



Relationship between species diversity and tree size in natural forests around the Tropic of Cancer

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Abstract Although numerous hypotheses have been proposed to explain the patterns of species diversity of forests at local and landscape levels, it is still difficult to predict the alpha diversity of species, especially in tropical and subtropical natural forests where trees of different sizes and shapes are highly mixed. Size might characterize species diversity, and the possible correlation between these variables may contribute to the development of easy-to-use growth indicators to predict diversity and to understand the status of trees within a stand. In this study, diameter classes were divided using the equal diameter class (EDC) and minimum measured diameter (MMD) methods, and five species diversity indices were calculated for each diameter class of 14 permanent plots in five national nature reserves surrounding the Tropic of Cancer (23.5°), southwest China. The results show that species richness, abundance, and spatial diversity

indices decreased in a typical inverted J-shape pattern with increasing diameter class and MMD, and could be easily modeled by a negative exponential function. The Shannon–Wiener index showed a linear decrease while Pielou’s evenness index displayed a linear increase, with a small degree of instability. The results suggest that species diversity in subtropical forests is closely related to tree size, and the relationship is possibly independent of habitat. Measuring DBH of some trees in a stand could be informative regarding species diversity and contribute to the investigation and assessment of biodiversity.

Keywords Biodiversity · Secondary forest · Species richness · Abundance · Diameter at breast height · Species mixture

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Introduction

Natural forests, consisting of various tree species differing in size and appearance, have complex structures, functions, and dynamics (Li et al. 2020), and reflect biodiversity at the species, generic, ecosystem, and landscape levels. Species diversity (richness, abundance, and the proportions of each population) and diversity of structure (vertical stratification, stand density, canopy widths, heights and diameter

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distribution, and spatial relationships of nearest neighbors) are widely considered as the most important components of forest diversity (Feroz et al. 2016). They play a key role in maintaining forest ecosystem stability, stress resistance, ecological processes (pollination, reproduction and renewal, competition and dependence, growth, and death) and in providing ecosystem services (primary productivity, decomposition, nutrition, energy, and culture) (Wang et al. 2013; Brockerhoff et al. 2017; Moradi et al. 2020). They are also closely related to silviculture practices such as thinning and evaluations of the effects of close-to-nature forest management, structure-based forest management, and secondary forest silviculture (Li et al. 2014, 2020; Wan et al. 2019). Species diversity and tree growth are promoted by maintaining structural diversity (Lei et al. 2009), particularly to maintain structural diversity in uneven-age forest management (Li et al. 2014).

The relationship between species and structural diversity, which involves time, spatial location, and scale (Chen et al. 2010), is a complex topic that remains under debate (Ostertag et al. 2014). Climate, site conditions, species pools and forest regeneration capacity, age, range, history, and evolution at both local and landscape levels, have a profound impact on species and structural diversity (Lei et al. 2009; Mwavu and Witkowski 2015; Wu et al. 2016). However, higher species diversity is often accompanied by complex structures in the same forest community (Liu et al. 2017). Structures act as “habitat scaffolds” or templates, which enable species aggregation and diversity by providing more niches (Lei et al. 2009). A higher number of species results in a larger range in size among individuals, greater stratification, and a more complex canopy structure; therefore, higher species diversity may enhance forest structure and resistance to disturbances (e.g., drought, high winds) (Bohlman 2015). These two processes are not mutually exclusive and can occur in parallel, creating a positive feedback loop that enhances species diversity and influences various aspects of forest structure (Ostertag et al. 2014; Liu et al. 2017).

There may be a quantitative relationship between species diversity and tree size at the stand level. For instance, later successional forest communities commonly exhibit higher species diversity, larger average diameters, and a wider range of diameter classes (Lei et al. 2009). Various understory microhabitats (e.g., dead wood, stumps, and mounds) promote regeneration and accommodate different species of seedlings (Brockerhoff et al. 2017). In contrast, canopy layer individuals are fewer but larger in comparison with the understory (Li et al. 2019a, 2020). The relationship between species diversity and size is also supported by several widely held theories of species diversity maintenance and coexistence. For example, conspecific negative density dependence (Chen et al. 2010; Bohlman 2015; Lin et al. 2017; Magee et al. 2021; Wang et al. 2021) and competition from

conspecific large-sized trees (Wu et al. 2016) may reduce the abundance of young trees and increase the richness of the entire stand. Moreover, negative density-dependent and functional characteristics co-regulate species abundance (Wang et al. 2021). To date, few studies have compared the species diversity of trees among different size classes, and the classification of tree size remains too rudimentary to express the relationship between size and species diversity (Mwavu and Witkowski 2015; Ke et al. 2017; Fibich et al. 2021). The quantitative relationships between species diversity and tree size in forest stands remain unexplored.

There are a large number of karst forests (KFs) mainly in Taiwan, Guangdong, Guangxi, Yunnan China PR, Vietnam, and Myanmar and non-karst forests (NKF) around the Tropic of Cancer (23.5°), where the climate is warm and rainfall abundant. There are a number of well-preserved small-scale, local virgin forests (Zhang et al. 2013; Liu et al. 2018). These forests have rich vegetation, and several are critical to global biodiversity (Ni et al. 2015; Wang et al. 2019). In this study, we focused on the relationship between species diversity and size at the stand level. It was hypothesized that species diversity would negatively correlate with size in both KFs and NKFs, i.e., that the diversity of small-sized trees would high and the diversity of large-sized trees low. Furthermore, species evenness would positively correlate with size (Hypothesis 1). As heterogeneity of a karst habitat may restrict tree growth and spatial distribution (Zhang et al. 2020; Li et al. 2022), it was hypothesized that the species diversity of KFs would be lower than that of NKFs and that KFs would show a weak relationship between species diversity and size (Hypothesis 2).

