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Drone-acquired data reveal the importance of forest canopy structure in predicting tree diversity

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ABSTRACT

The most salient feature of forests is the vertical-filling architecture of its constituent species. However, among the possible determinants of tree community assembly, vertical niche differentiation has been poorly studied. Here we used an Unmanned Aerial Vehicle to measure spatial variation of canopy structure in five subtropical forest plots in China, and evaluated the importance of canopy structure and topography in structuring tree diversity and species distributions. We combined data from canopy attributes with topography and the locations of 533,763 individuals of 614 tree species. Spatial simultaneous autoregressive error models were used to evaluate the relative importance of each variable to species diversity. We found that varaibles describing canopy structure contributed significantly to tree richness patterns in all plots and all forest layers, although the strength and direction of the effects varied among the sites. Among the study species, the abundance distributions of 38–49% of them in four plots were explained by the combination of canopy structure and topographic variables, and 21–33% by canopy structure or topography alone, while the abundances of 48% species in the Heishiding plot were explained by canopy structure alone. Our study shows that canopy structure variations and topography jointly shape species distributions in these forests and our findings highlight the importance of considering canopy structure and related ecological processes for understanding community assembly.

1. Introduction

Forest canopies and their associated structure are critical in maintaining high biodiversity and supporting ecosystem functioning (Ozanne et al., 2003). As the important vegetation layer for plant community photosynthesis and transpiration, canopy structure dramatically affects the distributions of forest productivity (Antonarakis et al., 2011; Gough et al., 2019), forest biomass, and carbon storage (Lefsky et al., 2002; Saatchi et al., 2011; Zhang et al., 2014), leading to structural and functional complexity of forest stands. The vertical niche differentiation driven by this complexity was conceptualized as a vertical dimension of niche space (MacArthur & MacArthur 1961), and has long been recognized as providing important habitat and diverse food resources for vertebrates and invertebrates. There has recently been a renewed interest in the concept of vertical niche for predicting plant and animal diversity and their distributions across multiple scales (Zhang et al., 2013; Nakamura et al., 2017; Fahey et al., 2019; Meyer et al., 2020; Feng et al., 2020).

Tall forests usually have high under-canopy variation in both quality and quantity of solar radiation (Lambers et al., 2008) which contributes

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to strong niche differentiation, particularly along the vertical dimension, through competition for light as well as disturbances resulting from shading suppression, windfall, pests and diseases (Kohyama 1993; Couteron et al., 2005). Moreover, taller trees in general have deeper or wider root systems supporting nutrient and water acquisition (Koch et al., 2004), and their crowns often inhibit neighboring trees (Lutz et al., 2014). Although the importance of species-habitat associations (e.g. the edaphotopographic niches that define species occupancy in the horizontal plane) in regulating plant community assemblage, especially the assemblages of species-rich tropical and subtropical forests, has been widely appreciated (Harms et al., 2001; John et al., 2007; Wang et al., 2009), the role of forest canopy structure in promoting forest diversity is poorly understood.

A principal challenge in understanding canopy structure is the shortage of techniques for collecting and analyzing canopy data (Barker & Pinard 2001). Traditional techniques based on ground surveys of canopy structure are difficult to apply to large-size (e.g., several hectares) forest communities due to problems with accuracy, or even differentiating interwoven canopies. The challenges are especially acute in subtropical and tropical forests with dense forest canopies (Larjavaara & Muller-Landau 2013). Recent advances in remote sensing provide new insights into canopy studies in vegetation structure and ecosystem functions (Anderson & Gaston 2013; Turner 2014; Stovall et al., 2019). Satellite and manned airborne remote sensing instruments have been used to study forest canopies (e.g., Saatchi et al., 2011; Zhang et al., 2016a; Feng et al., 2020), but mainly at larger scales due to relatively coarse spatial and temporal resolutions. Therefore, these data do not often match well with ground-based inventory data collected at small spatial scales (usually less than a few hectares), relevant to addressing questions of species coexistence (Innes & Koch 1998; Kerr & Ostrovsky 2003; Wulder et al., 2004). Aircraft LiDAR and terrestrial laser scanning are used to accurately represent forest structural characteristics (e.g., Lefsky et al., 2002; Kane et al., 2010; Gough et al., 2019; Fahey et al., 2019, Jeronimo et al., 2019; Rahman et al., 2022), but they requires high levels of expertise and computing power to process the data (Roşca et al., 2018). The recent development of Unmanned Aerial Vehicles (UAV) or drones has made it possible to acquire high-resolution remotely sensed data immediately (Anderson & Gaston 2013). Compared with satellite and manned airborne remote sensing techniques, UAVs based on Structure from Motion (SfM) point clouds can collect data on biotic and abiotic variables at high or moderate spatial resolutions (several centimeters) and avoid the limitations in long-duration cloud cover associated with satellite imagery, especially in subtropical and tropical forests (Koh & Wich 2012; Whitehead et al., 2014). Due to these advantages, drones have been used to estimate forest structure properties in boreal (Puliti et al., 2015) and temperate forests (Getzin et al., 2012; Dandois & Ellis 2013), and monitor tropical forest recovery (Zahawi et al., 2015). However, many of these previous studies were conducted in small plant survey plots with relatively flat terrain, which limits the ability to evaluate the importance of both complex canopy structure and topographic variables. Montane forests represent 23% of the Earth's forest cover (Price et al., 2011). They harbour a very high biodiversity and also play an important role in determining global and regional climates due to complex topography. We are interested in understanding the roles of canopy structure and topography in mountainous forests.

