


# The relative importance of space compared to topography increases from rare to common tree species across latitude

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## Abstract

**Aim:** Understanding how spatial distributions of rare and common species are associated with environmental and spatial processes is essential to understanding community assembly. We addressed the following questions: (a) does the relative importance of space and topography vary from rare to common tree species? (b) Are the contributions of topography and space equal? (c) Are the variances explained by topography or space correlated with elevational ranges (ER) at the local scale? (d) Does cell-size influence those postulated associations?

**Location:** China and the Americas.

**Major taxa studied:** Tree species.

**Methods:** We partitioned the variation in species richness and composition of rare and common tree species by topography and space across a range of extents and grain sizes in eight communities. We calculated contribution ratio (CR) between space and topography to quantify their relative importance. We employed Kendall's rank correlation to determine the relation between CR and commonness. Mixed effect models were used to identify the influence of cell-size on the results.

**Results:** The majority of CR values were positively related to increasing commonness, especially for composition. The explained variances by space were always higher than that by topography regardless of commonness. At local scale, variances explained by space or topography were not correlated with ER.

**Main conclusions:** Our results indicate that the relative importance of space compared to topography increases from rare to common species across forests. We suggest that future studies of community assembly need to account for both space and topography to adequately describe differences in rare and common species assembly mechanisms at range of spatial extents and grain sizes.

## KEYWORDS

alpha and beta diversity, community assembly, CTFs-ForestGEO, Niche and neutral, Scale, variation partitioning

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## 1 | INTRODUCTION

Niche and neutral processes are two broad categories of determinants of commonness and rarity in community assembly (Cottenie, 2005; Leibold & McPeck, 2006; Leibold et al., 2004). However, most studies concentrate on common species (e.g., Harms, Condit, Hubbell, & Foster, 2001; Hu, Sha, et al., 2012; Shen et al., 2009, 2013) or the overall community (e.g., Legendre et al., 2009). The response of rare species to the spatial and environmental processes has rarely been tested, yet rare species are usually the principal component of species diversity (McGill, 2003). Moreover, rare species are critical in shaping the dynamics of species assembly under climate change (Benedetti-Cecchi, Bertocci, Vaselli, Maggi, & Bulleri, 2008), and are essential for ecosystem functioning (Lyons, Brigham, Traut, & Schwartz, 2005; Lyons & Schwartz, 2001). Common and rare species tend to differ from each other in many ways, for example dispersal abilities, life history strategies (Kunin & Gaston, 1993; Kunin & Shmida, 1997), aggregation patterns (Condit et al., 2000), responses to competition (Dawson, Fischer, & Kleunen, 2012), density dependence (Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Johnson, Beaulieu, Bever, & Clay, 2012), population dynamics (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012) and habitat preferences (Cornwell & Ackerly, 2010). The mechanisms driving richness and composition patterns of rare species may be remarkably different from that of common species. With a few notable exceptions, (e.g., Alahuhta, Johnson, Olker, & Heino, 2014; Pandit, Kolasa, & Cottenie, 2009 and Siqueira et al., 2012), rigorously and quantitatively comparing the response differences of rare and common species to niche and neutral factors have not been investigated.

In terms of the relative importance of neutral and niche processes, metacommunity theory categorizes communities into four modes (Brown, Sokol, Skelton, & Tornwall, 2017; Winegardner, Jones, Ng, Siqueira, & Cottenie, 2012): species sorting, mass effects, patch dynamics and neutral model. Among them, species sorting and neutral model gain the hot debating (Cottenie, 2005). Nevertheless, Chang, Zelený, Li, Chiu, and Hsieh (2013) reported that including different environmental variables in community assembly analyses can alter the relative

contribution differences between neutral and niche processes. Therefore, the total contribution of neutral or niche processes can be strongly affected by the particular spatial or environmental variables included in the mathematical models. In this context, we propose that it is better to investigate contribution ratio (CR) between two fixed groups of neutral and niche variables, which can be defined as the ratio between spatial and environmental component, to identify the relative importance between space and environment. Especially, when we are want to identify the relative importance differences of neutral and niche processes to rare and common species, using the CR will make the comparison between rare and common species more equivalent.

No general consensus has been reached about the community assembly mechanism underlying rare and common species, likely because previous related studies usually being conducted at one single spatial scale, or just on one type of diversity (e.g., alpha or beta diversity). For instance, the composition of rare and common species similarly respond to niche process (Alahuhta et al., 2014; Heino & Soininen, 2010; Siqueira et al., 2012), the richness pattern of common species is more closely related to niche process than rare ones (Lennon, Beale, Reid, Kent, & Pakeman, 2011). Alternatively, Pandit et al. (2009) found that common respond in a neutral manner, while rare species to niche processes. The relative contributions of environment and space to community assembly are unpredictable across different spatial scales, extents and regions (Alahuhta & Heino, 2013; Cheng et al., 2012; László, Rákósy, & Tóthmérész, 2014). Moreover, intrinsic mobility differences among different trophic taxa can result in differential response to deterministic and stochastic processes (Beisner, Peres-Neto, Lindström, Barnett, & Longhi, 2006; Grenyer et al., 2009). As a result, investigating whether spatial patterns of species richness and composition of tree species are similarly determined by spatial and environmental process, at local scales with a series of combinations of grains and extents, will add to insight on forest community assembly.

There are almost no rigorous explicit studies that test the degree to which species richness or composition of common and rare species are determined by niche and/or neutral processes (Alahuhta et al., 2014; Heino & Soininen, 2010; Siqueira et al., 2012). Lots of



typical statistical models are incapable of disentangling the contribution of niche and neutral processes to community assemblage (Bell, Lechowicz, & Waterway, 2006; McGill, Maurer, & Weiser, 2006). The emergence of variation partitioning overcomes this problem to some extent (Smith & Lundholm, 2010). Nevertheless, strict test of the relative importance differences between spatial and environmental processes is still a great challenge as before due to lack of reliable replicates. Recently, Pandit et al. (2009) conducted an ANOVA on variation partitioning results with different years as replicates to test the significance differences between microcosm generalist and specialist. Therefore, rigorously and quantitatively testing the relative importance of niche and neutral processes may help us understand how metacommunity assembly paradigms shift from each other.

