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Variation in compositional and structural components of community assemblage and its determinants

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Abstract

Questions: What are the ecological processes that determine the spatial distribution of species and species diversity? Partitioning beta diversity can provide fundamental insights into the processes that determine the spatial variation of species assemblages. However, studying beta diversity is conventionally based only on species composition data, ignoring the structural component of communities.

Study site: Temperate mixed broadleaf–conifer forest in Jiaohe, Jilin Province, northeastern China.

Methods: We characterized the variation of community assemblages in terms of species composition, size structure, or considering both components. We then employed environmental and spatial variables as explanatory factors to partition the variation in both compositional and structural components of community assemblage and assess the relative contributions of the niche and neutral processes to community assembly.

Results: The values of overall beta diversity (BD statistics) and the relative contribution of individual sampling units to beta diversity (LCBD indices) depended on whether the species composition, size structure, or both together had been taken into account. The value of compositional–structural beta diversity was the largest, followed by traditional compositional beta diversity; the smallest was the structural beta diversity. The sites with high contributions to beta diversity (LCBD values) varied among structural and compositional components. The explanatory power of the environmental variables and the spatial variables also varied widely with different components of a community. The combination of environmental and spatial variables explained the highest proportion of variation (43.8%) in the compositional component and explained the lowest proportion of variation (25.4%) in the structural component of community assemblage.

Conclusion: Both deterministic and stochastic processes are acting to determine community assemblages in terms of species composition and structure in our temperate forest site. Our study highlights the importance of considering the structural component of forest communities, in addition to compositional data, when studying beta diversity.

KEYWORDS

beta diversity, community assemblage, cumulative abundance profile, local contributions to beta diversity, size structure, species composition, variation partitioning

1 | INTRODUCTION

Understanding the mechanisms that determine the spatial distribution of species and species diversity is a central theme in ecology (Chave, 2004; Chesson, 2000; Hutchinson, 1961; Ricklefs, 1990; Vellend, 2017). Deterministic niche-based and stochastic neutral processes have been widely discussed as potential drivers of community assembly (Chesson, 2000; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Hubbell, 2001, 2006; Mayfield & Levine, 2010), but the factors underlying the relative contribution of the two processes are still unresolved (Legendre et al., 2009; Punchi-Manage et al., 2014; van der Plas et al., 2015). Niche and neutral theories emphasize different mechanisms as sources of species diversity. Niche theory predicts that deterministic processes such as habitat filtering and competition shape species assemblages. Neutral theory, in contrast, assumes that all species are essentially functionally equivalent (HilleRisLambers et al., 2012; Hubbell, 2001, 2006; Keddy, 1992) and emphasizes the importance of stochastic processes in community assembly, such as random birth, death, dispersal events, speciation, and stochastic extinction (Caswell, 1976; Hubbell, 2001). It is now generally accepted that both the deterministic and stochastic processes are potentially important determinants of the spatial distribution observed in community assemblages. At present, however, their relative importance in shaping different components of community organization (i.e., the structural, compositional, or both components together) is not clear (De Cáceres et al., 2012; Legendre et al., 2009; Punchi-Manage et al., 2014). In the present study, we defined the “compositional” term as the species composition data (e.g., species abundance values). We constrained the definition of “structural” to refer to the diameter at breast height of the individual trees making up the community.

The variation in species composition observed among a set of sampling units within a region is often described as beta diversity (Whittaker, 1960, 1972). The interest of community ecologists for beta diversity stems not only from the fact that it links local (i.e., alpha diversity) and regional diversity (i.e., gamma diversity) (De Cáceres et al., 2012), but also because it can provide fundamental insights into the processes that determine the spatial pattern of species assemblages (Anderson et al., 2011; Chase, 2010; Kraft et al., 2011; Legendre & De Cáceres, 2013; Myers et al., 2013). Beta diversity can be measured in many different ways (Koleff, Gaston, & Lennon, 2003; Legendre, Borcard, & Peres-Neto, 2005; Legendre & Legendre, 2012; Legendre et al., 2009). Beta diversity estimates are most often based on species compositional data (e.g., species abundance values or species incidence), which take the form of a site-by-species data matrix with sites in rows and species abundances in columns. Although species composition data are fundamentally important, they alone may be insufficient for describing community organization and may neglect other valuable information to study community assembly processes, such as the structural component (e.g., the size structure of constituent individuals) of a community (De Cáceres, Legendre, & He, 2013; Faith, Austin, Belbin, & Margules, 1985; Fang et al., 2012). The phenomenon of competition asymmetry emphasizes that large individuals usually compete disproportionately with their smaller-sized neighbors (Weiner, 1990). Big trees control more above- and below-ground resources (e.g., light and mineral nutrients) than small trees (Schwinning & Weiner, 1998). Therefore, larger individuals tend to have greater impact on the function and dynamics of forest ecosystems than small ones. Moreover, natural multi-species communities may exhibit similar compositions but differ in other features such as the size structure of their individuals (De Cáceres et al., 2013). The distribution of individual sizes is also an important component to represent and understand community assembly, therefore using species abundances only (i.e., the compositional component) to describe forest beta diversity may be an oversimplification of the spatial variation of communities. In order to get comprehensive insight into the processes that determine the spatial pattern of species assemblages, it is necessary to ensure first that we have the ability to describe beta diversity in a comprehensive way. Whether or not the structural component should or could be considered altogether with other beta diversity components has never been investigated and remains to be explored.

In this study, we generalized the conventional approach to the study of beta diversity by considering structural data in addition to compositional data. We first measure the spatial variation of assemblages on the basis of species composition and size structure of constituents. We then use the environmental and spatial variables as explanatory factors to partition the variation in compositional and structural components of community assemblage. We specifically address the following questions: (a) Can we take both the species compositional and size structural components of a community into account when describing beta diversity? Is there a correlation between these beta diversity components? (b) How is the assessment of these beta diversity components affected by the size of the sampling units? (c) When considering both the compositional and structural components together, to what extent are beta diversity assessments affected by the relative importance accorded to structural vs compositional differences? (d) What is the relative contribution of the environmental and spatial variables to community assembly in terms of species composition, size structure, or considering both components?

2 | MATERIAL AND METHODS

2.1 | Study sites and data collection

Our study was carried out in a temperate mixed broadleaf–conifer forest in Jiaohe, Jilin Province, northeastern China. The average hottest monthly temperature is 21.7°C in July, and the coldest month is January with an average day temperature of -18.6°C. The average annual precipitation is 695.9 mm (Zhang, Zhao, & Gadow, 2014). The soil is a brown forest soil with a rootable depth ranging between 20 and 100 cm (Zhang, Zhao, Zhao, & Gadow, 2012). This study uses data from a 30-ha (500 m × 600 m) forest dynamic plot (43°57.928′–43°58.214′ N, 127°45.287′–127°45.790′ E), established in the summer of 2010. The plot is situated in a protected old-growth forest in a late stage of succession, with little human disturbance due to its remoteness from residential areas (Yao, Zhang, Zhang, Zhao, & Gadow, 2016).

