (Table S1). The first is a set of climate variables representing climate seasonality including the precipitation seasonality (BIO15, Fig. 4B) and the temperature annual range (BIO7, not shown) that showed the strongest effect. The second is a set of soil variables describing soil texture with the topsoil sand fraction as a key variable (Fig. 4C). The variation in β -deviation accounted for by the habitat variables showed a similar scale-dependent pattern as that for the variation explained by latitudinal gradient of spatial aggregation, that is the variation accounted for by the habitat variables was larger at broader scales (Fig. 5 and Fig. S1.8).

DISCUSSION

Previous debates on the drivers of the latitudinal gradient of β -diversity mostly focused on the local scale (by which the spatial extent of the ‘regional community’ was just at the scale

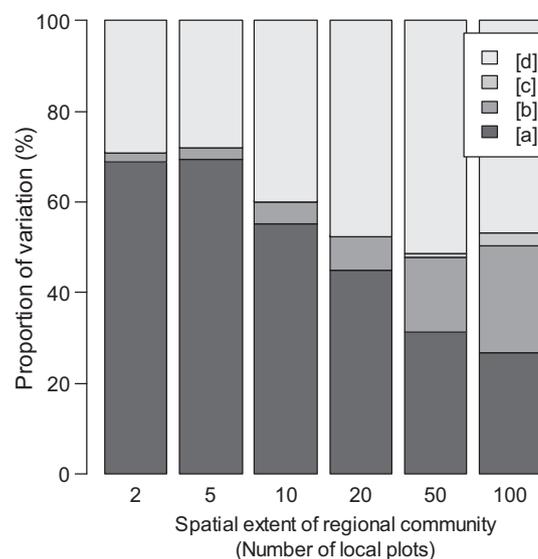


Figure 3 Proportions of variation in standardised β -deviation explained by latitude and the aggregation index for regional communities constructed at different spatial extents using the FIA data. [a] Variation explained by aggregation only; [b] variation explained by aggregation and latitude jointly; [c] variation explained by latitude only; [d] unexplained variation. Shown are results for the proportional species turnover (β_p). Results for other measures of β -diversity can be found in Figure S1.7.

of a few hundred metres in those studies) and were of limited inference on the hypotheses for regional β -diversity. Taking advantage of the regional scale of the FIA data, this study proposed a more realistic construction of regional communities and showed the latitudinal pattern of β -diversity is scale dependent.

Our results do not support the argument that the regional community SAD solely shapes the latitudinal gradient in β -diversity (Kraft *et al.* 2011; Xu *et al.* 2015). Different from Kraft *et al.* (2011) that showed no global latitudinal gradient of local β -deviation and Qian *et al.* (2013) that showed a negative gradient of local β -deviation in New World north and China but no relation in New World south, our results showed a strong unimodal latitudinal gradient in regional β -deviation for the FIA data and the gradient becomes stronger with increasing spatial scale (i.e. size) of regional communities (Fig. 2B and Fig. S1.5). Latitudinal differences in the degree of intraspecific aggregation are responsible for the U-shape latitudinal pattern no matter what measures of β -deviation are used (Fig. 3 and Fig. S1.7). These results provide support for spatial aggregation as a dominant factor underlying the latitudinal gradient of regional β -diversity and show the previous findings of Kraft *et al.* (2011) and Xu *et al.* (2015) apply only at the local scale.

Our results further showed that spatial variations in climate seasonality (as measured by precipitation seasonality BIO15, or temperature annual range BIO7, see Fig. 4B) and soil texture are primarily responsible for the U-shape β -deviation observed for the tree species in eastern North America, thus supporting the environmental filtering hypothesis. These results are consistent with the broad literature that have demonstrated the importance of climate seasonality and soil