In this study, we explore species richness and compositional spatial patterns of rare and common trees species constrained by the topographic variables and distance-based Moran eigenvector maps (dbMEMs), which represent the effect of environment and space respectively, in eight forest dynamics plots. Specifically, we address following questions: (a) does the CR values between space and topography differ from rare to common species? (b) Does the contribution of topography and space to tree distribution differ significantly? (c) Are the variances explained by topography/space correlated with elevational ranges (ER)? (d) Will cell-size influence previous relations? Our principal hypothesis is that the CR values will positively relate to tree species abundance. As environment had similar effects on rare and common macroinvertebrate species (Siqueira et al., 2012), while spatial effect played more important role in constraining common invertebrate species than that on rare ones (Pandit et al., 2009). Secondly, numerous studies on common tree species (Shen et al., 2009) or the entire community (including common and rare species) (Hu, Lang, et al., 2012; Legendre et al., 2009) both showed that the contribution by space always outperform that of environment. And thus, we predicted that the contribution of space should be significantly higher than that of topography of both rare and common species. By answering these questions, we can clearly identify the spatial organization of the tree alpha and beta diversity in tropical, subtropical and temperate forest across latitude gradient. We found that the relative roles that topographic heterogeneity and space related processes, including dispersal limitation, in structuring community assembly vary from rare to common species at multiple scales of subplot and cell-size. Ultimately, we will show that the relative importance of niche and neutral processes do vary among rare and common species; space always plays leading role in community assembly and its relative importance strengthens with commonness, but that strength is dependent on cell-size sampled.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and tree data

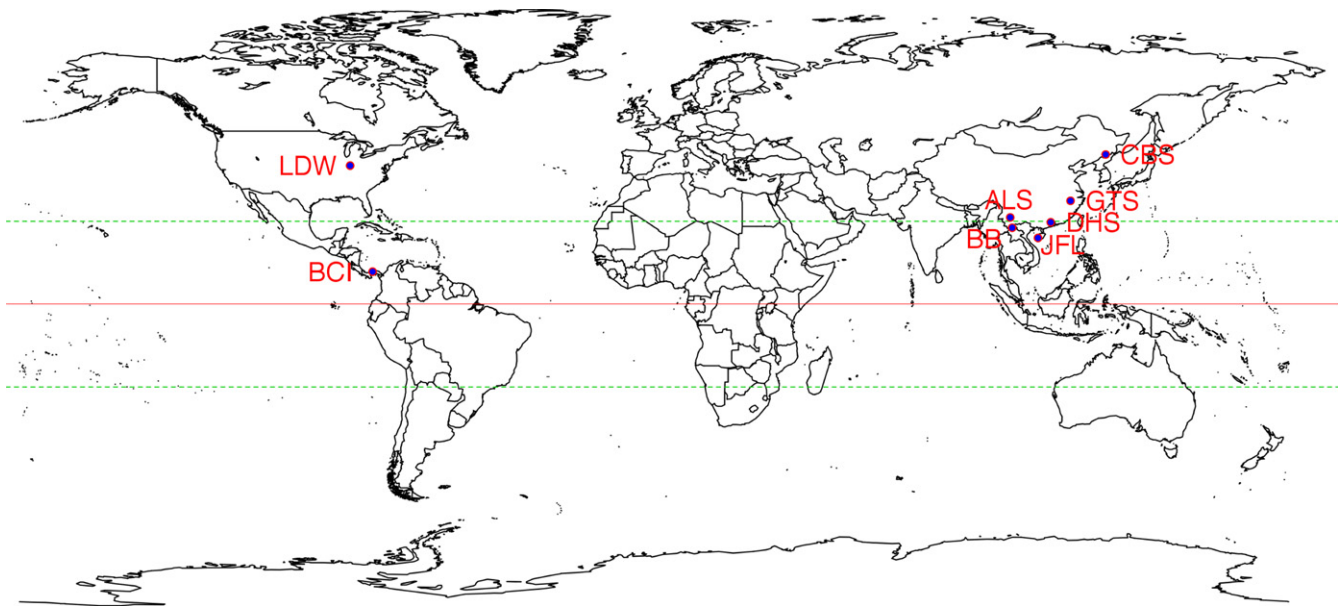
From 1981 to present, a worldwide network of forest research plots using uniform methodology, the Center for Tropical Forest Science - Forest Global Earth Observatory (CTFS-ForestGEO), has been established (<http://www.forestgeo.si.edu>). We used eight plots in this

network to understand the relative contributions difference between niche and neutral processes to rare and common species (Figure 1). The principal characteristics of each plot are summarized in Table 1, from the CTFS-ForestGEO. The eight forest plots, range in latitude from 9.15° N to 42.38° N, are located in China, the United States and Panama. Out of the eight tree communities, the Barro Colorado Island (BCI), Jianfengling (JFL) and Bubeng (BB) plots are tropical forests, the Ailaoshan (ALS), Dinghushan (DHS) and Gutianshan (GTS) plots are subtropical forests and, the Changbaishan (CBS) and Lilly Dickey Woods (LDW) plot are temperate forests. Following the standardized tree census protocol (Condit, 1998), all stems with diameter at breast height  $\geq 1$  cm were tagged, identified, measured and mapped at each plot. The first census data were used for all the plots, except for BCI where the sixth census data were used (Hubbell, 2005). We split the BCI plot into two plots, the BCI west (BCI.w) plot and the BCI east (BCI.e) plot, which were identical in shape and area to make the results more comparable among all the plots. By doing so, we acquired one more plot to explore our questions resulting in nine plots, with areas of ~20–25 ha, for our analyses. Elevation maps for each site were used to calculate topographic variables.

### 2.2 | The abundance effect on CR, or the contribution of space or topography

Natural communities are always comprised of the majority of taxa being relatively rare and a few taxa being very abundant (Magurran & Henderson, 2003), regardless of taxa body size (Nemergut et al., 2013). It is among one of the few and ubiquitous laws of ecology discipline (McGill et al., 2007). In terms of population size, distribution range and environmental preference, species can be categorized into eight forms, among which seven forms of rarity have been defined by Rabinowitz (1981). As far as our data were concerned, we could not apply geographical distribution range to define rarity, as there was hardly overlap of species among the sites; what's more, the occupied cell information (local distribution range) could only be used to category species into specialists and generalists. With respect to environmental preference, we can't define the rarity with it and then use it again to explain the rarity. As a result, we used total population size of targeted species in a sampled subplot, in a specific plot, to define rarity for subsequent analysis in this study.