All individuals with a diameter at breast height (dbh) of 1 cm or more in the plot were identified, measured and spatially mapped in 2010. A total of 49,684 individual trees belonging to 20 families and 47 species in the plot were used in the present study. The plot was divided into 120 (50 m × 50 m), 750 (20 m × 20 m) and 3,000 (10 m × 10 m) subplots, hereafter called quadrats. Topographic and soil variables were also available for each quadrat. Four topographic variables (altitude, quadrat convexity, slope, and aspect) were calculated for each quadrat following the recommendation of Harms, Condit, Hubbell, and Foster (2001) and Yamakura et al. (1995). Eight soil environmental and nutrient variables were measured: pH, the amount of organic matter, and the total amounts as well as the available nutrients of nitrogen (N), phosphorus (P), and potassium (K) (g/g; Yan, Zhang, Wang, Zhao, & Gadow, 2015). All laboratory analyses were conducted following the procedures recommended by the Soil Science Society of China (1999).

2.2 | Statistical analyses

2.2.1 | Cumulative abundance profiles

The concept of cumulative abundance profile (CAP), developed by De Cáceres et al. (2013), is defined as a function that takes the values of a structural variable (e.g., height, dbh, etc.) as input and returns the cumulative abundance of individuals whose values of the structural variable are equal to or larger than the input value. The CAP framework generalizes traditional species abundance values and allows researchers to describe the structural component of a community. In the present study, the structural variable was diameter at breast height (dbh). According to this choice, the value of CAP for a given dbh value is the cumulative abundance of tree individuals as big as or bigger than the input value. Function CAP in fact replaces the abundance value of a dbh class by the sum of abundances in this and larger dbh classes.

2.2.2 | Community tables

Following the conventional methods, species composition tables (i.e. quadrats in rows, species in column, and the table containing individual counts) were assembled; in this study, we call this table the *traditional species composition matrix* ($\mathbf{Y}^{\mathrm{COMP}}$). In order to generalize a traditional species abundance value and describe the size structure component of the community, the CAPs, considering species identity, were calculated to obtain the *species composition combined with structural data matrix* ($\mathbf{Y}^{\mathrm{COMP-STR}}$). The $\mathbf{Y}^{\mathrm{COMP-STR}}$ is a matrix with as many rows as plot records and where columns are organized in blocks, and there are as many blocks as species and each block has as many columns as size classes. Disregarding species identity of the different individuals, CAPs were also calculated to obtain the *community structural matrix* ($\mathbf{Y}^{\mathrm{STR}}$). The $\mathbf{Y}^{\mathrm{STR}}$ is a matrix with as many rows as plot records and as many columns as size classes.

Functions “stratifyvegdata” and “CAP” in the {vegclust} R package (De Cáceres, Font, & Oliva, 2010), available on CRAN (https://CRAN.R-project.org/package=vegclust), were applied to calculate the CAPs. Functions “stratifyvegdata” and “CAP” require discretizing the structural variable, and the number of size bins affects the importance accorded to structural differences. Thus, there are decisions to be made when creating $\mathbf{Y}^{\mathrm{STR}}$ and $\mathbf{Y}^{\mathrm{COMP-STR}}$, particularly how we define the bins of the structural variables (e.g., dbh bins). In this study, we tested from 1-cm bin size to 15-cm bin size to discretize dbh into classes. That is, 1 cm bins lead to dbh classes 1–2, 2–3, 3–4 and so on, whereas 5 cm bins lead to dbh classes 1–5, 6–10, 10–15 and so on. The smaller the size of dbh bin, the more columns will be produced in each block in the table $\mathbf{Y}^{\mathrm{COMP-STR}}$, indicating that more weight is accorded to differences in structure, and vice versa. If the bin size was big enough so that the number of columns in each block in the table $\mathbf{Y}^{\mathrm{COMP-STR}}$ was one, we would have that $\mathbf{Y}^{\mathrm{COMP-STR}} = \mathbf{Y}^{\mathrm{COMP}}$. Generally, the larger the size of dbh bins, the more similar will $\mathbf{Y}^{\mathrm{COMP}}$ and $\mathbf{Y}^{\mathrm{COMP-STR}}$ be.

2.2.3 | Pairwise dissimilarity in terms of community composition and structure

We calculated dissimilarity matrices between all pairs of quadrats using the percentage difference index (a.k.a. Bray–Curtis dissimilarity) on community matrices $\mathbf{Y}^{\mathrm{COMP}}$, $\mathbf{Y}^{\mathrm{STR}}$, and $\mathbf{Y}^{\mathrm{COMP-STR}}$ to obtain *the compositional dissimilarity matrix* ($\mathbf{D}^{\mathrm{COMP}}$), *the structural dissimilarity matrix* ($\mathbf{D}^{\mathrm{STR}}$) and *the compositional–structural dissimilarity matrix* ($\mathbf{D}^{\mathrm{COMP-STR}}$), respectively. In order to explore the pairwise covariation between the three kinds of dissimilarity assessments (i.e., $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{STR}}$, $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{COMP-STR}}$, and $\mathbf{D}^{\mathrm{STR}}$ vs $\mathbf{D}^{\mathrm{COMP-STR}}$), we first computed principal coordinates of each dissimilarity matrix using principal coordinates analysis (PCoA), then compared the resulting matrices of principal coordinates, keeping all axes, using the RV coefficient. We expected that $\mathbf{D}^{\mathrm{COMP-STR}}$ would be correlated to both $\mathbf{D}^{\mathrm{COMP}}$ and $\mathbf{D}^{\mathrm{STR}}$, but the strength of the correlation does depend on the chosen size of diameter bins (i.e., on the weight given to structural vs compositional information).

Function “vegdist” with the dissimilarity index “bray” in the {vegan} R package (Oksanen et al., 2018) was used to calculate the dissimilarity matrices **D**. Function “pcoa” in the {ape} R package (Paradis, Claude, & Strimmer, 2004) was used to compute principal coordinates of each dissimilarity matrix **D**. The dissimilarities in **D** matrices were square-rooted before PCoA in order to make the matrices Euclidean and prevent the generation of negative eigenvalues and complex PCoA axes (De Cáceres et al., 2013). Function “coeffRV” in the {FactoMineR} R package (Husson, Josse, Le, & Mazet, 2015) was used to calculate the RV coefficients between the matrices of principal coordinates.