Materials and methods

Study sites and plot establishment

The study was carried out in five national nature reserves: Damingshan National Nature Reserve (DMS), Mulun National Nature Reserve (ML), Huaping National Nature Reserve (HP), Shiwandashan National Nature Reserve (SWDS), and Dayaoshan National Nature Reserve (DYS), all located in China’s Guangxi Zhuang Autonomous Region (Table 1). These reserves surround the Tropic of Cancer (23.5°) and have geographical coordinates of 25°37′–21°50′ N latitude and 106°21′–110°15′ E longitude (Fig. 1). They contain a variety of forest types, including northern tropical montane evergreen seasonal rainforest, southern subtropical monsoon evergreen broadleaved forest, medium subtropical evergreen broadleaved forest, and medium subtropical limestone evergreen-deciduous forest. Approximately 35–40 years ago, state-owned forest farms were transformed into the current nature reserves due to changes in land use.

Table 1 Details of the study nature reserves located in Guangxi Zhuang Autonomous Region

Nature reserve	Location	Area (ha)	Altitude (m)	Precipitation (mm)	Temperature (°C)	Vegetation types
DMS	23°10'–23°38' N, 108°18'–108°45' E On the tropic of cancer	16,994	224–1760	2630.3	16.05	South subtropical monsoon evergreen broad-leaved forest
DYS	23°40'–24°28' N, 109°50'–110°27' E North to the tropic of cancer	25,594.7	513–1321	1824.0	17.0	South subtropical evergreen broad-leaved forest
HP	25°28'55"–25°39'15" N, 109°49'07"–109°58'10" E North to the tropic of cancer	15,133.3	420–1803	2150.0	13.5	Mid-subtropical evergreen broad-leaved forest
ML	25°06'09"–25°12'25" N, 107°53'29"–108°05'42" E North to the tropic of cancer	10,829.7	250–1028	1675.0	16.8	Mid-subtropical limestone evergreen-deciduous forest
SWDS	21°40'03"–22°04'18" N, 107°29'59"–108°13'11" E, South to the tropic of cancer	58,277.1	121–1462	2900.0	21.9	North tropical montane evergreen broad-leaved forest

The dramatic variation of topography in this region plays an important role in regional differentiation and creates multiple habitat gradients for the growth of vegetation (Fig. 1).

During 2017–2019, 14 standard fixed plots (Table 1) of 100 m × 100 m were established in the secondary forests of the five nature reserves. Plot borders were outlined and divide evenly into 25 subplots (20 m × 20 m) using the NTS-372R₁₀ total station (Southern Mapping Company, China).

Steel bars were nailed to plastic tubes fixed at the intersections of neighboring subplots and habitat information recorded for each subplot, including slope, aspect, elevation, litter, soil depth, and parent rock. The coordinates (x, y, z) of each vascular plant with a diameter at breast height (DBH) ≥ 1 cm were obtained using the grid method. DBH (cm), height (m), crown width (m), and height to crown base (m) were measured and growth status (disease and