Our principal objective was to clarify whether the relative importance of space and topography vary from rare to common tree species. To acquire the contribution of space and topography to spatial variation of richness and composition of rare and common species, we used the simulation and analysis schematic showing in Figure 2. First of all, we randomly moved the window for a given plot (e.g., BB plot) at a given size of cell (e.g., 20 m<sup>2</sup>) and randomly chose certain numbers of cells the total area of which equalled the given subplot size (like 8 ha) (Figure 2(1)). We defined rare and common species based on Gaston's quantile criterion (Gaston, 1994), by ranking species from the least to the most abundant within the subplot metacommunity and then equally divided them into five abundance quantiles representing rarest to most common. To minimize the



**FIGURE 1** World map showing the locations of the eight forest dynamics plots studied in this paper. Details of the forests can be found in Table 1. Ailaoshan (ALS), Barro Colorado Island east (BCI), Bubeng (BB), Changbaishan (CBS), Dinghushan (DHS), Gutianshan (GTS), Jianfengling (JFL) and Lilly Dickey Woods (LDW)

**TABLE 1** The basic information of the nine forest dynamics plots ordered by latitude

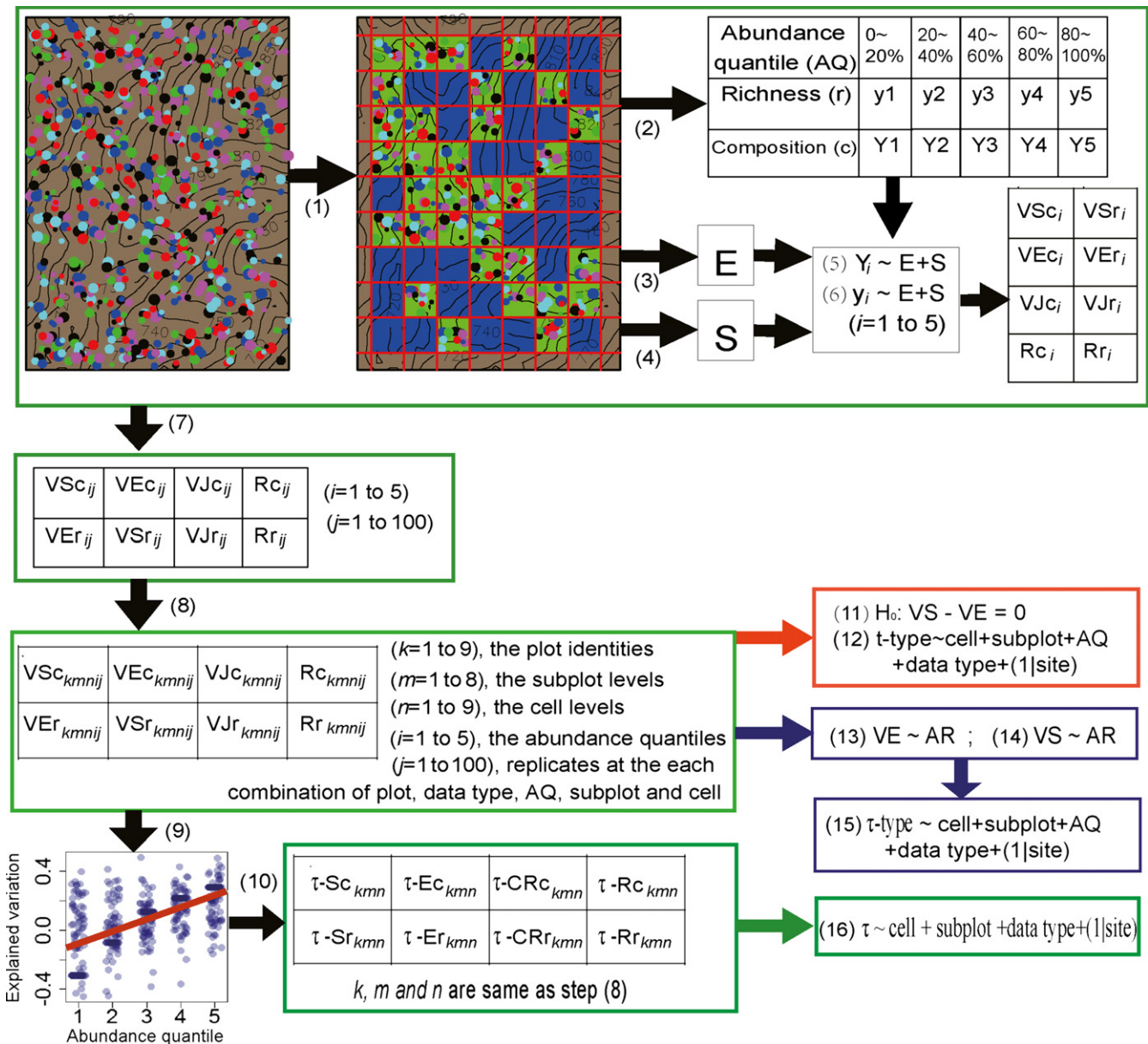
| Forest plot               | BCI.e     | BCI.w     | JFL        | BB         | DHS         | ALS         | GTS         | LDW       | CBS        |
|---------------------------|-----------|-----------|------------|------------|-------------|-------------|-------------|-----------|------------|
| Size (m × m)              | 500 × 500 | 500 × 500 | 340 × 600  | 400 × 500  | 400 × 500   | 500 × 400   | 600 × 400   | 500 × 500 | 500 × 500  |
| Year                      | 2005      | 2005      | 2010       | 2007       | 2005        | 2014        | 2005        | 2012      | 2004       |
| Number of species         | 286       | 274       | 272        | 468        | 210         | 101         | 159         | 35        | 52         |
| Number of individuals     | 111,341   | 111,366   | 147,191    | 95,451     | 71,617      | 44,153      | 140,676     | 28,015    | 38,902     |
| Latitude                  | 9.154° N  | 9.154° N  | 18.728° N  | 21.612° N  | 23.156° N   | 24.533° N   | 29.250° N   | 39.23° N  | 42.383° N  |
| Longitude                 | 79.846° W | 79.846° W | 108.899° E | 101.574° E | 112.511° E  | 101.016° E  | 118.119° E  | 86.220° W | 128.083° E |
| Climate                   | Tropical  | Tropical  | Tropical   | Tropical   | Subtropical | Subtropical | Subtropical | Temperate | Temperate  |
| Rainfall (mm)             | 2,600     | 2,600     | 2,651      | 1,493      | 1,985       | 1,874       | 1,964       | 1,203     | 700        |
| Dry season                | Dec.–Apr. | Dec.–Apr. | Nov.–Apr.  | Nov.–Apr.  | Dec.–Jan.   | Nov.–Apr.   | Oct.–Jan.   | No        | Oct.–May   |
| Mean air temperature (°C) | 27.1      | 27.1      | 19.7       | 21.8       | 20.9        | 11.1        | 15.3        | 11.9      | 2.8        |
| Elev. range (m)           | 40        | 32        | 95         | 156        | 237         | 156         | 253         | 73        | 17         |