2.2.4 | Beta diversity components (BD^{COMP}, BD^{STR}, and $BD^{COMP–STR}$)

Conventionally, beta diversity (abbreviated BD) is assessed from a site-by-species data matrix; other basic characteristics (e.g., size of individuals) of the community are ignored. In order to generalize the concept of traditional beta diversity to CAP data, we applied the index proposed by Legendre et al. (2005) and Legendre and De Cáceres (2013) to compute beta diversity as the variance of the community data. Legendre and De Cáceres (2013) showed how to compute the total variance of the community composition data matrix from a dissimilarity matrix **D**. The total sum of squares, SS(**Y**), can be obtained from a dissimilarity matrix **D** using Equation 1 (Legendre & De Cáceres, 2013; Legendre & Legendre, 2012). Dividing SS(**Y**) by (n - 1) produces the classical unbiased estimate of the total variance of **Y** computed from a user-selected Euclidean dissimilarity matrix **D** (i.e., Equation 2). We used that approach to calculate *the traditional compositional beta diversity* (BD^{COMP}), *the structural beta diversity* (BD^{STR}), and *the compositional–structural beta diversity* ($BD^{COMP–STR}$), respectively, using the following equations:

$$SS(Y) = \frac{1}{n}\sum_{h=1}^{n-1}\sum_{i=h+1}^{n} D_{hi}^{2} \tag{1}$$

$$BD = SS(Y)/(n-1) \tag{2}$$

D = (D_{hi}) is an $n \times n$ symmetric dissimilarity matrix (either $\mathbf{D}^{COMP}$, $\mathbf{D}^{STR}$, or $\mathbf{D}^{COMP–STR}$); i and h represent the sampling units; n is the number of the sampling units. If the calculations start with a percentage difference **D** matrix, which is non-Euclidean, one computes the square-roots of the D values in the **D** matrix to make it Euclidean, before using the transformed D values in Equations 1 and 2.

2.2.5 | Local contributions to beta diversity in terms of community composition and structure

Legendre and De Cáceres (2013) suggested that total beta diversity can be partitioned into Local Contributions to Beta Diversity (LCBD, which are comparative indicators of the ecological uniqueness of the sites). The Local Contributions to Beta Diversity ($LCBD_i$) represent the relative contributions of the sampling unit i to beta diversity. $LCBD_i$ indicates how exceptional the composition of site i is when compared to the centroid of all points, which would represent a theoretical site with the average species composition of all the sampling units. In the present study, the LCBD represents the degree of uniqueness of each sampling unit in terms of composition and/or structure of community assemblages. $LCBD_i$ indices can be calculated from the dissimilarity matrices **D** (Legendre & De Cáceres, 2013). One first transforms the distance matrix **D** into matrix $\mathbf{A} = (a_{hi}) = (-0.5D_{hi}^{2})$, then centers the matrix as proposed by Gower (1966):

$$\mathbf{G} = \left(\mathbf{I} - \frac{\mathbf{11}'}{n}\right)\mathbf{A}\left(\mathbf{I} - \frac{\mathbf{11}'}{n}\right) \tag{3}$$

where **I** is an identity matrix of size n, **1** is a vector of ones (of length n), and **1**′ is its transpose (Legendre & Legendre, 2012). Here, each diagonal element of matrix **G** is the SS_i values (i.e., the squared distance to the centroid of the ith sampling unit). Hence, the vector of local contributions of the sites to beta diversity($LCBD_i$) is:

$$(LCBD_i) = (SS_i)/SS(Y) = \mathrm{diag}(G)/SS(Y) \tag{4}$$

The LCBD indices are scaled to sum to 1. We used function "LCBD.comp" in the {adespatial} R package (Dray et al., 2018), available on CRAN (https://CRAN.R-project.org/package=adespatial), to calculate the LCBD indices.

We checked whether there is a correlation between the LCBD coefficients calculated from species composition, size structure, or using the two components together. Hence, we calculated Spearman rank correlations pairwise between the three types of LCBD vectors (i.e., $LCBD^{COMP}$ vs $LCBD^{STR}$, $LCBD^{COMP}$ vs $LCBD^{COMP–STR}$, and $LCBD^{STR}$ vs $LCBD^{COMP–STR}$). Since the LCBD indices indicate the degree of uniqueness of the sampling units in terms of their species composition and/or size structure, we plotted the LCBD values on maps of the 30-ha plot. Large LCBD values indicate the sites that have unique species assemblages and small LCBD values indicate the sites that have assemblages that are very similar to those in other sites. Again, we expected $LCBD^{COMP–STR}$ to be correlated to both $LCBD^{COMP}$ and $LCBD^{STR}$, but with the strength of the correlation depending on the weight given to structural vs compositional information. We thus showed the two extreme cases of the LCBD map: according a largest weight to the structural component and correspondingly the smallest relative weight to the compositional component (i.e., 1-cm bin size), and giving the largest relative weight to the compositional component (i.e., 15-cm bin size).

2.2.6 | Sets of explanatory variables: environmental and spatial variables

Following Legendre et al. (2009), we used altitude, convexity, and slope to construct third-degree polynomial functions (i.e., yielding nine variables). The monomials with exponents allow the modeling of nonlinear relationships between the topographic variables and the response variables. We calculated the aspect of a quadrat as the average angle of the four triangular planes that deviate from the north direction. We thus used the sin (aspect) and cos (aspect) in order to include it in a linear regression model. We therefore obtained 11 expanded topographic variables. We then combined these 11 expanded topographic variables with the eight soil variables (described in section 2.1 Study sites and data collection) to obtain the environmental variables data table (i.e., 19 variables) for each quadrat. We computed eigenfunctions of distance-based Moran's eigenvector maps (dbMEM, also called Principal Coordinates of Neighbour Matrices, PCNM; Borcard, Legendre, Avois-Jacquet, &

Tuomisto, 2004; Legendre & Legendre, 2012; Legendre et al., 2009) across the 3000 (10 m × 10 m), 750 (20 m × 20 m), and 120 (50 m × 50 m) quadrats. The dbMEM eigenfunctions with positive eigenvalues only were used as spatial variables. We applied forward model selection (with permutation tests, at the 5% significance level, of the increase in R^2 at each step) to extract the significant environment variables and eigenfunctions of dbMEM using the function "forward.sel" in the package {adespatial} (Dray et al., 2018).