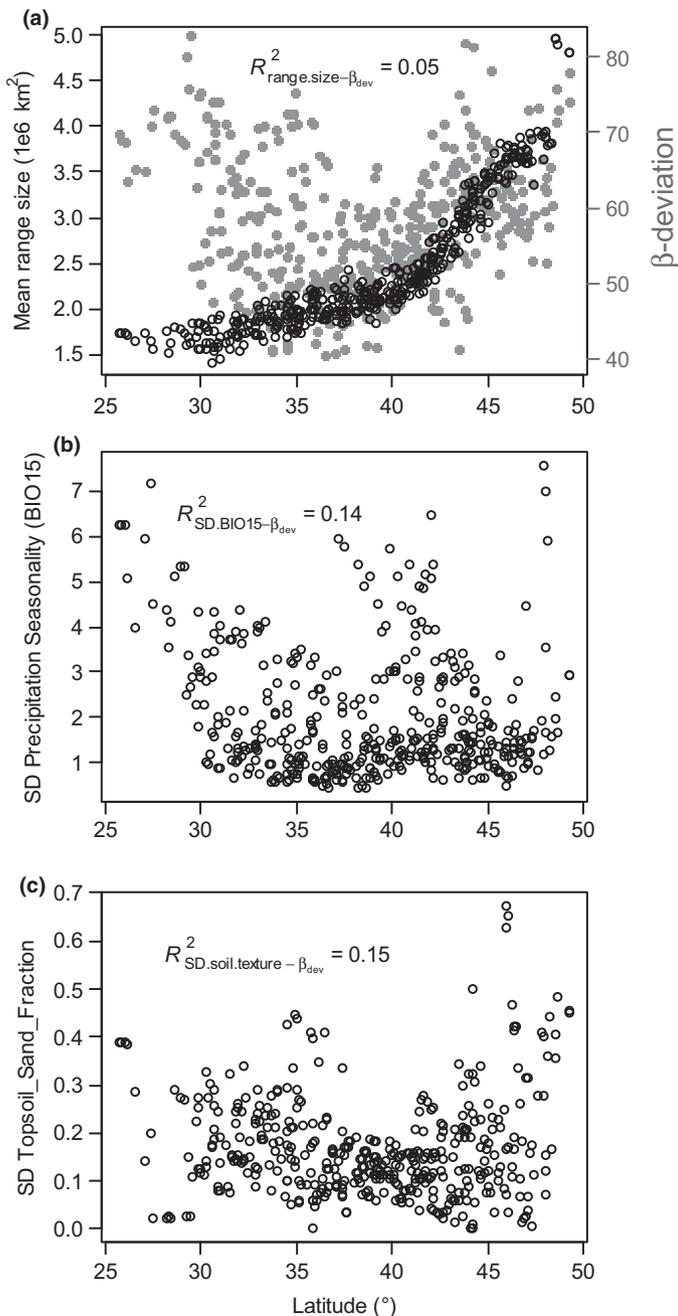


Figure 4 Latitudinal relationships of mean range size of species (black circles in A), standard deviation (SD) of precipitation seasonality (BIO15, B) and SD of soil texture (C) for the FIA data, obtained from each regional community consisting of 100 FIA plots (i.e. $n = 99$). The grey dots (from Fig. 2B) in (A) show β -deviation for the proportional species turnover (β_P). Shown in each panel is the R^2 between the β -deviation (i.e. the grey dots in panel A) and mean range size (A), SD of precipitation seasonality (B) and SD of soil texture (C).

in determining species distribution. Climatic seasonality is of primary importance in determining spatial distribution of plant species through its effects on phenology (Chuine 2010; Bykova *et al.* 2012) and is among the most frequently used predictors in modelling species distribution (Porfirio *et al.* 2014). It is remarkable that in an entirely separate study Ricklefs & He (2016) showed that temperature isothermality (BIO3), which is

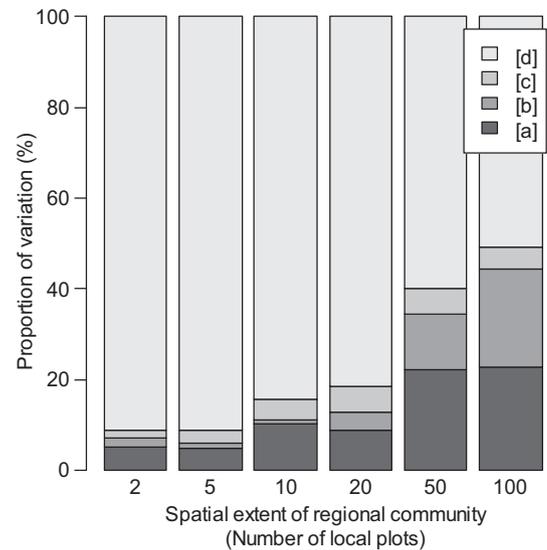


Figure 5 Proportion of variation in β -deviation explained by latitude and habitat heterogeneity for regional communities constructed at different spatial extents using the FIA data. [a] Variation explained by habitat heterogeneity only; [b] variation explained by habitat heterogeneity and latitude jointly; [c] variation explained by latitude only; [d] unexplained variation. Shown are results for the proportional species turnover (β_P). Results for other measures of β -diversity can be found in Figure S1.8.

a combination of mean diurnal temperature range (BIO2) and temperature annual range (BIO7), is one of the three most important climatic variables determining global distribution of tree diversity. The other two climatic variables were mean temperature of warmest quarter (BIO10) and precipitation seasonality (BIO15) as identified in this study (Fig. 4B). In other studies, Ficetola *et al.* (2017) found that the variation in temperature seasonality is a key driver underlying biogeographical boundaries, supporting our observation that the increased β -deviation at higher latitudes ($> 39^\circ$ N) reflects the transitional ecoclimates in the temperate forests of north-eastern US (Ricketts *et al.* 1999). It is worth noting that minimum annual temperature (BIO6) is often used to explain diversity patterns in the literature (Hawkins *et al.* 2014; Qian *et al.* 2016). Interestingly, we also found a significant correlation between β -deviation and the variation in BIO6 in our study although the significance was not as strong as that of precipitation seasonality or temperature annual range ($R^2 = 0.04$ vs. 0.14 for BIO15 and 0.11 for BIO7; Fig. 4B and Fig. S1.9), and BIO6 was not selected when climate seasonality was included.