Note. ALS: Ailaoshan; BCI.e: Barro Colorado Island east; BCI.w: Barro Colorado Island west; BB: Bubeng; CBS: Changbaishan; DHS: Dinghushan; GTS: Gutianshan; JFL: Jianfengling; LDW: Lilly Dickey Woods.

zero-inflated effect in species composition matrix, of which rows were quadrats and columns were species, the Hellinger transformation was applied to the species composition matrix. Through this transformation, we can decrease the effects of sample size difference in individual trees and in number of species between the plots or between the simulations to some extent.

We used variation partitioning, based on RDA, to disentangle the contribution of space and topography to the richness or composition variation in rare and common species (Legendre et al., 2009; Peres-Neto, Legendre, Dray, & Borcard, 2006; Smith & Lundholm, 2010). We did not conduct model selection before doing variation partitioning to make sure the explanatory variables for each species quantile group were the same. By doing so, the contributions of topography

and space were comparable among different quantile groups of species. Specifically, in terms of measured elevation data, we used ordinary kriging to interpolate the elevations of the selected cells by spherical model. Based on the interpolated elevation data, aspect, convexity, mean elevation and slope were computed for each cell to represent topography (Harms et al., 2001; Valencia et al., 2004). To model nonlinear relations, third-degree polynomial equations were constructed with elevation, convexity and slope. For aspect,  $\sin(\text{aspect})$  and  $\cos(\text{aspect})$  were calculated to linearize the circular variable (Figure 2(3)). To model complex effects of space, we calculated distance-based Moran's eigenvector map (db-MEM) using the centre locations of all the selected cells (Legendre et al., 2009). The db-MEMs were generated by decomposing a pairwise distance matrix



**FIGURE 2** Schematic representation of all the analyses conducted for each forest plot. The numbers in parentheses indicate the simulation procedures and analyses. Specifically, VEr and VEc: variation explained by topography for richness and composition data respectively; VSr and VSc: variation explained by space for richness and composition data respectively; VJr and VJc: variation explained by the joint effect of space and topography for richness and composition data respectively; Rr and Rc: model residuals for richness and composition data respectively; E: topography; S: space; Y and y: composition matrix and richness vector respectively. The t-type and  $\tau$ -type represent the three types of t-test and Kendall's rank correlation results respectively; specifically, they are significantly negative, nonsignificant, significantly positive. For the procedures, step (1) represents randomly moving window and selecting random cells to generate a subplot; step (2) represents evenly categorizing species into five groups based on abundance quantiles and obtaining corresponding richness and composition data; step (3) and (4) represents calculating E and S for selected cells respectively; step (7) represents repeatedly executing step (1) to (6) 100 times for a given plot at give scales of subplot and cell; step (8) represents repeatedly executing all previous steps at the combinations of nine levels of cells and eight levels of subplots at each of the nine plots; step (9) shows an example of Kendall's rank correlation between abundance quantile and one of the components of variation partitioning results in step (8); step (10) represents repeatedly executing step (9) for all of the components of variation partitioning results in step (8) and obtaining all the  $\tau$ . For the analyses, (5) and (6) represent conducting variation partitioning on species composition and richness respectively; (11) represents t-test between VS and VE; (12) represents modelling the effects of cell, subplot, AQ and data type on the t-type by (11) with cumulative link mixed models; (13) and (14) represents conducting Kendall's rank correlation between AR and VE or VS respectively; (15) represents modelling the effect of cell, subplot, AQ and data type on the  $\tau$ -type by (13) or (14) with cumulative link mixed models; (16) represents modelling the effect of cell, subplot, AQ and data type on the  $\tau$  by (10) with linear mixed effect model

among cells into a series of spectral waves, which modelled spatial structure from fine to broad scales and were linear and independent spatial variables (Borcard & Legendre, 2002).

To test the significance of abundance quantile with enough replicates, we repeatedly executed random window moving for a given plot at given size of subplot and cell 100 times and obtained replicates of variation partitioning results:  $VS_{Cij}$ ,  $VEC_{ij}$ ,  $VJc_{ij}$  (variation explained by space, topography and their joint effect of composition data of the  $i$ th quantile group and the  $j$ th replication,  $i = 1, 2 \dots 5$ ,  $j = 1, 2 \dots 100$ ) and  $Rc_{ij}$  (the corresponding residual);  $VSr_{ij}$ ,  $VER_{ij}$ ,  $VJr_{ij}$  (variation explained by space, topography and their joint effect of richness data of the  $i$ th quantile group and the  $j$ th replicates,  $i = 1, 2 \dots 5$ ,  $j = 1, 2 \dots 100$ ) and  $Rr_{ij}$  (the corresponding residual) (Figure 2(7)). By doing so, we simulated the recurrent rare-common differences (Kunin & Gaston, 1993), and thus change the local commonness and rarity of a species. To evaluate the extent and grain size effect on the contribution of space and topography species distributions, we conducted the analyses at range of combinations of subplot size (8–15 ha in one hectare increments) and cell-size (10–50 m in 5 m increments). We repeated steps (1)–(7) in Figure 2 for the each of the combinations of subplot sizes (8–15 ha in one hectare increments) and cell-size (10–50 m in 5-m increments) in each of the nine plots (Figure 2(8)).