2.2.7 | Variation partitioning of $\mathbf{D}^{\mathrm{COMP}}$, $\mathbf{D}^{\mathrm{STR}}$ and $\mathbf{D}^{\mathrm{COMP–STR}}$

To compare the influence of niche-based and spatial processes on community assembly represented by community composition, size structure, or the two components together, distance-based redundancy analysis (dbRDA, Legendre & Anderson, 1999; Legendre & Legendre, 2012) was used to partition the variation of each of three community matrices (Borcard, Legendre, & Drapeau, 1992; Legendre et al., 2009; Peres-Neto, Legendre, Dray, & Borcard, 2006). Specifically, we used the two sets of explanatory variables (after forward model selection) to partition variation in the principal coordinate tables extracted from $\mathbf{D}^{\mathrm{COMP}}$, $\mathbf{D}^{\mathrm{STR}}$, $\mathbf{D}^{\mathrm{COMP–STR}}$ separately into fractions explained by the four different components: (a) pure habitat, (b) spatially structured habitat, (c) pure space, and (d) undetermined (Borcard & Legendre, 1994; Borcard et al., 1992; De Cáceres et al., 2012; Legendre et al., 2009; Myers et al., 2013; Punchi-Manage et al., 2014). We hypothesized that the niche processes are responsible for the proportion of variation explained by the pure habitat and the spatially-structured habitat components (a + b) (Laliberté, Paquette, Legendre, & Bouchard, 2009; Legendre et al., 2009). While we hypothesized that the proportion of variation explained by the pure spatial component (c) is related to independent biological processes (e.g., dispersal limitation, competition, facilitation, historical events, and Janzen–Connell effects) (Legendre & Legendre, 2012; Legendre et al., 2009; Punchi-Manage et al., 2014). The undetermined proportion of variation (d) may be related to stochastic processes or undefined non-spatially-structured biological or environmental variables (Dumbrell, Nelson, Helgason, Dytham, & Fitter, 2010). That allowed us to assess the relative contributions of the environmental and spatial variables to community assembly in terms of composition, structure, or taking the two components together. All analyses were performed using R (R Core Team, 2017).

3 | RESULTS

3.1 | Pairwise dissimilarity in terms of community composition and structure

We found that dissimilarity matrices computed from species composition ($\mathbf{D}^{\mathrm{COMP}}$), size structure ($\mathbf{D}^{\mathrm{STR}}$), and considering both components together ($\mathbf{D}^{\mathrm{COMP–STR}}$) were correlated. However, the strength of the correlation depended on the size of bins used to discretize the structural variable and on the size of the quadrats (Figure 1a–c). Overall, the correlation between $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{COMP–STR}}$ was

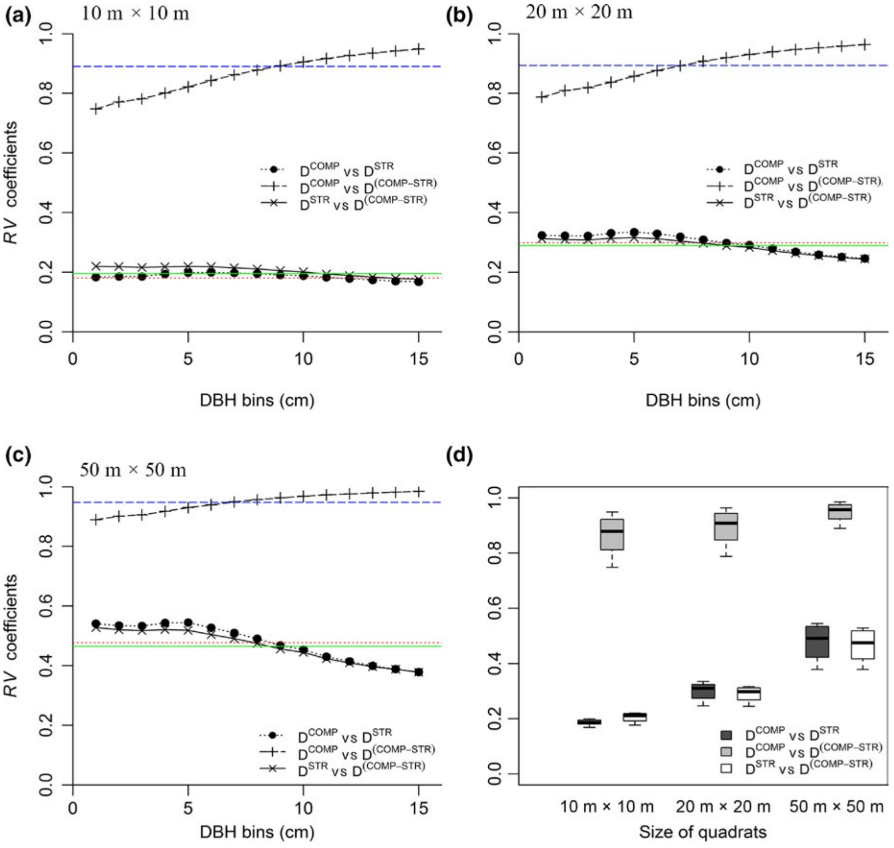


FIGURE 1 The correlations between the pairwise dissimilarity in terms of species composition ($\mathbf{D}^{\mathrm{COMP}}$), size structure ($\mathbf{D}^{\mathrm{STR}}$) and both components together ($\mathbf{D}^{\mathrm{COMP–STR}}$). The correlations of $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{STR}}$, $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{COMP–STR}}$, and $\mathbf{D}^{\mathrm{STR}}$ vs $\mathbf{D}^{\mathrm{COMP–STR}}$ vary with dbh bins at the scale of (a) 10 m × 10 m, (b) 20 m × 20 m and (c) 50 m × 50 m. In graphs (a), (b), and (c), the horizontal red dotted lines, horizontal blue long-dash lines and horizontal green solid lines represent the mean values of RV coefficients of 1–15 cm dbh bins of $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{STR}}$, $\mathbf{D}^{\mathrm{COMP}}$ vs $\mathbf{D}^{\mathrm{COMP–STR}}$, and $\mathbf{D}^{\mathrm{STR}}$ vs $\mathbf{D}^{\mathrm{COMP–STR}}$, respectively. (d) Boxplots for RV coefficients of the three pairwise dissimilarity comparisons (aggregated over all 1–15 cm dbh bin sizes), for each of the three quadrat sizes [Colour figure can be viewed at wileyonlinelibrary.com]