In this study, we selected five large (≥15 ha each), stem-mapped subtropical forest plots to evaluate whether canopy vertical stratification, in addition to topography, could improve understanding of plant community assembly. These forests are commonly located in mountains with complex terrain. In each of the five plots (Table 1), all stems with diameter at breast height (DBH) ≥ 1 cm were georeferenced and identified to species. Overall, there were 533,763 free-standing living stems with ≥1 cm DBH in these five plots. To evaluate the variations of forest canopy structure, we used an UAV equipped with still-photograph camera to collect visible light images. At the community level, we analyzed the effects of canopy structure and topography on plant diversity for all trees together and across different forest layers. At the species level, we analyzed the correlations between spatial distributions of species abundance and these variables. Specifically, we addressed three main questions: (1) To what degree does forest canopy structure have the influence on the community assembly of tree species in subtropical forests? (2) Is there a consistent pattern of the underlying drivers of high plant diversity among the forests? (3) How does the importance of canopy structure and topography in species distributions vary across species and among the forests?

2. Materials and methods

2.1. Study area

This study was conducted in five protected areas in the subtropical forest regions of China, extending over 6° in latitude and 10° in longitude (Table 1). The Chinese subtropical region covers approximately 25% of the area of the country (Song, 2013). The zonal vegetation is primarily evergreen broad-leaved forests, dominated by the genera *Castanopsis*, *Lithocarpus*, *Cyclobalanopsis* (Fagaceae), *Machilus* (Lauraceae), *Schima* (Theaceae), *Distylium* (Hamamelidaceae), *Magnolia*, and *Michelia* (Magnoliaceae) (Box et al., 1991; Wang et al., 2007; Song, 2013). The subtropical region harbors high plant diversity, including a large number of endemic and relict species. Mean annual temperature of these five areas ranges from 13.5 °C to 21.4 °C, and annual precipitation ranges from 1517 mm to 2482 mm (Table 1). Among 198 endemic plant genera in China, 148 genera (75%) occur in this region (Song, 2013). The dominant soil types are yellow soil in Tiantongshan (TTS), yellow–brown soil in Baishanzu (BSZ), and latosolic red soil in three other sites that are in Guangdong Province.

Table 1
Descriptive statistics for five stem-mapped subtropical forest plots.

Sites	Locations	Area (ha)	Mean annual temp. (°C)	Annual Prep. (mm)	Elevation range (m)	Slope (°)	Species richness (DBH ≥ 1 cm)	Total abundance of live trees	Number of species with ≥ 50 individuals
Tiantongshan (TTS)	29°48′N, 121°47′E	20	16.9	1517	313–585	9–48	154	108,540	79
Baishanzu (BSZ)	27°45′N, 119°12′E	25	13.5	2482	1417–1642	5–37	151	224,483	92
Chebaling (CBL)	24°43′N, 114°15′E	20	18.1	1900	431–545	4–53	223	86,518	96
Heishiding (HSD)	23°31′N, 111°52′E	15*	19.6	1751	445–672	5–50	249	54,207	119
Dinghushan (DHS)	23°10′N, 112°32′E	20	21.4	1966	241–465	6–52	177	60,015	67

*The Heishiding plot is 50 ha from which 15 ha was selected for the current analysis due to the range limit of the drone survey.

2.2. Ground inventory data

Following the protocols from the Smithsonian CTFS-ForestGEO (the Smithsonian Center for Tropical Forest Science - Forest Global Earth Observatory) network (Condit 1998; Anderson-Teixeira et al., 2015; Davies et al., 2021), all stems with DBH $\geq$ 1 cm were tagged, georeferenced and identified to species (Table 1). Plot sizes ranged from 15 to 25 ha, and the elevation ranges were between 114 m in the Chebaling (CBL) plot and 272 m in the TTS plot. These plots were sufficiently large and heterogeneous to cover a sufficient range of habitat complexity (Wang et al., 2009; Yang et al., 2016; Yin, 2016). All these forests are mature, and the forest ages of these plots range from approximately 100 to 300 yrs. Overall, there were 533,763 free-standing living individual stems with $\geq$1 cm DBH in these five plots. The richness of woody plant species ranged from 151 in BSZ to 249 in HSD (Table 1). In the current work, we used a 20-m grid scale (20 m × 20 m) for all the analyses at both community and species levels, since this plot size is commonly used in forest community ecology. We further checked the number of large trees (DBH $\geq$ 10 cm: roughly 10 m in height for the dominant tree species in this forest) for each plot, and found that all 20-m grids had 19 large trees on average, suggesting that this scale was suitable for community-level analyses in these sites.

2.3. Topographic variables

The topography of these five plots was represented by four variables: elevation, slope, aspect, and convexity (Harms et al., 2001). Within-plot elevations were surveyed on a 20 m × 20 m grid using electronic total stations (Condit 1998). The elevation of each 20 m × 20 m quadrat was taken as the average elevation from each of the four corners. Slope was defined as the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three of the corners of each quadrat. Aspect was defined as the compass direction in which the slope faces. Convexity of each quadrat was calculated as the elevation of the focal quadrat minus the mean elevation of eight surrounding quadrats. For edge and corner quadrats, convexity was defined as the elevation of the center point minus the mean of its four corners (Harms et al., 2001).

2.4. Aerial drone survey

The Microdrones MD4-1000 small drone (http://www.microdrones.com) was used for aerial survey in September and October 2016. This UAV weighed 2.65 kg, had a cruising speed of 12 m/s, a maximum flight duration of 88 min, and a maximum payload of 1.2 kg. A Sony NEX-5 still-photograph camera was mounted to the bottom of the drone to acquire aerial imagery.

Flight missions were planned with the software mdCockpit using orthoimages and a digital elevation model (DEM) of the flight area. Flight altitude was ~250 m above the canopy. We collected the UAV images with 70–80% overlap between adjacent collection paths. Pixel size of the raw images was approximately 5 cm. To geocorrect the point cloud, we selected a dozen ground control points (GCPs) for each plot. These GCPs were selected in open areas of each site, and the horizontal and vertical coordinates of each GCP were measured using a Trimble RTK (Real-Time Kinematic) GPS with the accuracy of $<$ 1 m (UTM Zone 49 N, WGS84 horizontal datum) before the drone survey. The raw aerial photographs were processed into georeferenced orthoimages, digital surface models of the canopy (DSM), and point clouds using the software "Pix4dmapper" (http://pix4d.com) at a resolution of 5 cm. The aerial drone data are publicly available in Zhang et al. (2021).