To compare the relative importance of space and topography to rare species with that to common ones, we compute the CR between db-MEM and topographical variables as following:

$$CR = e^{VS} / e^{VE} \quad (1)$$

where VS is the adjusted  $R$ -square value of db-MEM (space), VE is the adjusted  $R$ -square value of topography. As the adjusted  $R$ -square could be negative, we compute its exponential value before calculating the ratio. Therefore, all the CR values are positive. By calculating CR in the form of ratio, we can compare the relative importance of space and topography of rare species with that of common species equally. As the absolute values of VS and VE could be influenced by sample size; however, CR values are independent. In this study, the range of VS was from  $-1.41$  to  $0.92$ , and the range of VE was from  $-0.48$  to  $0.93$ . Therefore, the CR ranged from  $0.09$  to  $3.98$ . A CR  $< 1$  means  $VS < VE$  and the topography plays more important role; when CR = 1 it means space and topography explain the same amount of variation; and CR  $> 1$  means the  $VS > VE$  and space plays more important role. Specifically, we have multiple combinations of plot (nine levels), data type (two levels, richness and composition), subplot (eight levels) and cell (nine levels); we tested the abundance quantile effect on the explained variances of by space and/or topography, or CR for each of the 1,296 combinations (i.e.,  $9 \times 2 \times 8 \times 9 = 1,296$ ) with 100 replicates.

To identify how abundance quantile influence VS, or VE, or CR and or residuals (R), we conducted Kendall's rank correlation analysis ( $\tau$ ,  $\tau$ ) between VS/VE/CR/R and abundance quantile for each of the 1,296 combinations (Figure 2(9) and (10)). Moreover, to identify whether the data type, cell and subplot size will influence the  $\tau$ , we further conducted linear mixed effect model (LMM) (Figure 2(16)). At

last, to determine the relative contribution of the three explanatory variables in the LMM, we implemented ANOVA on the fitted LMM.

### 2.3 | Contributions difference between space and topography

Ecologists have been seeking to determine if niche or neutral process regulate community assemblage (Cottenie, 2005; Soininen, 2016). Here, we attempt to clarify whether the contributions of topography and space are equivalent to help provide evidence to this debate. Specifically, we addressed this issue by conducting  $t$ -tests on the pairwise difference between VS and VE (Figure 2(11)). The  $t$ -test results were transformed into three types ( $t$ -type): significant negative (mean  $< 0$  and  $p$ -value  $< 0.05$ ), nonsignificant ( $p$ -value  $\geq 0.05$ ) and significant positive (mean  $> 0$  and  $p$ -value  $< 0.05$ ). We further analysed the effect of abundance quantile, subplot size, cell-size and data type on the  $t$ -type with cumulative link mixed models.

### 2.4 | The influence of elevational range on VE or VS

As VE and VS are basically niche and neutral based, respectively, we hypothesized that the larger ER will be positively correlated with VE, and no significant relation between ER and VS respectively. To clarify these relations, we conducted the Kendall's correlation analysis ( $\tau$ ,  $\tau$ ) to determine the effect of ER on VE or VS at each of the 1,296 combinations (Figure 2(13) and (14)). Then, we categorized the  $\tau$  into three types ( $\tau$ -type), similar to the  $t$ -test in section 2.3. We further analyse the effect of abundance quantile, subplot size, cell-size and data type on the  $\tau$ -type with cumulative link mixed models.

We perform a random moving window procedure in R (version 3.1.2) statistical language (R Core Team, 2014). We conduct the kriging interpolation, variation partitioning analysis, Kendall's rank correlation analysis, and cumulative link mixed models, LMM in R with *geoR* (Ribeiro & Diggle, 2001), *vegan* (Oksanen et al., 2017), *stats*, and *ordinal* (Christensen, 2015), *lme4* (Bates, Maechler, Bolker, & Walker, 2015) and *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) packages.

## 3 | RESULTS

### 3.1 | The effect of commonness and rarity

We found a consistent positive trend of the total explained variances from abundance quantile group 1 (rare species) to 5 (common species) (Supporting Information Appendix S1 and S2). For composition data, all the  $\tau$  were significantly positive; and 87.7% (568/648) of the  $\tau$  were significantly positive in richness data (Supporting Information Appendix S2). Similarly, the VE or VS showed similar positive relations (Supporting Information Appendix S3 and S4): for composition data, 100% of the  $\tau$  of both were significantly positive; for richness data, 80.9% and 88.4% of the  $\tau$  were significantly positive for topography and space respectively (Supporting Information