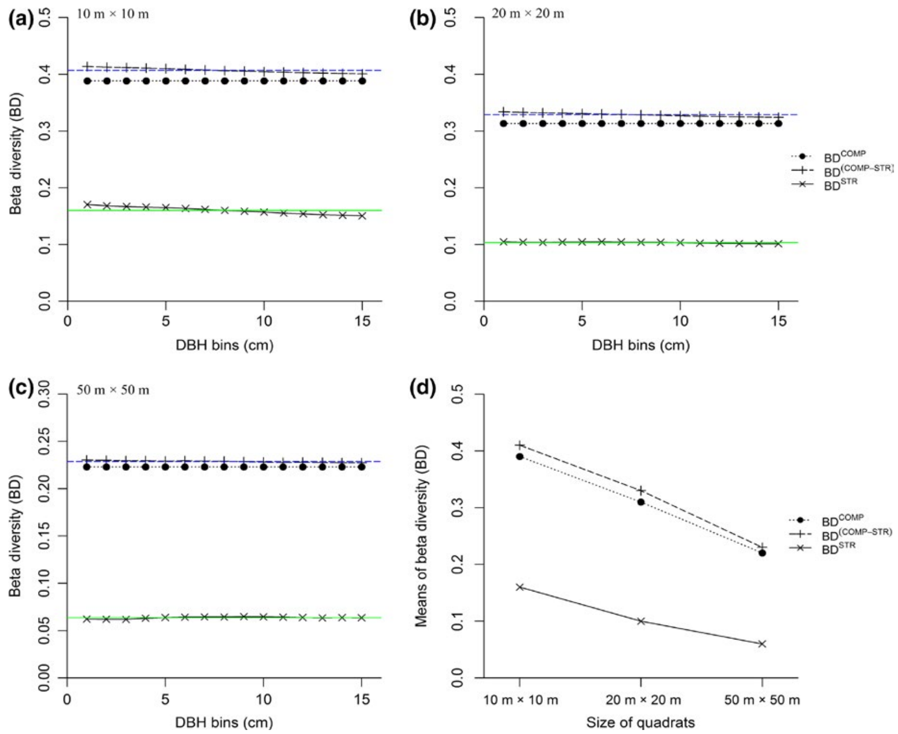


FIGURE 2 The Beta Diversity (BD) in terms of species composition (BD^{COMP}), size structure (BD^{STR}) and both components together ($\text{BD}^{\text{COMP–STR}}$). The values of $\text{BD}^{\text{COMP–STR}}$ and BD^{STR} vary with the size of bins of the structural variable (dbh bin sizes = 1–15 cm) at the scale of (a) 10 m × 10 m, (b) 20 m × 20 m, and (c) 50 m × 50 m. The size structure of individuals (i.e., the dbh) is not considered when calculating the BD^{COMP}; thus, the values of BD^{COMP} were not affected by the bin size. In graphs (a), (b), and (c), the horizontal blue long-dash lines and horizontal green solid lines represent the mean values of $\text{BD}^{\text{COMP–STR}}$, and BD^{STR} across 1–15 cm bin sizes, respectively. (d) Values of BD^{COMP}, BD^{STR}, and $\text{BD}^{\text{COMP–STR}}$ (after averaging across dbh bin sizes) vary with the sampling unit sizes [Colour figure can be viewed at wileyonlinelibrary.com]

substantially stronger than that of $\mathbf{D}^{\text{COMP}}$ vs $\mathbf{D}^{\text{STR}}$, and of $\mathbf{D}^{\text{STR}}$ vs $\mathbf{D}^{\text{COMP–STR}}$.

The correlation of $\mathbf{D}^{\text{COMP}}$ vs $\mathbf{D}^{\text{COMP–STR}}$ increased with the increase of bin size. Correspondingly, the correlations of $\mathbf{D}^{\text{STR}}$ vs $\mathbf{D}^{\text{COMP–STR}}$ showed the opposite trend (Figure 1a–c). As to the effect of the size of the sampling units, the strength of correlations increased with the quadrat size (Figure 1d), except for the correlation between $\mathbf{D}^{\text{COMP}}$ and $\mathbf{D}^{\text{COMP–STR}}$, which exhibits no significant difference between the 10 m × 10 m and 20 m × 20 m quadrats ($p = 0.23$, Figure 1d).

3.2 | The three components of beta diversity (BD): BD^{COMP}, BD^{STR} and $\text{BD}^{\text{COMP–STR}}$

The beta diversity (BD) values were closely related to whether the species composition, size structure, or both components together had been taken into account. Among these three components of beta diversity, $\text{BD}^{\text{COMP–STR}}$ was greatest, closely followed by BD^{COMP}, and the smallest was BD^{STR} (Figure 2). Since the size structure of individuals was not considered when calculating BD^{COMP}, this index was not affected by the size of dbh bins (Figure 2a–c). The values of $\text{BD}^{\text{COMP–STR}}$ and BD^{STR}, however, decreased slightly with an increase of bin size. When increasing dbh bin size, the values of $\text{BD}^{\text{COMP–STR}}$ gradually approached the values of BD^{COMP} (Figure 2a–c). BD also varied as a function of quadrat size (Figure 2); values of BD^{COMP}, BD^{STR}, and $\text{BD}^{\text{COMP–STR}}$ (after averaging across bin sizes) systematically decreased with increasing quadrat size (Figure 2d).

3.3 | Local contributions to beta diversity in terms of community composition and structure

Local Contributions to Beta Diversity calculated using species composition, size structure, or both components were correlated. Again, the strength of correlations depended on the size of dbh bins and on the size of quadrats (Figure 3a–c). In the case of $\text{LCBD}^{\text{COMP}}$ vs $\text{LCBD}^{\text{COMP–STR}}$, the strength of the correlation increased with an increase of bin size. Correspondingly, the correlation of LCBD^{STR} vs $\text{LCBD}^{\text{COMP–STR}}$ showed the opposite trend (Figure 3a–c). The correlations of $\text{LCBD}^{\text{COMP}}$ vs LCBD^{STR}, and LCBD^{STR} vs $\text{LCBD}^{\text{COMP–STR}}$ were significantly different for different quadrat sizes. A striking finding was that the strength of correlations was weaker at the scale of 20 m × 20 m than that at the scales of 10 m × 10 m or 50 m × 50 m (Figure 3d). However, correlations between $\text{LCBD}^{\text{COMP}}$ vs $\text{LCBD}^{\text{COMP–STR}}$ were not substantially affected by the size of quadrats (Figure 3d).

The LCBD_i values indicate the *i*th quadrats that contribute more or less than the mean to beta diversity (in other words, the *i*th quadrats with high or low uniqueness of species assemblages). The results indicated that the sites with high LCBD values (contribute more than