2.5. Canopy height model (CHM) generation and canopy height metrics

A canopy height model (CHM) was generated with a pixel size of 1 m by subtracting the DEM from the DSM in each plot. The elevation of each canopy pixel was interpolated by ordinary kriging from the DEM generated from the 20 m × 20 m grid using the total station. Accuracy was evaluated by the mean error (ME) and the root mean square error (RMSE) between estimations and observations. The values of ME ranged from −0.02 m to 0.07 m within five sites, and the RMSE ranged from 3.71 m to 6.18 m. A suite of forest canopy metrics in each plot was then developed at spatial scales of 20 m. These metrics included maximum canopy height (the average of three highest values at 1 m^2 scale; ht_max), canopy closure (ht_closure), standard deviation of heights (ht_sd), skewness of the heights (ht_skewness), and the vertical distribution ratio (ht_VDR; Goetz et al., 2007). Three measures, ht_max, ht_closure and ht_VDR, were used to represent the overall canopy hight and light availability from top canopy. High values in ht_max, ht_closure and ht_VDR generally suggest for low light availability and relatively low disturbance events recently (Zhang et al. 2016a). Two measures, ht_sd, ht_skewness, were related to the variations of forest canopy structure. High values in ht_sd and ht_skewness usually suggest for complex canopy strcture with multip layers, which may be related to high plant diversity (MacArthur & MacArthur 1961). We quantified ht_closure by the percentage of 1 m × 1 m pixels with $>$ 10 m height in each 20 m × 20 m quadrat. The threshold of 10 m height was a rough estimation of canopy heights in subtropical evergreen broadleaved forests in China (Song 2013). Values of ht_closure ranged from 0 to 100 with higher values indicating closed canopy and lower values indicating open canopy. ht_VDR was calculated using the equation: $ht\_VDR = \frac{HT_{max} - HT_{med}}{HT_{max}}$, where HT_{max} and HT_{med} were maximum and median values of canopy height at each grid cell.

2.6. Statistical analysis

To measure woody plant diversity in each plot, we calculated species richness, species evenness, and the effective number of species (Jost 2006) based on the Shannon diversity index ($\exp[H_{\text{Shannon}}]$) for each 20 m × 20 m quadrat (Fig. 1; Fig. S1). The Shannon diversity index accounts for both abundance and evenness of the species, and weights overproportionally for rare species. It is calculated as follows: $H_{Shannon} = -\sum_{i=1}^{s}(p_i)\ln(p_i)$, where p_i is the proportion of total individuals represented by species i (Shannon 1948). Species evenness was calculated as the Shannon diversity index divided by the natural logarithm of species richness (Pielou 1975). Meanwhile, to evaluate the influence of forest vertical structure on plant diversity in different forest layers, we also calculated these diversity indices of three different forest layers, including understory (DBH $<$ 5 cm), midstory (5 cm $\leq$ DBH $<$ 10 cm) and overstory (DBH $\geq$ 10 cm). That is a rough classification based on the vegetation structure of subtropical forests in China (Song 2013).

In each plot, the five drone-acquired canopy variables (ht_max, ht_closure, ht_sd, ht_skewness and ht_VDR) and four topographic variables (elevation, convexity, slope and aspect) were selected as the predictor variables at both the community and species levels. Considering the spatial accuracy of predictor variables, we limited our statistical analysis to the 20 m scale (grain resolution). To consider the multicollinearity effect among these measures and the possible interactive effects bewteen canopy structure and topographic variables, we calculated Pearson correlation coefficients after accounting for spatial autocorrelation for each pair of variables at each site. Nearly all 50 pairs of the variables had correlation coefficients less than $|0.7|$, expect for ht_max and ht_closure in TTS and ht_closure and ht_VDR in DHS.

For the community-level analysis, spatial simultaneous autoregressive error models (SARs) were used to evaluate the relative importance of each variable to each of three biodiversity measures (species richness, species evenness, and Shannon diversity index) for all trees together and across the three forest layers (Kissling & Carl, 2008). Compared with common ordinary least squares regression and other spatial linear models, SARs can account for spatial autocorrelation in species distribution data by adding the autoregressive process as the spatially independent error (Kissling & Carl, 2008).

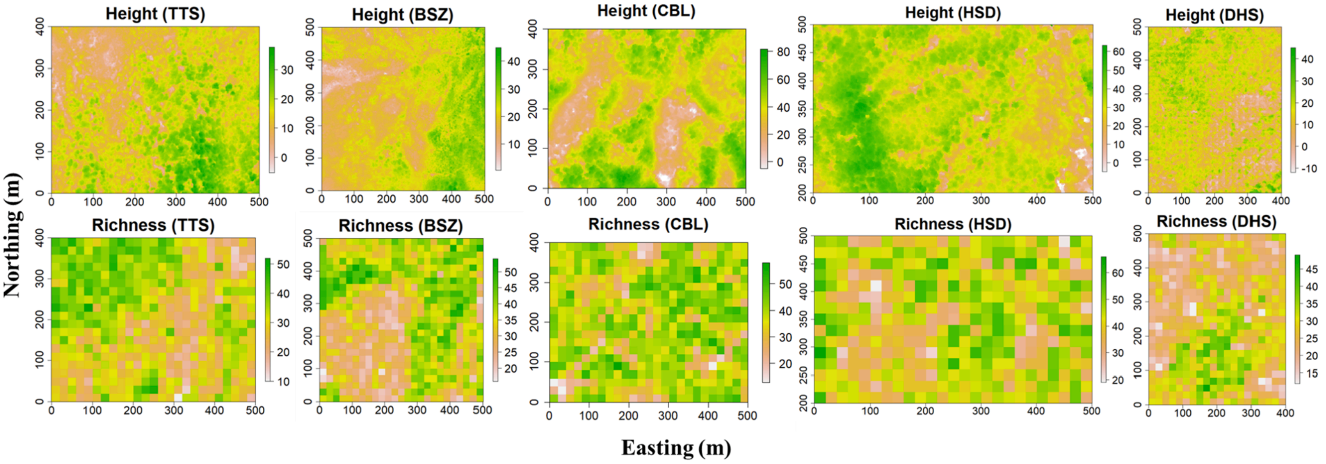


Fig. 1. Drone-acquired canopy height maps at 1-m resolution and species richness maps at 20-m scale for each of five subtropical forest plots. Plots: Tiantongshan (TTS), Baishanzu (BSZ), Chebaling (CBL), Heishiding (HSD), and Dinghushan (DHS). Values for x-axis and y-axis reflect dimensions of each plot in meters.