Many studies have also documented the importance of soil texture in determining tree species distributions. For instance, Itoh *et al.* (2003) reported tight relationships between soil texture and spatial distribution for two sympatric dipterocarp species in a Bornean rainforest. van Breemen *et al.* (1997) found that canopy tree species in temperate forests in southern New England varied significantly with soil texture. Robertson & Augspurger (1999) showed consistent species-specific associations of tree recruits with soil texture across multiple river bends along the Bogue Chitto River in Louisiana. All these studies are in consistent with our observation that soil texture is an important factor affecting tree

distributions in eastern North America, and thus the β -deviation (Fig. 4C).

Although our study does not support Rapoport's range size variation hypothesis for tree distribution at the regional scale of the eastern North America, at the global scale the hypothesis could contribute to the decreasing latitudinal β -deviation as illustrated in Fig. 1B. As it is clear, β -gradient is scale dependent (i.e. change in the latitudinal range of studies). At the local scale, β -deviation could form any relationship with latitude (positive, negative or no relationship as characterised by habitat heterogeneity) (Fig. 1B). As such, β -deviation calculated from local data could present any latitudinal trend, explaining the controversy raised from the recent debate (Kraft *et al.* 2011; Qian *et al.* 2012, 2013; Tuomisto & Ruokolainen 2012). At the regional scale, unimodal (convex or concave) relationships are revealed as shown in this study. At the global scale, a decreasing β -deviation with latitude could persist if the effects of range size become more pronounced in the tropics and/or the tropics have greater habitat heterogeneity. However, for the North American woody plant species, Weiser *et al.* (2007) showed that the range size decreases with latitude only until $\sim 25^\circ$ N, the southern boundary of our study (Fig. 2). In addition, one of the most significant predictors of β -deviation identified in this study, the temperature seasonality, does not vary a lot in the tropics. Both of these seem not to support the prediction of a global decreasing β -deviation with latitude. Nevertheless, we must acknowledge that any extrapolation of our results should be exercised with caution and the global gradient of β -deviation can only be fully revealed with comprehensive global level data.

A natural question following our results of the scale-dependence of the latitudinal gradient of β -deviation and its underlying drivers is that whether there exists a threshold of spatial scale of regional community below which there is no latitudinal gradient for β -deviation. The smallest scale analysed in this study that only included two adjacent FIA plots corresponds to a spatial scale of ~ 7 km (Fig. S1.2). At this scale the latitudinal gradients of both β -deviation and the aggregation index were still significant, though weak ($R^2 = 3\text{--}10\%$, $P < 0.01$; Figs S1.5A and S1.6A). This suggests that the threshold, if existing, should be smaller than 7 km for forest tree assemblages. Studies from a global network of stem-mapping forest dynamic plots showed that local-scale habitat heterogeneity could be substantial in structuring communities at spatial extents of 500–1000 m (De Cáceres *et al.* 2012; Brown *et al.* 2013). Indeed, a previous reanalysis of Gentry's data revealed a significant (though weak) negative relationship of standardised β -deviation with latitude for Gentry's New World north plots (Qian *et al.* 2013). We found this weak relationship can also be accounted for by the latitudinal gradient of intraspecific aggregation as defined in this study (not shown). But no similar results were found in Gentry's New World south plots. These inconsistent results reinforce the need to test the strength of local-scale habitat heterogeneity in shaping diversity patterns, thus aiding to identify the aforementioned threshold.

We conclude that latitudinal β -diversity gradient is scale dependent, and intraspecific aggregation due to habitat heterogeneity primarily drives the latitudinal gradient of the regional β -deviation for tree species in eastern US. Our results highlight the critical importance of the scale at which a regional community is

defined, and the impact of that scale on findings about the underlying drivers of β -diversity. At the subcontinental extent, this finding resolves the recent debate on whether community assembly processes in general, and species spatial aggregation in particular, are contributing to latitudinal gradients of β -diversity. Future studies on the problem should aim to test the β -gradient at the global extent and to disentangle the relative contributions of environmental filtering and range size variation in shaping the patterns of intraspecific aggregation and the β -gradient.

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AUTHORSHIP

DX and FH conceived the study. DX performed the analyses. DX and FH wrote the paper.

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