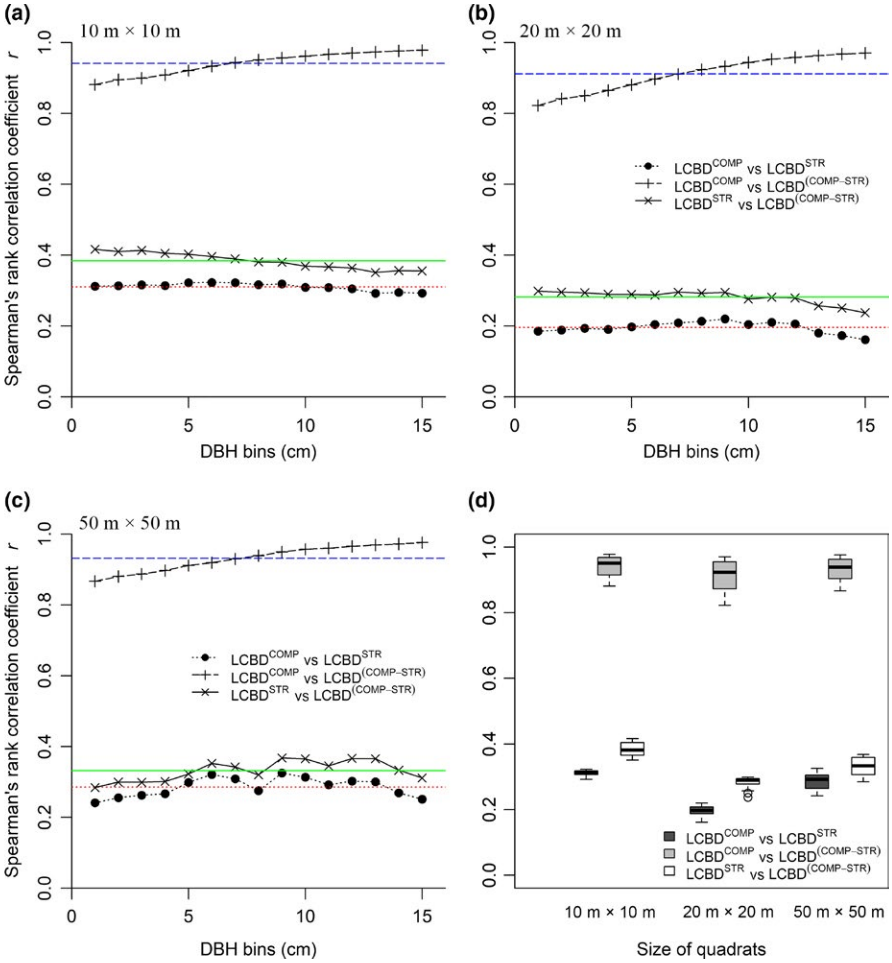


FIGURE 3 The correlations between the Local Contributions to Beta Diversity (LCBD) in terms of community composition (LCBD^{COMP}), structure (LCBD^{STR}) and both components together (LCBD$^{COMP–STR}$). The correlations of LCBD^{COMP} vs LCBD^{STR}, LCBD^{COMP} vs LCBD$^{COMP–STR}$, and LCBD^{STR} vs LCBD$^{COMP–STR}$ with the size of bins of the structural variable (bin sizes = 1–15 cm) at the scale of (a) 10 m × 10 m, (b) 20 m × 20 m, and (c) 50 m × 50 m. In graphs (a), (b), and (c), the horizontal red dotted lines, horizontal blue long-dash lines and horizontal green solid lines represent the mean values of Spearman's rank correlation coefficient *r* across 1–15 cm bin size of LCBD^{COMP} vs LCBD^{STR}, LCBD^{COMP} vs LCBD$^{COMP–STR}$, LCBD^{STR} vs LCBD$^{COMP–STR}$, respectively. (d) Boxplots for the Spearman's rank correlation coefficient *r* between the pairwise of the three kinds of LCBD of 1–15 cm bin sizes at different quadrat sizes [Colour figure can be viewed at wileyonlinelibrary.com]

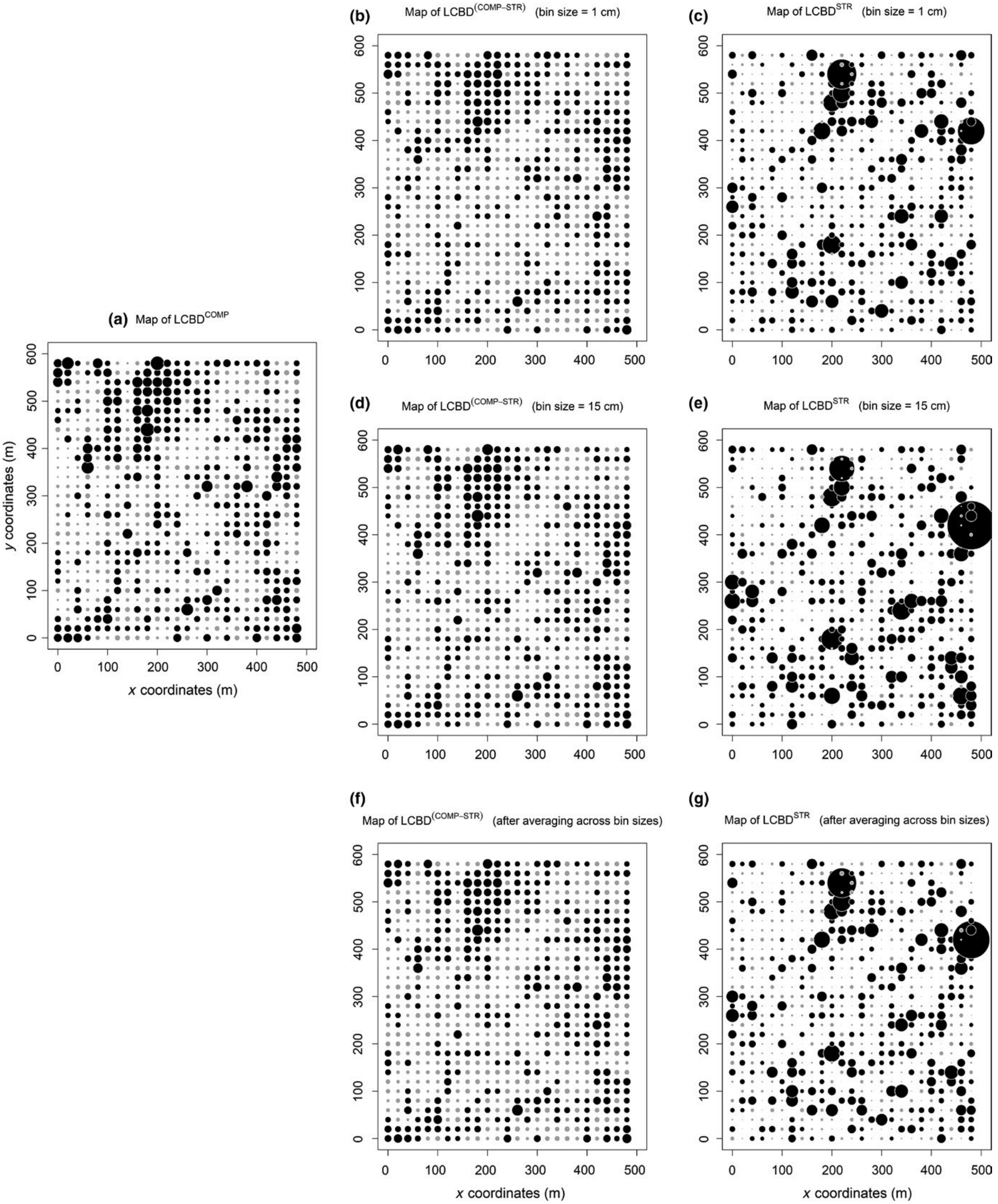
the mean to beta diversity) are varied among three components of a community (Figure 4). Specifically, 342 (45.6%), 290 (38.7%), and 331 (44.1%) out of 750 quadrats contributed more than the mean to beta diversity in term of species composition (i.e., LCBD^{COMP}, Figure 4a), size structure (i.e., LCBD^{STR}, Figure 4g), and both components together (i.e., LCBD$^{COMP–STR}$, Figure 4f), respectively.