For the species-level analysis, SARs were used to analyze the correlations between species abundance at the 20 m scale and these predictors. To reduce small sample size bias in data analysis, only species with $\geq$ 50 individuals were selected for the analyses (Table 1). All possible combinations of nine predictor variables were used to fit the models. The best combination of these variables was selected by comparing all model subsets using Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). Then, for the 'best' model, we calculated the relative importance of predictor variables by using the standardized partial regression coefficients of all predictor variables (cf. Kissling & Carl, 2008; Zhang et al., 2013). The Akaike weight (w) for each predictor variable was calculated by the summed AIC weights of all subset models where the variable appears (Burnham & Anderson 2002). The value of w varies between 0 and 1, and a large value indicates the high importance of this variable.

All statistical analyses were carried out using R 4.0.0 software (R Core Team, 2020). SARs were calculated using the R package 'spdep 1.1-3′ (Bivand et al., 2019). The spatial weight matrices of the SARs were calculated with the nearest neighbor and a row-standardized coding style (Kissling & Carl, 2008).

3. Results

3.1. Biodiversity measures

Drone-acquired canopy metrics showed substantial variations in distribution patterns in each of these five plots (Fig. 1; Fig. S1). Species richness at 20-m scale varied from <10 species in some quadrats to over 50 species in others (Fig. 1). Spatial regression modeling showed that the relative importance of vertical and topographic variables in species richness varied greatly among these five plots (Table 2; Fig. 2a). Canopy structure variables contributed significantly to the explanations of the richness patterns in all five plots. Maximum canopy height (ht_max) in BSZ and CBL and the skewness of the heights (ht_skewness) in TTS and DHS were negatively related to species richness, canopy closure (ht_closure) in HSD and the vertical distribution ratio (ht_VDR) in TTS and BSZ were positively related, and ht_closure in DHS had a negative relation with richness. Among four topographic variables, mean elevation, convexity and slope had significantly positive relations with plant richness in TTS, CBL and DHS, and the convexity in HSD, the aspect in DHS and mean elevation in BSZ were negatively correlated with plant richness.

For species evenness (Fig. 2b; Table 2), ht_max had significantly negative relations in TTS and HSD, ht_VDR showed significantly positive relations in TTS, BSZ, and HSD, and ht_closure was positively related in BSZ. Three topographic variables (mean elevation, slope and aspect) in TTS and the convexity and slope in BSZ showed significant relations with species evenness, while the correlations between topography and evenness in three other plots were relatively weak.

For the effective number of species exp[H_{Shannon}] (Fig. 2c; Table 2), ht_max had significantly negative relations in the TTS, HSD and DHS plots. Standard deviation of heights (ht_sd) had positive relations in BSZ, HSD and DHS. ht_VDR showed positive relations in BSZ. The effective number of species was greatly related to several topographic variables in TTS, BSZ and DHS plots, while only the slope had a strongly positive effect in CBL and weak effect in HSD.

When we divided plant communities into three forest layers, the effects of vertical and topographic variables in three biodiversity measures in the understory layer of each forest were very similar to the results for entire communities (Fig. S2; Table S1). The explanatory power (pseudo R^2) of the final selected models in the understory was stronger or nearly equal to those for entire communities (Table 2 & S1), while the explanatory power in the midstory and overstory layers was generally lower than that in the understory layer (Tables S2 & S3; Figs S3 & S4).

3.2. Species abundance, canopy structure and topography

Spatial distributions of most tree species abundance in these five plots were significantly correlated with at least one predictor (Fig. 3), but the relative importance of these predictors varied dramatically among these five plots. Among five canopy structure variables, ht_max in TTS and HSD, ht_sd in BSZ, and ht_skewness in TTS were included in the "best" models for nearly 30% of selected species in each plot. Among topographic variables, meanelev in BSZ, CBL and DHS, convex in TTS and DHS, and slope and aspect in BSZ played important roles in determining the abundance distributions of nearly 30% and even 40% of the selected species (Fig. 3).

When we grouped these nine predictor variables in the final selected models into three groups (Fig. 4), we found that, among the study species, the abundance distributions of 38–49% species in the plots (except HSD) were explained by the combination of vertical and topographic variables, and the species abundances explained by canopy structure or topography alone (21–33%) were relatively consistent in these four plots. In HSD, the abundances of 57 of 119 (48%) species were explained by canopy structure only, 31 species by topography only, and another 31 species by both of them. When we divided these species by growth forms and leaf habits, the overall trends were similar (Fig. 4).

Table 2
Spatial simultaneous autoregressive models of response variables (species richness, species evenness, and the effective number of species based on Shannon diversity index ($\exp[H_{\text{Shannon}}]$)) against all combinations of predictor variables. Standardized coefficients (Coef.) for the model with the highest Akaike weight (*w*) for a given variable group are given, as well as the Akaike weight (*w*) for each variable based on all possible combinations of predictor variables. Pseudo r^2 of each model was in bold. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. Plots: Tiantongshan (TTS), Baishanzu (BSZ), Chebaling (CBL), Heishiding (HSD), and Dinghushan (DHS).