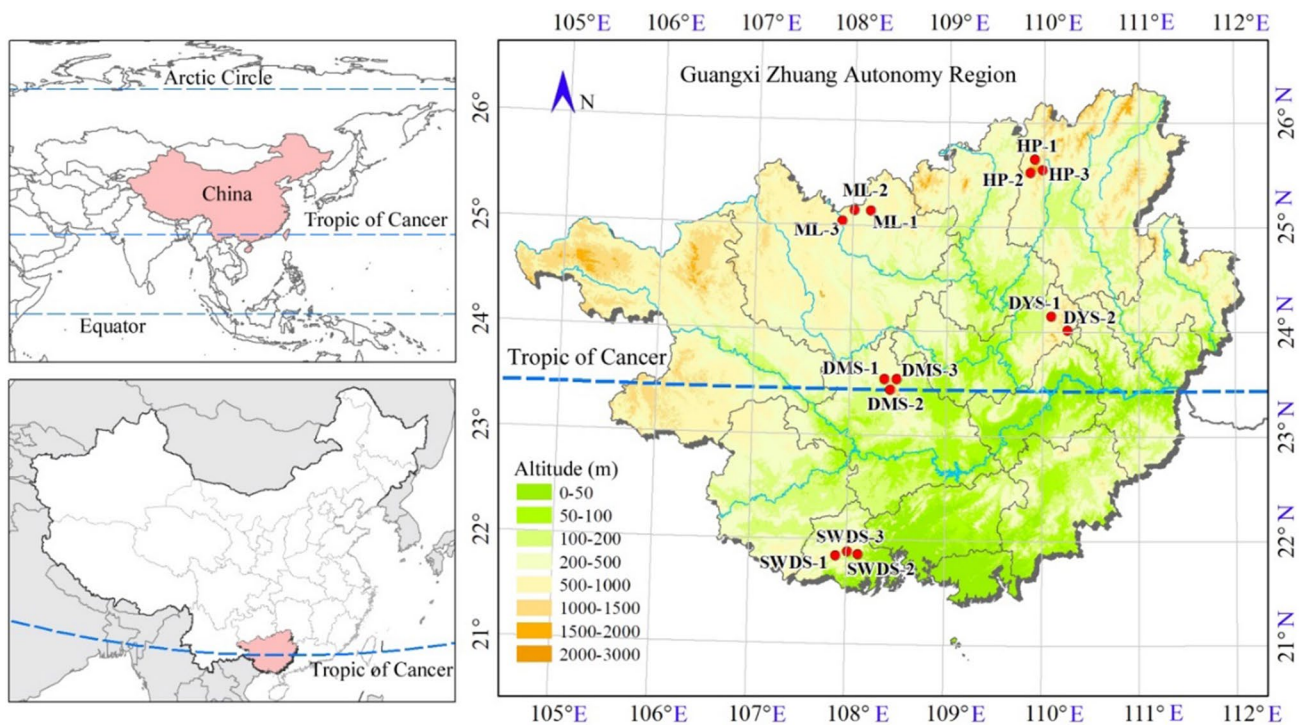


Fig. 1 Study plots distributed in the five national nature reserves. The Tropic of Cancer passes through the central part of Guangxi Zhuang Autonomous Region, China

pest, vigor, and lodging) recorded. Finally, each individual was marked with a unique number and identified by species (Table 2).

Data analysis

Diameter class in this study represents tree size. Because it is impossible to analyze the relationship between the DBH of each tree and indicators of species diversity directly, the diameter data was first divided into diameter classes using two different methods, and species diversity indices calculated for each class. The first method was the equal diameter class method (EDC). There is no strict spacing requirement for EDC. Diameter class data was separated by 2-cm intervals (1–2.9, 3–4.9, 5–6.9 cm... maximum), to avoid a situation with too many or too few classes or segments. Accordingly, the middle points were 2, 4, 6 cm..., and so on. The second method was the minimum measured diameter (MMD) method. Specifically, classes of 1 cm–maximum

DBH, 2 cm–maximum DBH, 3 cm–DBH maximum... were adopted.

Species diversity for each diameter class was calculated using four indices based on species abundance and richness, i.e., the number of trees (*N*), richness (*R*), Shannon–Wiener index (*H'*), and Pielou’s evenness index (*J*) and an index based on the spatial patterns of one reference tree *i* and its four nearest neighbors (tree species spatial diversity index, *TSS*) (Table 3). *N* and *R* may be the simplest indicators of biodiversity (He et al. 2002) and were calculated directly. *H'* and *J* denote the heterogeneity and homogeneity of the quantity distribution of tree populations, respectively (He et al. 2002; Ke et al. 2017). *TSS* expresses the differences in space configuration of tree species (Hui et al. 2011). The relationships between species diversity indices and EDC and MMD was fitted using the general linear model (GLM) and the significance of their differences between/within the nature reserves tested using the *Kruskal.test* function. Species diversity indices were calculated using the *diversity*

Table 2 Details of the study plots

Quadrat	Area (m ²)	Richness	No. of rare species	No. of trees	Mean DBH ± SD (cm)	Canopy cover
DMS-1	100 m × 100 m	98	9	5980	6.6 ± 5.25	0.85
DMS-2	100 m × 100 m	81	4	7588	6.3 ± 4.20	0.90
DMS-3	100 m × 100 m	73	10	6695	7.4 ± 4.60	0.90
DYS-1	100 m × 100 m	119	22	4387	6.3 ± 6.65	0.85
DYS-2	100 m × 100 m	122	31	4064	6.3 ± 7.10	0.85
HP-1	100 m × 100 m	105	18	7437	5.2 ± 5.79	0.90
HP-2	100 m × 100 m	126	21	6982	5.3 ± 6.64	0.90
HP-3	100 m × 100 m	104	15	6969	5.9 ± 7.26	0.90
ML-1	100 m × 100 m	98	12	3615	5.5 ± 5.49	0.75
ML-2	100 m × 100 m	126	22	4328	5.5 ± 4.94	0.80
ML-3	100 m × 100 m	96	15	3466	6.2 ± 4.53	0.75
SWDS-1	100 m × 100 m	96	30	8960	4.9 ± 4.77	0.95
SWDS-2	100 m × 100 m	164	33	8799	5.3 ± 3.77	0.95
SWDS-3	100 m × 100 m	154	22	8008	5.5 ± 4.56	0.95

Table 3 Diversity indices used to characterize tree species diversity

Formulas	Explanations	References
$H' = - \sum_{i=1}^S p_i \ln(p_i)$	<i>H'</i> = Shannon–Wiener index; <i>p_i</i> = proportion of individuals belonging to the <i>i</i> th species	Hui et al. (2011)
$J = \frac{- \sum p_i \log p_i}{\ln S}$	<i>J</i> = Pielou evenness index, <i>p_i</i> = proportion of individuals in the <i>i</i> th species, <i>S</i> = the number of species	Li et al. (2022)
$M_i = \frac{1}{4} \sum_{j=1}^4 v_{ij}, \quad v_{ij} = \begin{cases} 1, & \text{if } sp_j \neq sp_i \\ 0 & \text{otherwise} \end{cases}$	<i>M_i</i> = species mixture of the structure unit <i>i</i> , a structural unit contains one reference tree <i>i</i> and its four nearest neighbors	Hui et al. (2011)
$M_{S_{sp}} = \frac{1}{5N_{sp}} \sum_{i=1}^{N_{sp}} (M_i \times S_i)$	<i>M_{S_{sp}}</i> = species average spatial status, <i>N_{sp}</i> = the number of tree of species <i>sp</i> in the community, <i>S_i</i> = the number of species of the structure unit <i>i</i>	Hui et al. (2011)
$TSS = M_{S_{sp1}} + M_{S_{sp2}} + \dots + M_{S_{spn}}$	<i>TSS</i> = Tree species spatial diversity	Hui et al. (2011)

function of the Vegan package in R (<https://www.r-project.org/>) (Oksanen et al. 2019). Graph processing was with the ggplot2 package (Wickham 2016).