3.4 | Variation partitioning of matrices D^{COMP}, D^{STR}, and D$^{COMP–STR}$

The explanatory power of the environmental variables and the spatial variables varied for the three types of matrices and with quadrat sizes (Table 1). The variation explained by the environmental variables (a + b), and by the spatial variables (b + c) increased systematically with increasing scale (Table 1). Averaging across quadrat sizes, habitat and space jointly explained 43.8%, 25.4%, and 34.1% of the variation in compositional component, structural component, and the two components together of community assemblage, respectively. However, the contribution of the pure habitat component (a) was negligible. The combination of environmental and spatial variables explained the lowest proportion of variation in the structural component alone and explained the highest proportion of variation in the compositional component alone (Table 1). Both the environmental variables (a + b) and the pure spatial variables (c) explained more variation in the compositional component than that in the structural components of community assemblage. Additionally, our findings indicate that the unexplained (d) fractions dominated the variance partitioning computed for the structural component $\mathbf{Y}^{STR}$ alone (Table 1).

4 | DISCUSSION

Forest ecosystems can be characterized and evaluated in terms of both their structure and composition (Peet, 1992). In previous studies, the compositional and structural components of a community assemblage were usually analyzed separately (e.g., Fang et al., 2012). However, the nature of species assemblages indicates that either species composition or size structure of constituent individuals alone may oversimplify community organization (De Cáceres et al., 2013). Changes in structure and composition may be only weakly related (e.g., Arsenault & Bradfield, 1995); therefore, assessment of both simultaneously is important when evaluating community assembly. In the present study, we generalized the conventional approach to community assemblage by incorporating structural data of a community in addition to compositional data, using the CAP framework. To our knowledge, this is the first paper that investigates in a single study the variation in both the compositional and structural components of community assemblages simultaneously, as well as its determinants.



We found that both overall beta diversity (BD) and the relative contribution of sampling units to beta diversity (LCBD) depended on whether the species composition, size structure, or both components together had been taken into account. Beta diversity partitioning indicated that the explanatory power of the environmental and the spatial variables also varied widely with different components of a community. Our results highlight that considering both species compositional and size structural components may be a more comprehensive way to describe the community organization.

FIGURE 4 Maps of 30-ha (500 m × 600 m) plot showing the local contributions to beta diversity (LCBD) in terms of community composition and structure for 750 quadrats (20 m × 20 m). The solid circles represent the values of LCBD_i for each *i*th quadrat ($i = [1, 750]$). (a) The map of LCBDs only in terms of species composition. Note that the size structure of individuals (i.e., dbh) is not considered when calculating the $\mathrm{LCBD}^{\mathrm{COMP}}$; thus, the values of $\mathrm{LCBD}^{\mathrm{COMP}}$ were not affected by the size of the bins of the structural variable. (b)–(e) The two extreme cases of the LCBD map: (b) and (c) giving the most weight to the structural component and correspondingly the least weight to the compositional component (i.e., 1-cm bin size), and (d) and (e) giving the most weight to the compositional component and correspondingly the least weight to the structural component (i.e., 15-cm bin size). (f) and (g) Maps of LCBDs after averaging across dbh bin sizes. Size of the circles is proportional to the LCBD_i values. The black and grey solid circles represent the sites with LCBD values higher and lower than the mean, respectively

TABLE 1 Variation partitioning results for three types of matrices at different scales of quadrats. The partitioning is based on adjusted R^2 statistics, as recommended by Peres-Neto et al. (2006)

Quadrat sizes	(a)	(b)	(c)	(d)	(a + b)	(b + c)	(a + b + c)
$\mathbf{Y}^{\mathrm{COMP}}$							
10 m × 10 m	0.0044	0.0796	0.1361	0.7799	0.0840	0.2157	0.2201
20 m × 20 m	0.0028	0.1783	0.2862	0.5327	0.1811	0.4645	0.4673
50 m × 50 m	0.0050	0.2995	0.3229	0.3726	0.3045	0.6224	0.6274
$\mathbf{Y}^{\mathrm{STR}}$							
10 m × 10 m	0.0123	0.0131	0.0296	0.9450	0.0254	0.0427	0.0550
20 m × 20 m	0.0013	0.0907	0.1652	0.7428	0.0920	0.2560	0.2572
50 m × 50 m	0.0029	0.2300	0.2163	0.5509	0.2328	0.4463	0.4492
$\mathbf{Y}^{\mathrm{COMP-STR}}$							
10 m × 10 m	0.0055	0.0564	0.0932	0.8449	0.0619	0.1496	0.1551
20 m × 20 m	0.0028	0.1576	0.2559	0.5837	0.1604	0.4135	0.4163
50 m × 50 m	0.0013	0.2543	0.1948	0.5496	0.2556	0.4492	0.4504

Fractions (a)–(d) (adjusted R^2 statistics): (a), variation explained by the environmental variables after controlling for the spatial structure; (b), variation explained by the spatially structured environmental variables; (c), spatially structured variation explained by pure space after controlling for environmental variation, (d), residual variation. Environmental variables used to compute fraction (a + b). dbMEM eigenfunctions were the explanatory variables used to compute fraction (b + c). Only 5-cm-diameter classes (i.e., bin size = 5 cm) as the structural variable were used to calculate the $\mathbf{Y}^{\mathrm{STR}}$ and $\mathbf{Y}^{\mathrm{COMP-STR}}$.

4.1 | Structural and compositional components of forest variation

The framework of CAP allowed us to incorporate the distribution of individual tree size into the analysis of community assemblage, thus making it possible to quantify the spatial variation of community structure beta diversity. Even so, such structural beta diversity can be quantified independently or in combination with species composition. The $\mathrm{BD}^{\mathrm{COMP-STR}}$ is the largest among these three components of beta diversity, indicating that applying species composition alone or size structure alone to assess the beta diversity may underestimate the variation of assemblages (Figure 2). The values of $\mathrm{BD}^{\mathrm{COMP}}$ are closer to the $\mathrm{BD}^{\mathrm{COMP-STR}}$ values than that of $\mathrm{BD}^{\mathrm{STR}}$ (the $\mathrm{BD}^{\mathrm{STR}}$ values are relatively small; Figure 2). Thus, as far as our CAP framework is concerned, it seems more appropriate to quantify beta diversity using the species composition individually than using the size structure individually. Nevertheless, if structure provides independent information and is deemed important, one should incorporate it in BD assessment. As beta diversity indices were calculated from dissimilarity matrices, the structural component of beta diversity depended on the weight given to structural vs compositional information when calculating dissimilarity (Figure 2a–c). The larger the bin sizes (i.e. the smaller weight given to species structural information), the closer $\mathrm{BD}^{\mathrm{COMP-STR}}$ values approached the values of $\mathrm{BD}^{\mathrm{COMP}}$ (Figure 2a–c). If the bin sizes are big enough, the $\mathrm{BD}^{\mathrm{COMP-STR}}$ value and the $\mathrm{BD}^{\mathrm{COMP}}$ value are expected to converge at a certain size of dbh bin. Nevertheless, considering the necessity of comprehensive assessment of beta diversity, we advocate for small bin sizes, as they provide more independent structural information. Finally, it is important to note that this forest plot includes 47 different tree species, which results in a strong relative weight of the compositional component of $\mathrm{BD}^{\mathrm{COMP-STR}}$ when using the CAP framework. Repeating our study in forests with lower species richness or in this forest but using a coarser compositional resolution (e.g., at the family level) would result in larger relative weight of the structural component.