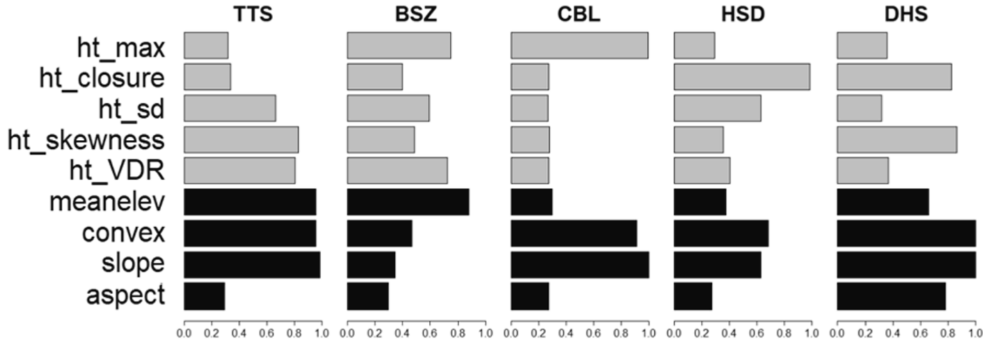
Sites	Variables	Richness		Evenness			$\exp[H_{\text{Shannon}}]$
		Coef.	*w*	Coef.	*w*	Coef.	*w*
TTS	ht_max		0.317	−0.301***	0.997	−0.222**	0.955
	ht_closure		0.336		0.393		0.327
	ht_sd	−0.101*	0.661		0.298		0.434
	ht_skewness	−0.127**	0.829	0.063*	0.516		0.337
	ht_VDR	0.181**	0.802		0.620	0.059	0.685
	meanelev	0.288**	0.956	0.380***	0.995	0.418***	0.996
	convex	0.135**	0.954		0.345	0.129**	0.958
	slope	0.128**	0.984	−0.179***	1.000	−0.067*	0.691
	aspect		0.294	0.120**	0.934		0.319
	Pseudo r^2	**0.542**		**0.612**		**0.667**	
BSZ	ht_max	−0.184**	0.746		0.433	−0.147	0.547
	ht_closure		0.397	0.195**	0.933	0.121	0.562
	ht_sd	0.072	0.594		0.654	0.124*	0.865
	ht_skewness		0.485		0.386		0.394
	ht_VDR	0.066	0.727	0.154**	0.710	0.118*	0.689
	meanelev	−0.323**	0.878		0.303	−0.221*	0.736
	convex		0.465	−0.209***	0.995	−0.129*	0.828
	slope		0.345	−0.225***	0.999	−0.154**	0.958
	aspect		0.298		0.294		0.278
	Pseudo r^2	**0.617**		**0.324**		**0.450**	
CBL	ht_max	−0.243***	0.994	0.145*	0.606		0.385
	ht_closure		0.273		0.345		0.292
	ht_sd		0.271		0.532		0.347
	ht_skewness		0.277		0.372		0.292
	ht_VDR		0.276	0.089	0.505		0.513
	meanelev		0.300		0.483		0.274
	convex	0.143**	0.910	−0.09	0.592		0.326
	slope	0.289***	1.000		0.271	0.207***	1.000
	aspect		0.275		0.299		0.273
	Pseudo r^2	**0.436**		**0.446**		**0.367**	
HSD	ht_max		0.291	−0.158*	0.762	−0.152*	0.379
	ht_closure	0.208***	0.983		0.510		0.317
	ht_sd	0.120*	0.630		0.356	0.102*	0.431
	ht_skewness		0.355		0.331		0.326
	ht_VDR		0.402	0.145**	0.728		0.621
	meanelev		0.375		0.308		0.274
	convex	−0.129*	0.681	0.117	0.691		0.355
	slope	0.107	0.630		0.286	0.082	0.447
	aspect		0.271		0.381		0.387
	Pseudo r^2	**0.274**		**0.449**		**0.415**	
DHS	ht_max		0.356		0.350	−0.172***	0.555
	ht_closure	−0.176**	0.826	−0.116	0.405		0.609
	ht_sd		0.318		0.347	0.097*	0.507
	ht_skewness	−0.117**	0.863		0.358		0.356
	ht_VDR		0.366		0.376		0.348
	meanelev	0.165	0.661		0.297		0.386
	convex	0.262***	1.000		0.412	0.165**	0.834
	slope	0.309***	1.000	−0.088	0.517	0.193***	0.912
	aspect	−0.099*	0.781		0.308	−0.107*	0.751
	Pseudo r^2	**0.530**		**0.358**		**0.415**	

4. Discussion

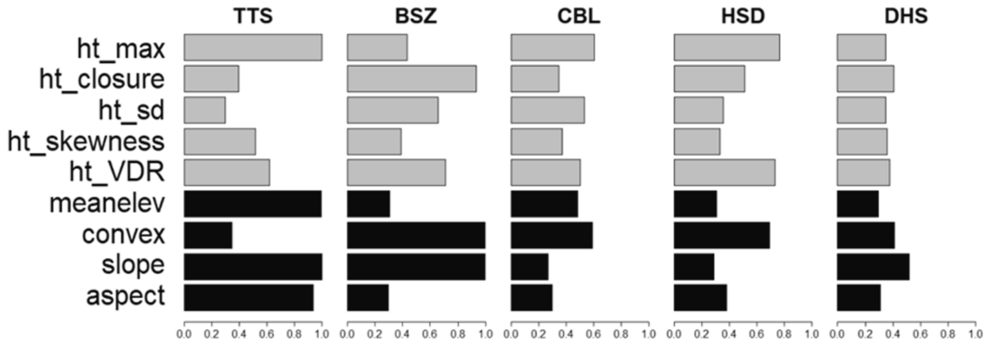
4.1. The influence of forest canopy structure in plant diversity