Results

Species richness

Regardless of how the diameter distribution was divided, richness and DBH had a close negative exponential relationship ($R^2=0.951-0.998$), i.e., richness gradually decreased with increasing diameter, showing a reversed J shape. Small-sized trees always had a higher richness value than larger ones (Fig. 2a–j); there were no obvious differences within the same nature reserve ($p_{KW} \gg 0.05$). However, there were significant differences among different nature reserves ($p_{KW} \ll 0.01$). Due to the different calculation mechanism, richness based on the MMD method was greater than based on EDC.

Number of trees

Although N varied considerably among nature reserves, N and DBH were closely related. With increases of DBH and MMD, N of all plots showed a decreasing pattern that could be characterized as ‘first quick and then slow’ (Fig. 3a–j). However, there was no obvious correlation between the curve and its total number of individuals (Table 1). For

example, the values in the Dayaoshan and Huaping nature reserves decreased rapidly, and only a few individuals were at the high end of the diameter scale (DBH=20–65 cm) (Fig. 3b–c, g–h). In other plots, the rate of decrease was gradual (Fig. 3a, d–e, f, i–j). In addition, the rate of decrease in MMD by abundance was higher than that using the EDC method, and the difference was more obvious for smaller trees.

Species diversity index

The relationship between DBH and H' in the secondary forests was strong (Fig. 4a–j). H' of small-sized trees was high, while those of large-sized trees was low. H' calculated by the EDC method decreased linearly with increasing diameter ($p \ll 0.01$) the MMD method also showed a linear distribution ($p \ll 0.01$) but was flat or showed a slight increase at the small-sized tree interval (DBH=1–5 cm) (Fig. 4f–j). Some plots had a constant H' for large diameter classes. The maximum H' in each plot was > 3 , and the minimum was zero. In contrast, the TSS showed a typical inverted J shape (Fig. 5a–j), which could be fitted well by a negative exponential function ($R^2 \gg 0.98$). Small-sized trees had a large spatial diversity index while larger ones had a small TSS , approaching 0.

Species evenness

Pielou's species evenness index (J) showed a linear upward trend with increases of DBH and MMD. Most J values of

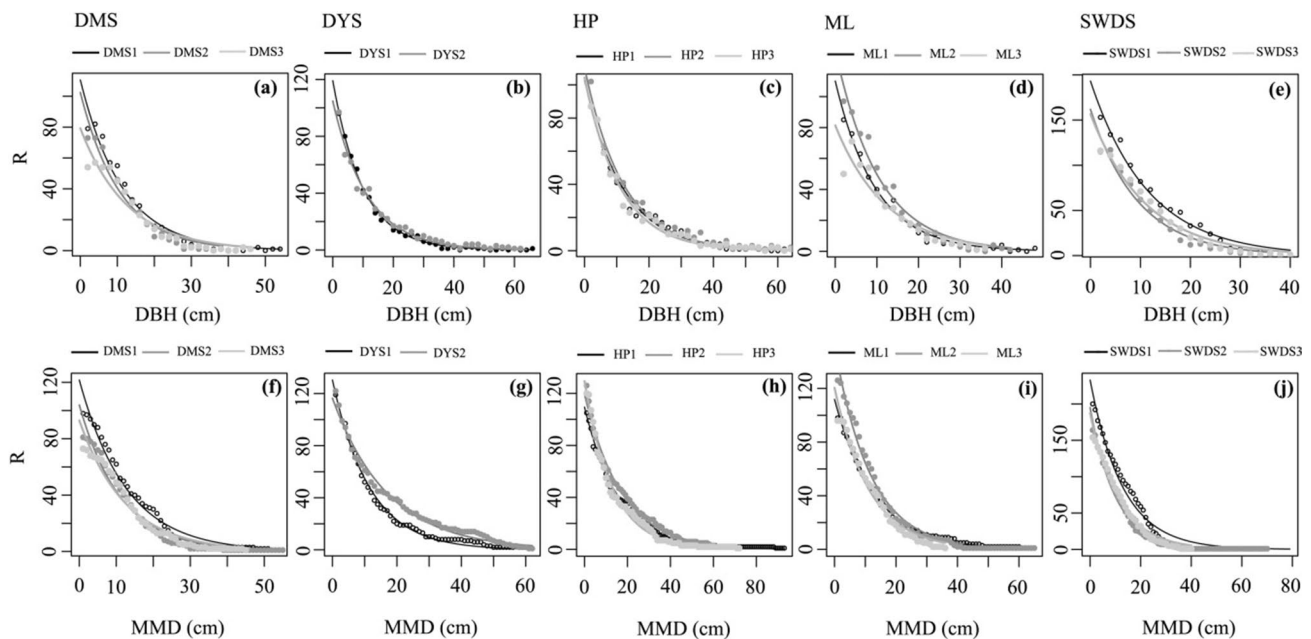


Fig. 2 Distribution patterns of species richness (R) based on equal diameter class (EDC) and minimum measured diameter (MMD)