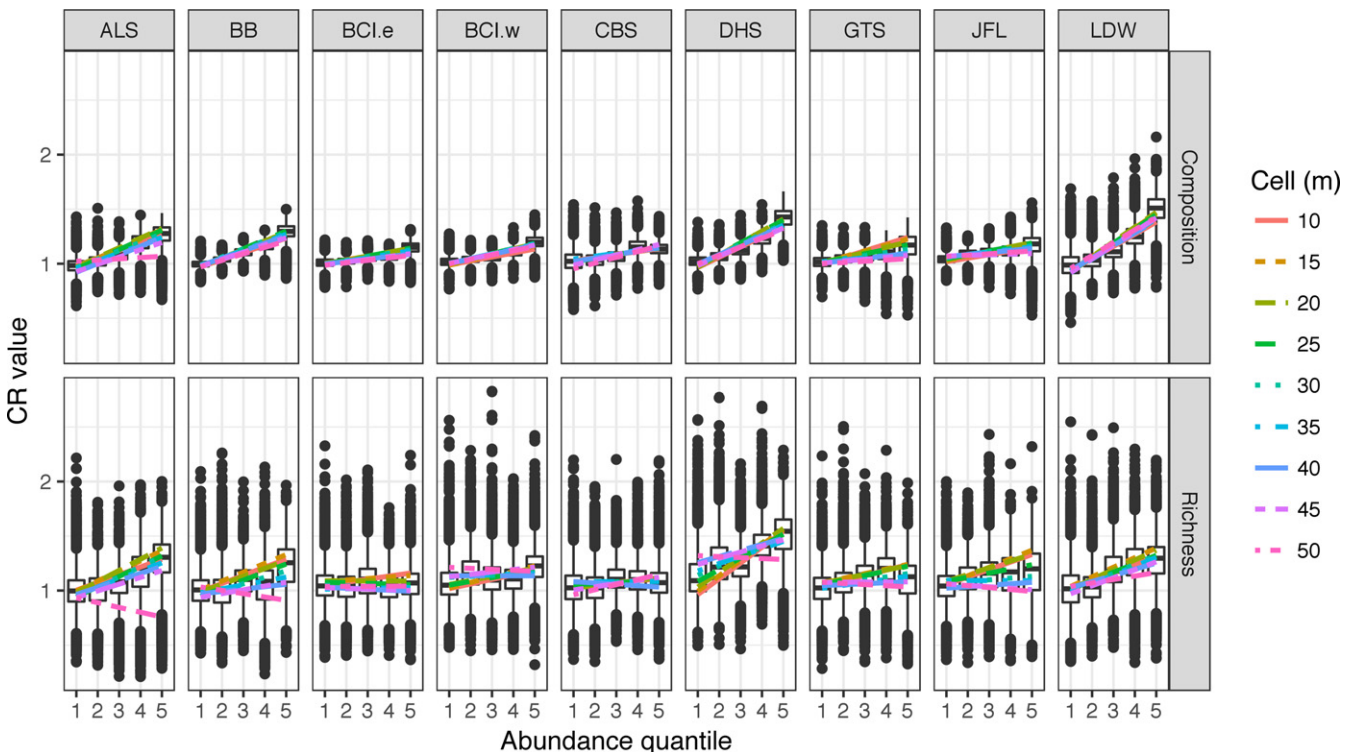
Appendix S5 and S6). When it came to CR, the trends were different (Figure 3): for composition data, the  $\tau$  were composed by 12 significant negative, 7 nonsignificant and 629 significant positive (Supporting Information Appendix S7); for richness data, the  $\tau$  were composed by 145 significant negative, 42 nonsignificant and 461 significant positive. After further making pairwise comparisons of  $\tau$  value differences between CR and space/topography, we found that most of the  $\tau$  values of CR were smaller than the corresponding  $\tau$  of space/topography (Supporting Information Appendix S8 and S9). Furthermore, *t*-tests indicated that, with the exception of difference between CR and topography of richness data, all other three groups of differences of  $\tau$  values were significant lower than 0 (*p*-value <0.0001), which suggests that  $\tau$  of CR was significantly lower than the corresponding  $\tau$  of topography or space. Although the absolute contribution of niche or neutral processes to rare and common species varied substantially, the relative importance of space and topography to rare and common species were similar.

We found that the coefficients of cell-size and data type (richness) were significantly negatively related to  $\tau$  (Figure 4), but significantly positive for the subplot variable (Table 2). The ANOVA tests on the fitted LMM showed consistent patterns for the topography, space and CR: data type always accounted for the largest proportions of variance among the three explanatory variables (Table 2), cell-size ranked second, and subplot size always explained the lowest amount of variations. This suggests that the increasing tendencies, i.e.,  $\tau$ , of richness data were significant lower than that of composition data; the  $\tau$ -type would become nonsignificant or even

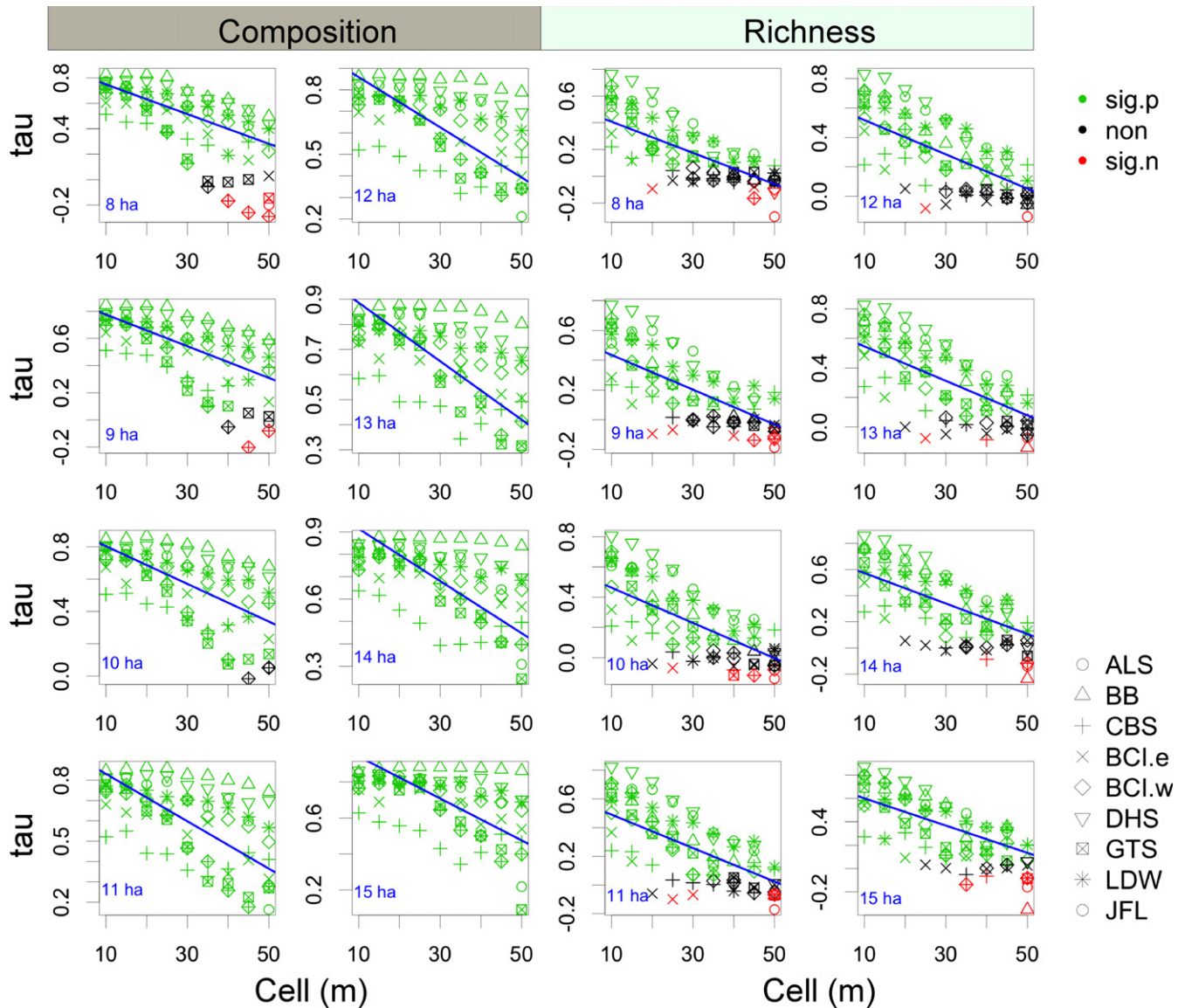
significantly negative as cell-size is increased; subplot variable had significant, but limited, effect on the  $\tau$ .