Ecological niche differentiation has been considered as a pivotal mechanism in determining plant community assembly (Hutchinson, 1961; Vellend 2016). Among possible determinants of niche partitioning, vertical niche differentiation is relatively less considered than horizontal niche differentiation. Previous studies have shown that plant diversity was positively related to canopy complexity in different forests through the provision of varying light environments for plants (e.g., Rüger et al., 2009; Zhang et al., 2013; Zellweger et al., 2017). Importantly, a high level of variation in light environments depends on the existence of a high and complex canopy so that various levels of shading can exist throughout the forests (Hubbell et al., 1999). The horizontal and vertical heterogeneity provided by the large trees that have developed over centuries drives this gradient (Lutz et al., 2013, 2018; Chu et al., 2019). Due to the lack of effective tools for measuring tree height, the diameter distributions of trees have often served as a proxy for local vertical canopy structure (Hao et al. 2007), although the general relationship between diameter and height is well known. In this study, we showed that a lightweight drone can collect ecologically-relevant tree height data at hectare-scale extents. Combining drone-derived canopy data and ground-based surveys shed insights into the explanations for patterns of biodiversity in these five species-rich subtropical forests. At the community level, canopy height and its variation emerged as important predictors of three different measures of plant diversity for both the entire plant communities and understory layers. The consistency of results between the entire communities and understory layers were related to relatively high density of small trees and shrubs in the

(a) Species richness



(b) Evenness



(c) $\exp[H_{\text{Shannon}}]$

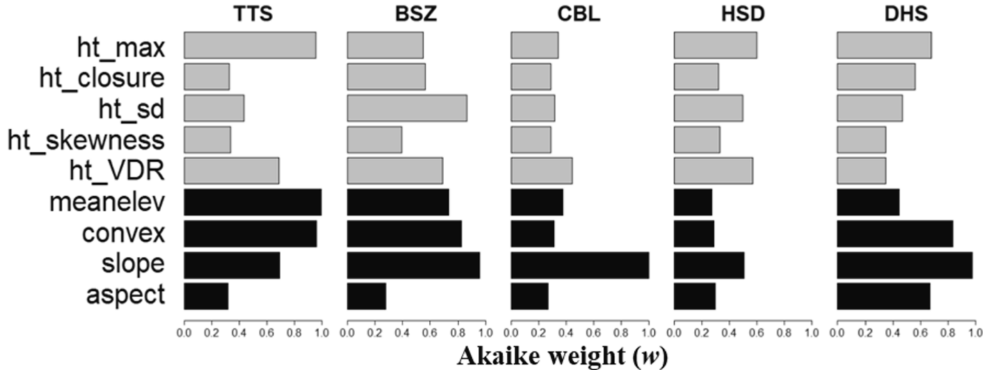


Fig. 2. The relative importance of five drone-derived canopy variables (ht_max, ht_closure, ht_sd, ht_skewness and ht_VDR) and four topographic variables (elevation, convexity, slope and aspect) to (a) species richness, (b) species evenness, and (c) the effective number of species based on Shannon diversity index ($\exp[H_{\text{Shannon}}]$). The Akaike weight (*w*) for each variable was calculated based on the results of spatial simultaneous autoregressive models. Plots: Tiantongshan (TTS), Baishanzu (BSZ), Chebaling (CBL), Heishiding (HSD), and Dinghushan (DHS).

understory in most plots. At the species level, the distributions of a large portion of species in the five plots were related to one or more metrics of canopy structure.

Our findings partly differ from others based on data from the CTFS-ForestGEO stem-mapped plot network, of which our five plots are part, precisely because those studies did not include canopy data. For example, without canopy height data, Wang et al. (2009) in the Dinghushan plot, Yang et al. (2016) in the Tiantongshan plot, and Yin et al. (2016) in the Heishiding plot found that spatial distributions of over 80% of tree species were related to topographical variables. At the extreme end of the diversity spectrum, Furniss et al. (2017) found that all ten common species in a high elevation plot in the Utah plot all had a strong niche association using only aspect and parent soil type. However, Harms et al. (2001) documented that only 16% (28 species) of 171 plant species in a 50 ha Panamanian tropical forest plot on Barro Colorado Island (BCI) showed significant correlations with topography, suggesting that local habitat specialization as defined only by topography played a limited role in tree diversity maintenance. In a 25 ha Sri Lankan mixed dipterocarp forest plot, Punchi-Manage et al. (2013) found that only 25% of the species spatial distributions was due to topographic association. Brown et al. (2013) compared the results of the ground tree survey data from 14 large subtropical and tropical forest plots, and found that the contribution of topography in community assembly varied greatly among different forests, with the increased importance in the high heterogenetic environment. Our study suggests that adding canopy data would almost certainly improve the inference of habitat niche. This is consistent with other studies that evaluated the importance of canopy structure related variables, including canopy height, canopy openness and light availability (e.g., Hubbell et al., 1999; Tateno & Takeda 2003; Rüger et al., 2009; Zhang et al., 2016b), and found vertical niche partitioning significantly contributes to plant community assembly. In addition, we found that canopy structure variables had stronger or near equal effects in plant diversity in the understory layers of these forests compared with the entire communites, suggesting the importance of light enviroments in determining understory plant diversity and subtropical forest regeration (Rüger et al., 2009; Getzin et al. 2012).