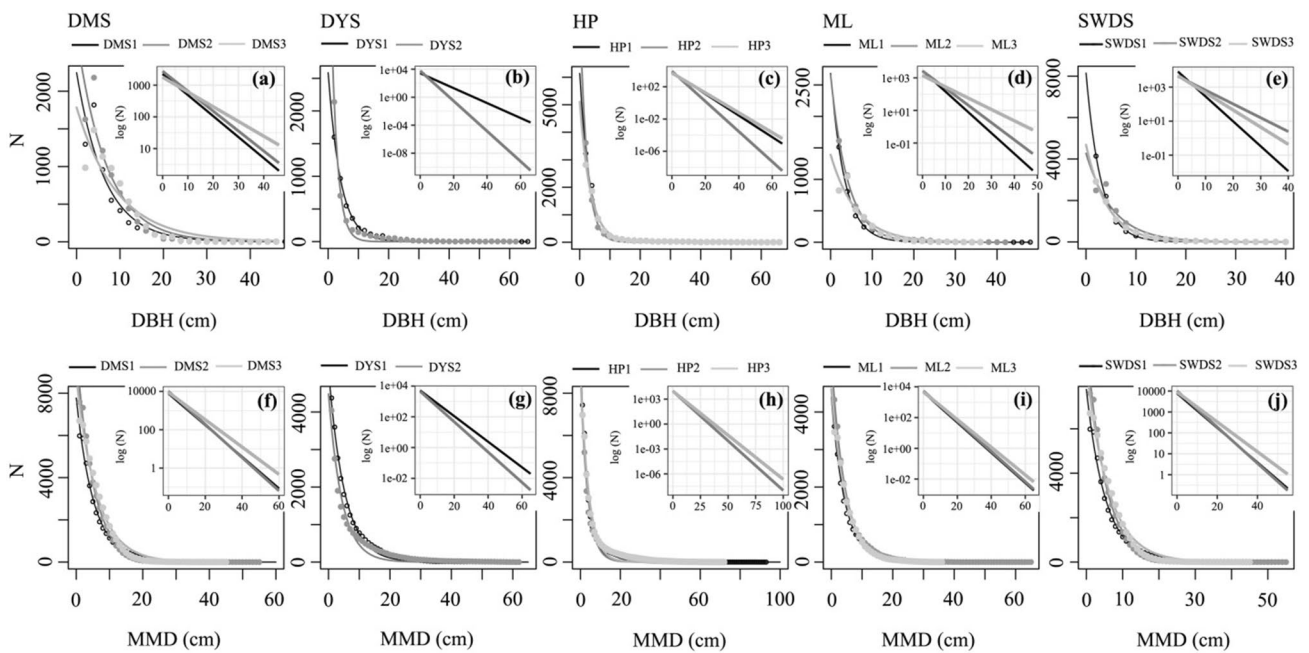


Fig. 3 Distribution patterns of the total number of trees (N) according to equal diameter class (EDC) and minimum measured diameter (MMD); N represents the number of trees in each sub-graph

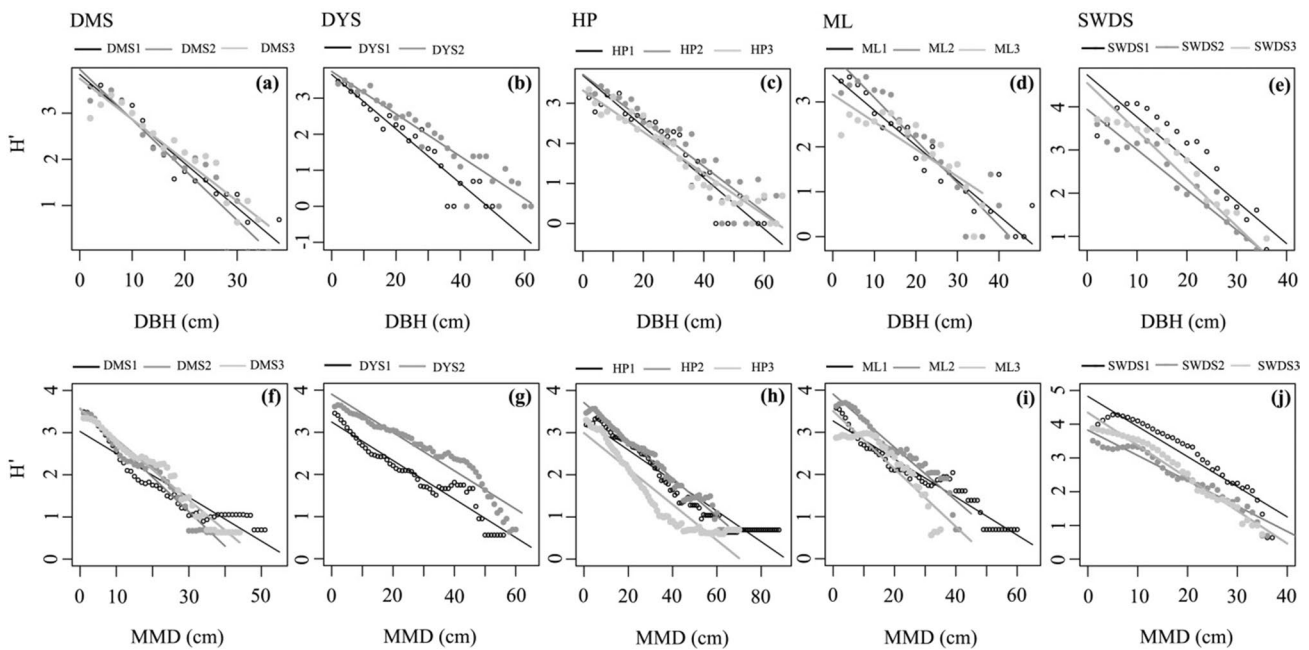


Fig. 4 Distribution patterns of the Shannon–Wiener index (H') based on equal diameter class (EDC) and minimum measured diameter (MMD)