4.2 | Local contributions to beta diversity in terms of community composition and structure

Ecologically, LCBD indices only represent the degree of uniqueness of the sampling units in terms of community composition (Legendre

& De Cáceres, 2013). However, natural communities may exhibit similar species compositions but differ in other features such as the size structure of individuals. In the present study, we assessed the degree of uniqueness of the quadrats in terms not only of their species composition, but also of their size structure, and by using both components together. The degree of uniqueness of quadrats in terms of community composition individually had a very weak correlation with uniqueness in terms of size structure individually ($\mathrm{LCBD}^{\mathrm{COMP}}$ vs $\mathrm{LCBD}^{\mathrm{STR}}$, Figure 3), indicating that sites that are unique in species composition are not necessarily unique in size structure, and vice versa. Additionally, we found that the spatial distribution of sites with high LCBD values is different for the two components of a community, with sites with high structural uniqueness occurring in small forest patches (Figure 4). All these results reinforce the idea that considering both species compositional and size structural components may be a more comprehensive way to describe the community organization. However, if we accept the fact that sites that are unique in terms of size structure are the result of gap dynamics (see below), the non-zero correlation between $\mathrm{LCBD}^{\mathrm{COMP}}$ vs $\mathrm{LCBD}^{\mathrm{STR}}$ may indicate that forest gaps may be colonized by species that may later be suppressed as the forest grows, so that recent forest gaps have a different species composition than closed forest structures (Comita et al., 2009).

4.3 | Partitioning the structural and compositional components of beta diversity

About 34.4% of the variation in community assemblage was determined by environmental and spatial variables, depending on the scale (quadrat size) and on which components of community assemblage (i.e., compositional component, structural component, and taking both components together) were taken into account. This proportion is slightly lower than the values found in studies by Legendre et al. (2009) and Punchi-Manage et al. (2014). A reason for this result is that we incorporated differences both in size structure and species composition into community assemblages rather than only using the conventional species composition data. When the species composition and size structure of the constituent individuals are incorporated into the community at the same time, more variation will occur in community assemblages. In our study, habitat (a + b) explained more variation in the compositional component (19.0%) than in the structural component (11.7%) of the community assemblages. Beta diversity partitioning indicated that the variation in the structural component is less dictated by environment than variation in the compositional component. We here hypothesize that canopy gap dynamics will be the potential drivers of structural variation. Winter in our study area is cold and long, with a long snowfall period. The snowfall period lasts for half a year, and the snow cover thickness in mountainous areas reaches 40–50 cm. We hypothesize that pulses of moderate-severity disturbances may be caused by snowstorms in our site. In the absence of stand-replacing disturbances, forest canopies are opened periodically by the death of single big trees or small groups of adult trees creating canopy gaps. Snowstorms may have altered forest structure by selectively removing larger canopy trees. Environmental selection of individuals shapes composition by determining the fitness of individuals, whereas structural variation may have some relationship with environmental conditions (i.e., larger trees in sites where larger sizes are supported for energy or water availability) but in general is the reflection of different stages around gap dynamics. Previous studies are consistent with our findings. Fraver and White (2005) for instance, found that the repeated moderate-severity disturbances (i.e., windstorms) caused dramatic structural changes; they caused no significant change in species composition.

Because the relative importance of both niche and neutral theory in structuring communities varies with spatial scale (Legendre et al., 2009; Punchi-Manage et al., 2014), we conducted scale-dependent analyses. In sharp contrast to the finding by Legendre et al. (2009) for a broad-leaved forest in China, we found that the proportion of undetermined variation in compositional and structural components of community assemblages was very high at fine spatial scales (up to 94.5% for the structural component, 78.0% for the compositional component, and 84.4% for both components together) but decreased systematically with increasing spatial scale (up to a minimum of 37.3% for compositional component at the 50-m scale). These results are in line with the findings by Punchi-Manage et al. (2014) in a Sri Lankan dipterocarp forest and by De Cáceres et al. (2012) in a comparison of several forests. On the one hand, the high proportion of unexplained variation may be related to unmeasured and not spatially-structured biological or environmental variables. Xu et al. (2016) showed that the soil nutrients in the upper (0–10 cm, considered in our study) and lower soil layers (10–20 cm), and the heavy metal elements (Cu, Ni, Cd, As, Pb, Zn, Mo, Cr, Mn and Mg) in the soil show a strong correlation with the species spatial distributions at Jiaohe. This may partly explain why the pure environmental variable (a) explained such little variation in the community assemblages. Another explanation for the high proportion of unexplained variation is that it may be due to stochastic processes, which related to the neutral theory assuming that the dynamics of populations are primarily driven by ecological drift and dispersal (Legendre et al., 2009). On the other hand, the proportion of undetermined variation in compositional and structural components of community assemblages decreased systematically with increasing spatial scale. This may indicate that community assemblage is highly stochastic in terms of species composition and tree size distribution at fine scales (i.e. 10-m scale), but this fine scale stochasticity tends to smooth out at the 50-m scale, where more consistent habitat-driven species assemblages emerged. When variance partitioning is conducted on the structural component alone, the unexplained (d) fraction is dominant. While the influence of environmental factors on size structure may be less important than for the compositional component, the effect of local disturbances (e.g., appearance of canopy gaps resulting from mortality of large trees) results in random spatial patterns of quadrats with rather different structure, contributing to a large unexplained fraction.

5 | CONCLUSIONS

Species composition and size structure are the two essential features of a community. Only one of them individually may be insufficient to describe the organization of tree species assemblages. Defining and quantifying beta diversity using the species composition alone may be sufficient then in many occasions. Nevertheless, species composition is just one dimension of biodiversity; variation in size structure is also important. Incorporating structural data in beta diversity assessments allows ecologists to make use of valuable information collected during field surveys. If it is available, there is no reason to ignore the wealth of information about size structure when comparing species assemblages. Our study highlights the need to incorporate the structural data of a community in addition to compositional data when quantifying and analyzing beta diversity. Finally, our results suggest that both deterministic and stochastic processes are relevant determinants of compositional and structural components of community assemblages in our temperate forest. Nevertheless, these processes are scale- and/or resolution-dependent.

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CONFLICTS OF INTEREST

The authors declare no competing financial interests.

DATA ACCESSIBILITY

Data ownership belongs to Beijing Forestry University, whose staff conducted the analyses and wrote the manuscript. http://www.bjfu.edu.cn/.

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