Despite the strong support for the importance of canopy structure

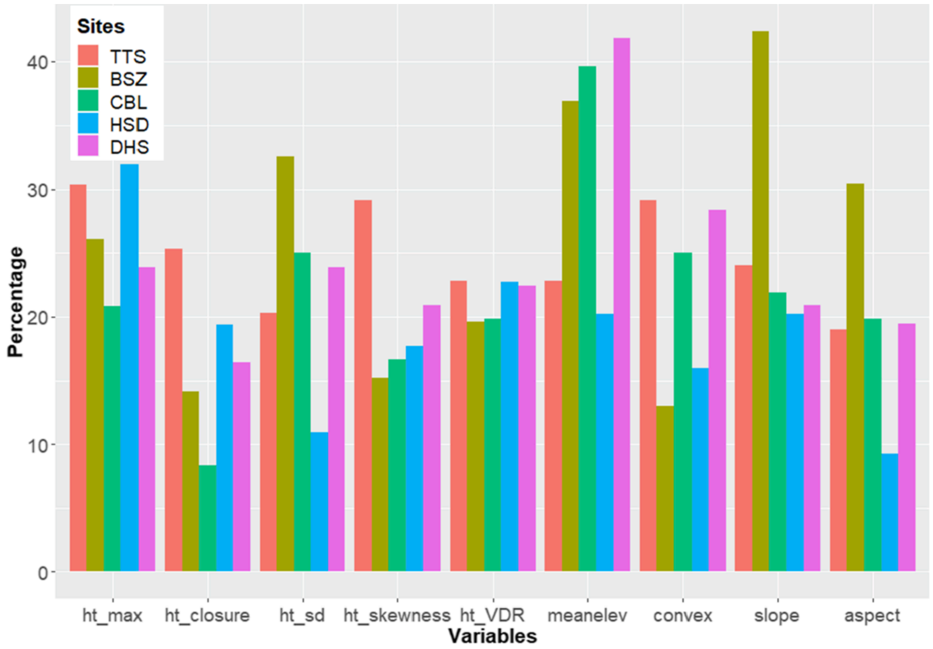


Fig. 3. The percentage of species number included the predictor variables in the “best” models of species distributions compared with total species number with at least 50 individuals. The “best” model of each species was selected by comparing all subsets of spatial simultaneous autoregressive models using Akaike’s Information Criterion (AIC). Plots: Tiantongshan (TTS), Baishanzu (BSZ), Chebaling (CBL), Heishiding (HSD), and Dinghushan (DHS).

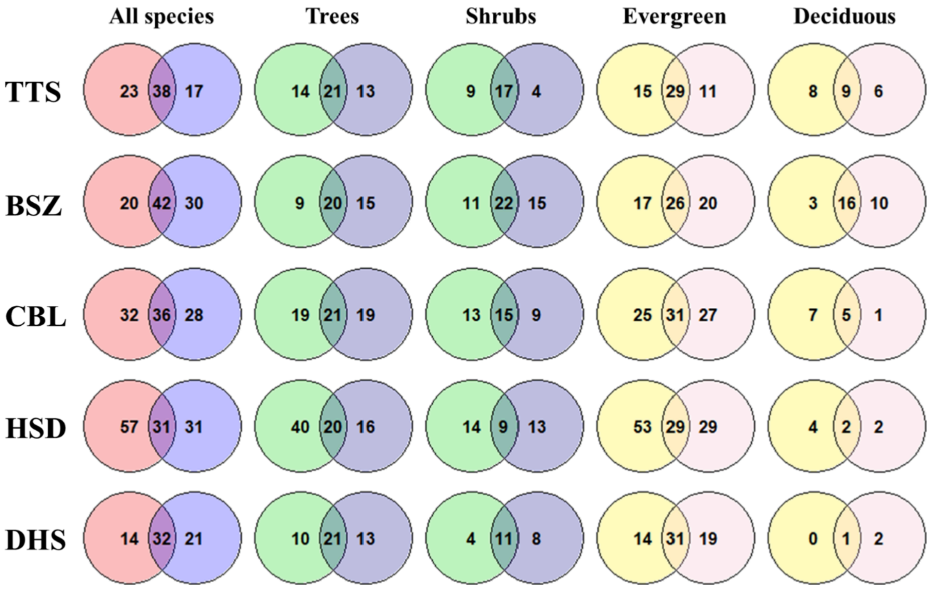


Fig. 4. The number of species included canopy structure related variables (dark-pink, green or yellow circles in the left sides), topographic variables (darkblue, grey, or pink circles in the right sides), and their combinations interactions (the interactions union of two circles) in the “best” models of species distributions in each of the five plots. Species were grouped by growth forms (trees *vs.* shrubs) and leaf habits (evergreen *vs.* deciduous). Plots: Tiantongshan (TTS), Baishanzu (BSZ), Chebaling (CBL), Heishiding (HSD), and Dinghushan (DHS).

variables in predicting tree diversity, it is worth noting that a canopy height variable could have significantly varied effects on tree diversity across forest plots (Fig. 2). This context-dependent effect of different canopy variables is expected given that the five forests in our study vary considerably in canopy height, species composition (e.g., the proportions of evergreen tree species vary with latitudes and elevations among them) (Song et al. 2015) and disturbance history (this region is strongly influenced by the East Asian monsoon and the frequency and intensity of disturbances, e.g., typhoon, seasonal drought, and ice-storm are very different among these plots) (Wang et al., 2007; Song 2013). These variations speak for the complexity of canopy structure and its varied effects on tree species assembly. Without detailed information of forest disturbance history and plant interactions, our current work cannot disentangle the effects of different measures of canopy structure variables on plant diversity. Further studies are needed to directly link canopy structure measures with the key ecological processes, such as light availability and forest disturbance. For example, light availability and forest gap distribtuions could be mapped using high-resolution RGB images, although the accuracy of the drone-derived variables still needs to further evaluate in different ecosystems (Getzin et al., 2014; Jucker 2021). In addition, the current study had only one-time snapshots of forest canopy in each forest, providing relatively limited insights into how forests may change over time. Long-term monitoring of forest canopy dynamics and ground resurveys in plant demographic changes is necessary to understand forest diversity and dynamics (Zhang et al., 2015; Davies et al., 2021). To fill this knowledge gap, we are continuing to monitor the changes of canopy height distributions and gap characteristics in these forests.

4.2. Combined effects of forest canopy structure and topography

Topography influences plant diversity and species abundance patterns by controlling environmental factors such as water drainage and the solar radiation regime. Topographic niche partitioning remains as a prominent hypothesis to partially explain tree community assembly in subtropical and tropical forests (Wang et al., 2009; Brown et al., 2013). Our findings at both community and species levels from the five species-rich subtropical forests partly support this hypothesis. Our findings also suggest that previous studies (above) in quantifying the importance of topography in plant diversity could be confounded with the effect of canopy structure variables which in turn vary with topography.