small-sized trees were >0.6 ; those of large-sized trees were close to or equal to the maximum of 1 (Fig. 6a–j). Overall, J was not as stable as R , N , H' , or TSS , even decreasing in

parts of diameter (Fig. 6a, f, h, j). Although the methods of dividing the diameter distribution differed, the order of J was consistent in all plots. Some large diameter classes had a constant value of 1 (Fig. 6h–i).

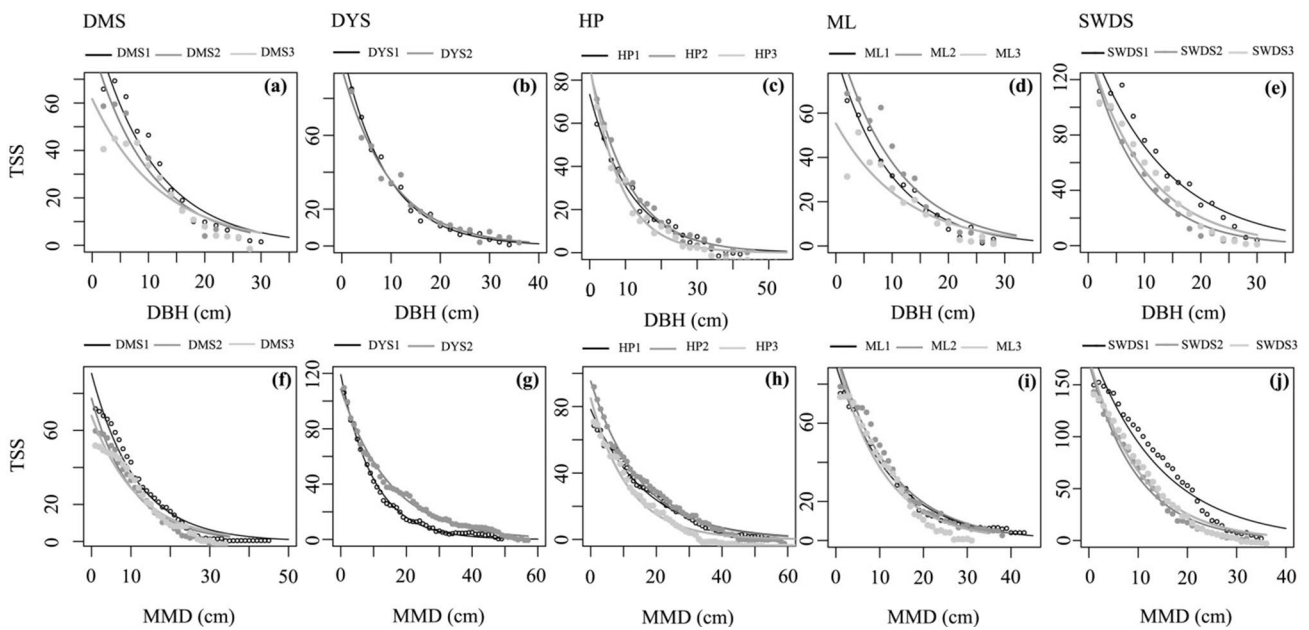


Fig. 5 Distribution patterns of tree species spatial diversity index (*TSS*) based on equal diameter class (EDC) and minimum measured diameter (MMD)