### 3.2 | Contribution difference between space and topography

The *t*-test between VS and VE showed that mean values of the difference VS and VE were significant positive for most of the cases (Supporting Information Appendix S10). The cumulative link mixed models results showed that the log odds ratio between significant negative and nonsignificant mean value of differences was -5.10 (*p*-value <0.0001), and the log odds ratio between nonsignificant and significant positive mean value of the differences was -3.18 (*p*-value <0.0001). This indicated that the mean value of the differences being significant positive occurred with the highest probability. We also found that the cell-size and richness data had significant negative log odds ratios (both were -1.33 and *p*-value <0.0001), indicating that there is a high probability that the significant positive mean value of differences might become nonsignificant or significant negative as cell-size increases or as data type transferring from composition to richness. The predicted trends of the composition data and richness results along cell-size gradient indicated that cell-size could strongly affect the results and thus may change our understanding of the relative importance difference between topography and space (Supporting Information Appendix S11 and S12). On the contrary, the log odd ratios of subplot and abundance quantile were significant positive, 0.37 and 1.14 respectively (both *p*-value <0.0001).



**FIGURE 3** The variance of richness and composition explained by topography from abundance quantile group 1 to 5, which represents species moving from rare to common. The lines represent the fitted lines at each cell-size



**FIGURE 4** The cell-size effect on the Kendall's correlation coefficients between abundance quantile and CR. Blue lines are the fitted lines by mixed effect models. sig.n: significant negative, non: nonsignificant, sig.p: significant positive. Barro Colorado Island east (BCI.e), Barro Colorado Island west (BCI.w), other site convention as Figure 1

**TABLE 2** The linear mixed effect model coefficients and relative explained variances of the  $\tau$  of CR, topography and space

|                             |            | Cell     | Subplot | Data type (richness) |
|-----------------------------|------------|----------|---------|----------------------|
| Coefficients                | Topography | -0.09*** | 0.02*** | -0.51***             |
|                             | Space      | -0.11*** | 0.04*** | -0.43***             |
|                             | CR         | -0.15*** | 0.06*** | -0.34***             |
| Relative explained variance | Topography | 11.2%    | 0.5%    | 88.3%                |
|                             | Space      | 19.3%    | 2.5%    | 78.2%                |
|                             | CR         | 40.7%    | 7.2%    | 52.1%                |

Note. \*\*\*p-value <0.001.

This suggested that there was a high probability of the mean value of the differences being significant positive when the abundance quantile or subplot size increased.

### 3.3 | Elevational range effects

We found that most of the  $\tau$  values were nonsignificant (Supporting Information Appendix S13). This result suggested that there was a high probability of no relation between elevational range and the variances explained by topography/space at local site scale. For the DHS plot, the number of significant negative relations were even more than the significant positive ones. The cumulative link mixed models results showed similar pattern that the odds of nonsignificant versus significant negative or the significant positive values were 14.87 and 4.62 respectively for topography, and 20.91 and 11.52 respectively for space. Increasing cell-size had a significant positive effect on the relations between elevational range and the variances explained by topography/space (Supporting Information Appendix S14). For example, for 1-m increment in cell-size, the odds





of “nonsignificant” applying versus “significant positive” or “significant negative” applying combined are 1.26 greater, given that all of other variables in the model are constant. In summary, the probability of nonsignificant relations was high, but cell-size was positive related to variance explained by topography/space.

## 4 | DISCUSSION

Advances in rarity studies at the community level have brought new insights into community assembly (Alahuhta & Heino, 2013; Pandit et al., 2009; Siqueira et al., 2012). Previous rarity studies principally have concentrated on investigating macroinvertebrate (Pandit et al., 2009), aquatic macrophyte (Alahuhta et al., 2014), invertebrate (Benedetti-Cecchi et al., 2008; Pandit et al., 2009) and grassland (Markham, 2014) communities, whereas other biological assemblages of rare species, such as tree communities, have received less attention. Furthermore, almost no study has explicitly examined the response difference between rare and common species to niche and neutral variables. We addressed these shortcomings in our current research by studying how environmental controls (i.e., topographical variables) and spatial processes (i.e., spatial location) affected the assemblages of common and rare tree species across latitudes. Our results indicate that the mechanisms influencing rare and common tree species assembly differ significantly, as the relative importance of space compared to topography increases from rare to common species across forests.

### 4.1 | The effect of commonness and rarity

For the contribution of topography separately, we found significant positive trends from rare to common species. This is congruent with most of the findings based on community composition (Alahuhta et al., 2014; Siqueira et al., 2012; Székely & Langenheder, 2014) and richness data (Lennon et al., 2011). But, rare species could rely on rare habitat (Markham, 2014; Umana et al., 2017), we hypothesized that if rare species-related uncommon environmental variables could be introduced into models, the positive trends can change to nonsignificant or negative. Moreover, László et al. (2014) found that rare parasitoid species are even more closely related to environmental variables at landscape scale than they are at local scale compared to common species. In this study, we found that the  $\tau$  between abundance quantile and topography were significantly negatively related to cell-size (Table 2). Additionally, taxon matters as well, as Siqueira et al. (2012) reported that rare Chironomids species were more closely related to environment than common species were. This also suggests that sample size issue may not influence the habitat associations. Hence, the increasing tendency of habitat association from rare to common species should be a general phenomenon of trees. For space, the trends are similar to topography. Rare tree species were more spatially aggregated than common species which could be an essential reason for the positive trends (Condit et al., 2000). Not only for trees, widely distributed invertebrate species are

principally dominated by spatial factors as well (Pandit et al., 2009). Nevertheless, the trend is still scale dependent. At the local scale, the results of this study, of Pandit et al. (2009) and of Székely and Langenheder (2014) all show a strong ascending pattern, but an ambiguous pattern at broad scales (Alahuhta et al., 2014; Siqueira et al., 2012). As a result, we conclude that the positive trends of space or topography is a general pattern of tree communities.