Clearly, both canopy structure and topography were associated with species distributions in these forests, although their relative importance varied considerably across study sites and tree species. For tree communites across the entire forest layers, nearly 48% of the variation (on average) in richness, 43% in evenness, and 46% in Shannon diversity were statistically explained by their combined effects. One recent study in the 50-ha BCI plot also reported canopy height and topography explained 48% of the variations in plant richness at 1.0-ha scale (Wolf et al., 2012). In addition, topographic variation could influence forest canopy structure by mediating light availability, soil nutrient cycling, microclimate, and the distribution of herbivores (Tateno & Takeda 2003; Rüger et al., 2009; Ledo et al., 2013). Therefore, it would be necessary to disentangle the separate effects of topographic variables on the related ecological processes for a further understanding how the variation in topography would redistribute abiotic and biotic resources for maintaining the complex network of biodiversity. It is worth mentioning that, for species-level analysis, we only selected the species with at least 50 individuals to reduce samle sample size bias, which may ignore the effects of canopy structure and topography in some extremely rare species. Condit et al. (2000) analyzed the spatial patterns of six tropical CTFS-ForestGEO plots and reported that rare species were more aggregated than common species, but the drivers of rare species spatial distributions are still unclear. Considering the importance of rare species in community assembly, further studies are needed to quantively evaluate how canopy structure, topography and dispersal limitation shape the distributions of rare species. In addition, our current analyses only focused on one spatial scale (20-m grid scale). Although this spatial scale is commonly used in forest community ecology, it can only capture several ecological processes and may have some uncertainties in estimating canopy heights because the crowns of large trees may across the boundaries of the 20-m grids. Considering that the importance of most ecological and evolutionary processes varies with spatial scales (Levin 1992), multiple-scale studies on canopy structure and topography will be useful to evaluate spatial scale effects in plant community assembly.

4.3. Drones and other remote sensing techniques as the tools for forest canopy monitoring

The rapid development of drones and other remote sensing techniques (e.g., aircraft LiDAR and terrestrial laser scanning) has greatly improved our ability to acquire data that were previously not possible and as such offers exciting opportunities for addressing questions important to the understanding of biodiversity and conservation (Anderson & Gaston 2013; Koh & Wich 2012; Nakamura et al., 2017; Randin et al., 2020). Fine-scale drone mapping provides high-quality data in canopy structure attributes that are less known and have been little explored at fine spatial scales (Getzin et al. 2014). Furthermore, drone surveys take only 1–2 days to cover >20 ha at a given forest site, including the survey of ground control points, mission planning and the actual aerial drone survey. If traditional ground-based surveys were used, it would take several months to collect one or several forest canopy attributes. For example, to map canopy gaps and their changes over time, the researchers in the 50 ha BCI plot in Panama measured forest height using fiberglass measuring poles in each 5 m × 5 m quadrat, and it took one person eight months to complete one census (Condit 1998; Hubbell et al., 1999). Due to the practical difficulties in measuring canopy structure directly from the ground in large areas, most previous studies have been based on a rough estimation of canopy height and the light environment (Larjavaara & Muller-Landau 2013; Rüger et al., 2009), but the uncertainty associated with the use of such approximate techniques is not well known. In the current study, we used the topographic variables from ground-based surveys on 20 m × 20 m grids using digital total stations, which did not distinguish topographic variations within the grain scale that was used and may miss out the importance of fine-scale topographic niche differentiaon.

Recent development in light-weight LiDAR sensors, terrestrial laser scanning, and the simultaneous localization and mapping (SLAM) techniques show large potential for forest mapping based on combined ground and airborne surveys (Bauwens et al., 2016; Roşca et al., 2018; Disney 2019; Rahman et al., 2022). These new technologies could certainly reduce the uncertainties in data collection and analysis, especially in forests with complex vegetation structure. As we mentioned before, the terrain data we collected from the field did not spatially match the digital surface model generated from the drone, since the topographic variables were measured at the 20-m scale following the standard protocols of the CTFS-ForestGEO network (Condit, 1998; Zhang et al., 2016b). The use of LiDAR techniques will greatly improve the accuracy of terrain data. The combination of light-weight drones and other remote sensing techniques provide a high-quality measure of forest canopy structure, and could serve as a cost-effective and time-saving tool for monitoring canopy dynamics, especially in species-rich tropical and subtropical forests with complex mountainous topographies (Koh & Wich 2012; Zhang et al., 2016b).

5. Conclusions

By combining drone-based photogrammetric data and detailed ground survey data, we provide a quantitative evaluation of the relative importance of forest canopy structure and topography in determining species richness, abundance, and plant community assembly in five subtropical forests. We conclude that forest vertical structure plays an important role in plant community assembly, and canopy structure variations and topography jointly shape species distributions in these forests. Moreover, our study shows that, as a complement to traditional field surveys, drones allow collection of a large volume of data with high spatiotemporal resolution and at low cost, while providing new data to advance our mechanistic understanding of species coexistence.

CRediT authorship contribution statement

Jian Zhang: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Zhaochen Zhang:** Investigation, Data curation, Writing – review & editing. **James A. Lutz:** Writing – review & editing. **Chengjin Chu:** Investigation, Data curation, Writing – review & editing. **Jianbo Hu:** Investigation, Data curation. **Guochun Shen:** Data curation, Writing – original draft, Writing – review & editing. **Buhang Li:** Investigation, Data curation. **Qingsong Yang:** Investigation, Data curation. **Juyu Lian:** Investigation, Data curation. **Minhua Zhang:** Investigation, Data curation. **Xihua Wang:** Investigation, Data curation. **Wanhui Ye:** Investigation, Data curation. **Fangliang He:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119945.

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