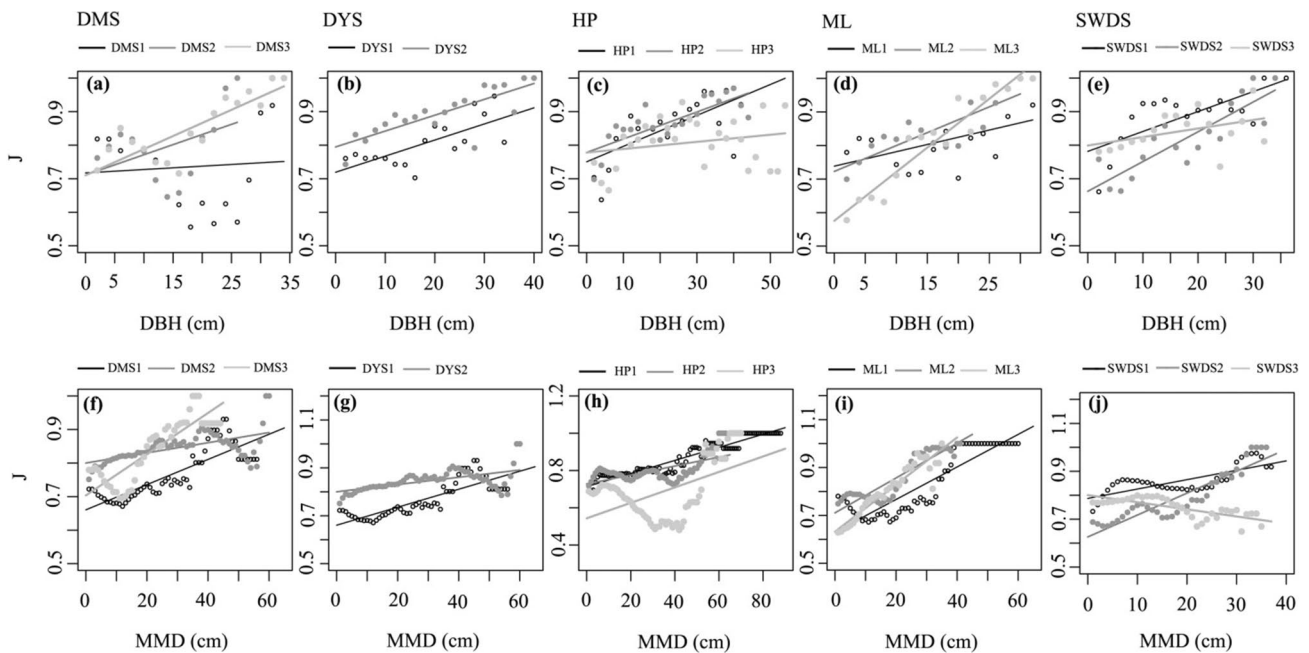


Fig. 6 Distribution patterns of the species evenness index (*J*) based on equal diameter class (EDC) and minimum measured diameter (MMD)

Discussion

Negative correlation between species richness and tree size

Species-rich forest communities are composed of common and sometimes rare species (Wang et al. 2021). In

this study, the proportion of rare species ($\leq 1/\text{ha}$) in some nature reserves was very high (Table 2). Usually, these species are of a small size and part of the understory (Liu et al. 2018), together with other shrubs, saplings and young individuals of shade-tolerant species that contribute significantly to the richness of the forest. Reduction in life forms, competition among neighboring trees, aging

and death of individuals, density dependence, and gap dynamics will reduce the abundance of large-sized trees (Li et al. 2012; Piao et al. 2013; Fibich et al. 2021). A recent study also suggested that the species–size association was driven mainly by species spatial distribution and conspecific size differentiation (Pommerening et al. 2021). The vertical pattern of richness may be beneficial in terms of physical space and light utilization by trees (Bohlman 2015). Our results are consistent with the findings in other tropical and subtropical forests (Mwavu and Witkowski 2015; Feroz et al. 2016; Ke et al. 2017; Li et al. 2019b) and Hypothesis 1, and support the traditional view that species composition is dominated by small-sized trees. But our results differ from those of Bohlman (2015) for the Barro Colorado Island (Panama) dynamic plot (50 ha), in which 5% of the individuals in the canopy accounted for 70% of the tree species and where the overlap of upper and lower species was very low. This suggests that the relationship between species diversity and tree size varies greatly across lands and islands differing in species composition and ecological driving forces.

Habitat heterogeneity is the most striking feature that differs KFs from NKF, but there were no karst environments in the Mulun Nature Reserve that changed the relationship between species diversity and tree size, contrary to Hypothesis 2. Various karst habitats at different scales provide suitable space for many species (Zhang et al. 2013; Geekiyanage et al. 2019; Zhou et al. 2019; Li et al. 2022). At the same time, vegetation in karst areas develops physiological and ecological systems adapted to this environment. Most species are xerophytic, calcium-tolerant, and have thick cuticles and waxy leaf layers (Geekiyanage et al. 2018; Wang et al. 2019; Zhang et al. 2020). Species richness of karst forests is not necessarily lower than that of NKF (Fig. 2a vs. Fig. 2d). Li et al. (2022) found that exposed rock of KFs has a similar species richness but smaller tree sizes to soil in the same region, supporting our findings. Possibly niche differentiation and mutual assistance allow individuals of different sizes to grow together (Liu et al. 2020; Zhang et al. 2020). In the degraded karst regions of southwest China, however, Nie et al. (2019) reported that matrix woody species were more diverse in genera and species than vegetation on rocky outcrops. There are many types of karst terrain and karst forests, and research is still in early stages (Li et al. 2013).

Negative correlation between N (number of trees) and tree size

Diameter distribution illustrates the correlation between N and tree size. An inverted J-shape generally characterizes the diameter distribution in natural stands, especially in primary forests (Meyer 1951; Rubin et al. 2006; Westphal

et al. 2006; Gove 2017; Li et al. 2020). Typically, the number of neighboring diameter classes decreases at a constant rate with increasing diameter (Horodnic and Roibu 2018), consistent with the results in this study (Fig. 3). It is often interpreted as the result of trees of different sizes created by gap openings (Pach and Podlaski 2015), and indicates a balance among regeneration, growth, and death (Gove 2017); this points to sustainability of the stand in terms of renewal and has been used to guide sustainable forest management (Li et al. 2014, 2020; Gove 2017). The diameter distribution, however, may be S-shaped or irregular in some harsh environments/conditions (e.g., seasonal drought, barren soil, nutrient deficiency) (Janowiak et al. 2008; Horodnic and Roibu 2018). Interestingly, this study found that KFs, compared with NKF, had a significantly reduced stand density but this did not markedly affect the shape of the abundance curve (Fig. 3d, i). Although some karst species can survive by utilizing soil in rock crevices (Ni et al. 2015; Li et al. 2022), exposed rock or large rocks hidden beneath the surface soil may still impede their growth. Other studies also found that habitat heterogeneity of karst forests reduces sapling survival (Magee et al. 2021) and above-ground biomass (Liu et al. 2016), and alters the pattern of biomass accumulation as well (Liu et al. 2020), which indirectly supports the results in this study. The extensive exposure of limestone makes it difficult to carry out research using permanent fixed plots (Zhang et al. 2013; Li et al. 2020). To our knowledge, few permanent fixed plots (< 10) have been established; thus, studies on the dynamics of karst forests are rare (Liu et al. 2018), and how best to maintain the stability of diameter classes remains unclear.