Our principal hypothesis was that the CR values would positively relate to tree species abundance likely due to dispersal limitation being stronger for widely distributed and less habitat restricted common species, than for rare species. Although most of the trends of space or topography are positive, the trends of CR still showed ascending tendencies. This indicates that the relative importance of space increases faster than that of topography. Indeed, the increasing trends of CR are relatively weak compared to that of space or topography. Specifically, the proportion of nonsignificant, significant negative and positive CR trend is differed from the pattern of space and topography; and the  $\tau$  of CR were significantly lower than that of topography or space at each corresponding combination of cell and subplot. After calculating CR with the data of previous studies: we found that there were both ascending and descending CR trends in macroinvertebrate communities at landscape scale (Siqueira et al., 2012), and only decreasing tendencies in bacterial communities at local scale (Székely & Langenheder, 2014), and decreasing tendencies in macrophyte community at both two spatial extents: ecological provinces and all of Minnesota, USA (Alahuhta et al., 2014). This suggests that the trends of CR can be reversed and are taxa dependent. In addition, our results clearly indicate that the cell-size effect can negatively affect the  $\tau$  of CR; we predict that environment would outperform space as study cell-size increases. Consistent with this prediction, Karst, Gilbert, and Lechowicz (2005) found that the CR decrease from fine (4–134 m) scale to mesoscale (135–3,515 m) for fern species. In summary, our finding strongly suggests that the mechanism involved in determining common species distribution cannot be extending to rare species and thus to the entire community. Over the past decade, numerous studies have expended significant effort to understand the relative role of environment and spatial processes in shaping species distribution (Beisner et al., 2006; Cottenie, 2005; Legendre et al., 2009; Siqueira et al., 2012). However, without explicitly exploring the response differences of rare and common species, we cannot truly understand the mechanism driving community assembly.

### 4.2 | The relative contribution between topography and space

Many studies have compared the environmental and spatial effects on common and/or rare species distributions (Cottenie, 2005; John et al., 2007; Shen et al., 2009); some claimed niche dominance (Alahuhta et al., 2014; John et al., 2007; Székely & Langenheder, 2014), and some claimed neutrality dominance (Bennett, Cumming, Ginn, & Smol, 2010; Sharma, Legendre, De Cáceres, & Boisclair, 2011; Shen et al., 2009). But the difference has seldom been statistically



quantified. We found that space contributed substantially more to tree assembly than topography did at the spatial scales tested. However, we showed that the increasing of cell-size and the occurrence of richness data would increase the relative contribution of topography. Moreover, Chang et al. (2013) showed that including soil variables lead to more variation explained by environment than space. Meanwhile, Alahuhta et al. (2013) found that macrophytes communities were predominantly determined by environmental variables. In contrast, our results supported space is the dominant factor. The difference in species taxa maybe a reason for this, as Bennett et al. (2010) and Sharma et al. (2011) found that lacustrine diatom and fish communities were often shaped by dispersal-related processes at regional scales, but these are motile organisms. Last, the relative importance between space and topography is cell-size dependent as well, especially for rare species. As it shown in Supporting Information Figures S11, S12 the relative importance of space and topography shift as cell-size expanding. Based on the model prediction, the contribution of space and topography may be equal, i.e., nonsignificant difference between them, to rare and common species when cell-size approaching 60 and 80 m respectively. To summarize, the spatial effect plays a dominant role in shaping both rare and common tree species assembly, but it is cell-size dependent.

### 4.3 | Elevational range effects

We expected that the variance explained by topography and space would be significantly and nonsignificant related to ER respectively. Partly contradicting to our expectation, we found that both relations were nonsignificant for most of the cases examined. However, the nonsignificant relations between ER and topography/space strengthen as cell-size increasing (Supporting Information Appendix S14). This results is partly consistent with the finding of De Cáceres et al. (2012). We conducting the analysis repeatedly at range of subplots and cell-sizes with large numbers of replicates provides a robust result. Most of the community census datasets, like RAINFOR (<http://www.rainfor.org/>) or AFROTRON (<http://www.afritron.org/>), do not have the coordinate information of individual tree across such a large area, the CTFS-ForestGEO tree census network offers an opportunity to do this kind of simulation. As far as our results are concerned, it is highly likely that the contribution of topography and space are independent of ER effects at the site scale.

### 4.4 | Robustness of the results

Recently, there is a hot debate over using MEMs as proxies for spatial processes in variation partitioning (Brown et al., 2017; Tuomisto, Ruokolainen, & Ruokolainen, 2012), as they always overestimates the variance explained by spatial processes (Gilbert & Bennett, 2010). However, Brown et al. (2017) suggested that variation partitioning is still a powerful technique when used it with appropriate strategies. With respect to this study, we repeatedly conducted variation partitioning at range of cell and subplot sizes in multiple forests with numerous simulated data which match the

sensitivity analysis, strategically subset data and using simulation data raised by Brown et al. (2017). On the other hand, our aim was not to identify the absolute contribution by spatial and environmental processes which are critical to understand paradigms of metacommunity, but to elucidate how the relative importance between spatial related processes and topographical variables varies from rare to common species. Specifically, we evaluated the Kendall's rank correlation  $\tau$  between CR values, which are not influenced by the inflated MEMs to a large extent, and abundance quantiles. Hence, even if the absolute contribution by MEMs and topography change, the CR values will change, but systematically, as consequence. As a result, there would be little change in the correlation coefficients  $\tau$  between CR and abundance quantile and thus the trends would be basically the same due to systematic changes in CR. In summary, the influence of overestimated spatial component in variation partitioning is limited to our findings.

## 5 | CONCLUSION

We discovered that the response of rare and common tree species to topography and/or space are different from each other in tropical, subtropical and temperate forests. Specifically, the relative importance of space compared to topography increased with abundance. Space was identified as a predominant factor for tree assembly regardless of species abundance. At local scale, ER has no effect on the contribution by space/topography. Furthermore, the relations are cell-size dependent. We predicted that rare and common species would be equally well explained by topography and space as cell-size reaching about 60 and 80 m respectively. In all, we conclude that exploring community assembly with no regard for rare species would lead to bias understanding of the mechanism maintaining species coexistence and community assembly. Meanwhile, it is critical to examine a range of cell-sizes for future studies targeting on rare and common species assembly.

### DATA ACCESSIBILITY

The datasets are available at <http://www.cfbiodiv.org> and <http://www.forestgeo.si.edu>.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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