Negative correlation between species diversity index and tree size

The Shannon–Weiner index H' is a comprehensive measure of richness and evenness (Lei et al. 2009; Hui et al. 2011; Wang et al. 2013). The continuously increasing values of Pielou's evenness index J in this study indicated that the decrease of H' was due to species richness (Fig. 6a–j), emphasizing the dominant role of species in maintaining biodiversity. Guo et al. (2019) found that tree species diversity in KFs had no significant effect on variations in diameter, supporting our findings (Fig. 4). However, in the Barro Colorado Island dynamic plot described by Bohlman (2015), the diversity of canopy species was greater than that of the understory, as there were more trees in the former. This is inconsistent with our results. The distribution of H' may also reflect the coexistence of species in stands. For example, the variation of small-sized trees (DBH = 0–5 cm) (Figs. 4a–j) suggests the occurrence of conspecific negative density dependence or self-thinning (Nguyen et al. 2014; Lin et al. 2017; Wang et al. 2021). Although different diversity indices

are correlated, they differ in emphasis (Wang et al. 2013). Thus, one possible explanation for the difference between the H' and TSS curves is their sensitivity to rare species; H' is insensitive while TSS is sensitive to both the number and stand structure of rare species (Hui et al. 2011), leading to a significant difference at the small-sized tree stage. TSS has a much larger range than H' and is more conducive to illustrating the diversity of nature reserves and preventing the loss of rare and endangered species. Wang et al. (2013) also found that the tree species spatial diversity index increased with increased richness, similar to other diversity indices but the type of increase was different from those of the Shannon–Weiner index, H' . There are few applications of TSS , and our results further demonstrate the merits of using various species diversity indices (Figs. 4, 5).

Positive correlation between species evenness and tree size

Evenness distribution reflects the dynamics of species abundance. The low evenness value of small-sized trees implies that some populations, especially common species, are dominant, while others are rare (Fig. 6a–j); this may be related to seed production and dispersal mechanisms of different species (Bohlman 2015). The higher the evenness index of large trees suggests that the abundance of the residual populations approach each other, which also indicates that the upper layer of these forests is composed of several co-dominant species rather than a single dominant one. The long-term coexistence of dominant species is an important characteristic of forests in the region under study (Li et al. 2021). Trees may avoid direct competition through differences in morphology (height, crown shape and ratio), growth and physiological characteristics (seasonal growth and light utilization), and finally achieve coexistence (Li et al. 2021). Our research is supported by studies from other subtropical forests, in which the evenness of the canopy is higher than that of the understory (Feroz et al. 2016; Shankar 2019); this is considered to reflect conspecific density-dependent effects (Bohlman 2015). In a 30-year secondary forest near the Mulun Nature Reserve, Li et al. (2020) found a positive linear relationship between tree size and the degree of species mixture, suggesting that the difference in abundance among populations decreases with increased diameter; this also indirectly supports the increase of evenness. However, forests on some tropical islands may display different diversity characteristics (Ostertag et al. 2014; Bohlman 2015). Moreover, evenness was less stable than the other diversity indicators (N , R , H' , TSS), implying that interspecific quantities are seldom equal (Nguyen et al. 2014; Li et al. 2021). Numerous biological (growth and functional properties) and abiotic (niche partitioning) factors can affect population sizes (Lin et al. 2017; Wang et al. 2021). It is likely

that an imbalance among population size, individual size, and adaptive capacity may benefit forest stands in terms of maintaining stability and achieving positive succession.

Conclusions

Forests play a key role in maintaining global biodiversity and the balance and functioning of terrestrial ecosystems. Because of the diverse types, uneven distribution, and internal complexity of forests globally, relationships between species and structure at large scales have considerable uncertainty. Species and structural diversity mainly occur and change at small scales. Therefore, investigating the relationships between species diversity and tree size at the stand level has theoretical and practical significance. Many secondary forests near the Tropic of Cancer are in early stages of succession, with abundant species and individuals. In this study, there were close quantitative relationships between diameter classes and species diversity (N , R , H' , TSS , J) which could be fitted well by a simple linear or negative exponential function. In other words, tree size indicated the degree of species diversity. The highly heterogeneous karst habitats in the Mulun Nature Reserve did not indicate changes in this relationship, pointing to a new and reliable approach for the investigation, assessment, and monitoring of biodiversity. Gradual decreases in N (number of trees), R (richness), H' (heterogeneity of tree populations), and the TSS (species spatial diversity) index indicate that the stands changed from a coexistence state of multiple populations with unbalanced abundance to a state with fewer populations and a balanced abundance. This further suggests that small-sized trees provide the majority contribution for stand diversity and emphasizes the critical role of species, especially rare species, in maintaining diversity. Species should have more attention when considering the protection, construction, and management of forest biodiversity. Protecting species is crucial for preserving diversity.

Authors contributions YL and GZ conceived the idea, YL wrote the draft, SY analyzed data and improved its expression, YL and SY participated in data collection.

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