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Tree architecture varies with forest succession in evergreen broad-leaved forests in Eastern China

Xiao-Dong Yang · En-Rong Yan · Scott X. Chang · Liang-Jun Da · Xi-Hua Wang

Abstract

Key message **Vertical and temporal patterns of tree architecture and their relationship with woody plant crown exposure index varied with succession in evergreen broad-leaved forests in eastern China.**

Abstract Linking temporal pattern of tree architecture with changing light conditions through forest succession is important for understanding plant adaptive strategies. We determined vertical (canopy, sub-canopy, and understory species) and temporal (pioneer, mid-successional, and climax species) patterns of tree height, stem basal area, crown area and depth, leaf coverage, leaf convergence (clumped vs. dispersed leaves) and stretch direction of branches (vertical, leaned and horizontal branches) and their relationship with crown exposure index (CEI) for woody plants among three successional series in subtropical evergreen broad-leaved forests in eastern China. The series included three stages: secondary shrub (early-), young (mid-) and climax forests (late-successional stage). Tree height, crown area and depth, stem basal diameter and leaf coverage were the greatest in canopy trees, intermediate in sub-canopy trees, and the smallest in understory plants among the three successional stages; the above parameters and the proportions of dispersed leaves and leaned branches were climax > mid-successional > pioneer species. In contrast, the proportions of clumped leaves and vertical branches were pioneer > mid-successional > climax species. Between canopy and understory species, the patterns of branch stretch direction and leaf convergence were not consistent among the three successional stages. Tree height, crown area and depth, leaf coverage, and stem basal diameter were positively correlated with CEI for both vertically different species and successional species. Tree architectural traits were interactively affected by forest age and CEI ($p < 0.01$). In conclusion, tree architecture varies with changes in both forest vertical structure and successional status. The large variability of tree architectural traits in relation to CEI and forest age reflects a strong control of light availability that affects biomass allocation strategies of trees. Our study demonstrated that light induced shift in tree architecture may result in species coexistence through divergence of vertical space, as well as species replacement through forest succession.

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Introduction

Tree architecture refers to the overall shape and size of woody plants, and the spatial arrangement of their components such as crowns, stems, branches and leaves (Poorter et al. 2003). For mechanical and hydraulic reasons, tree architecture can greatly affect whole-plant functions such as photosynthesis, transpiration and energy

balance (Olson et al. 2009; Iida et al. 2011; Sarlikioti et al. 2011). As one of the leading dimensions in shaping plant function, tree architecture is also fundamental in influencing species demographics (Enquist et al. 1999; Kohyama et al. 2003; Poorter et al. 2003; Iida et al. 2011), and consequently species coexistence (Kohyama 1993; Poorter et al. 2008).

Architecture is a major determinant of plant performance in response to environmental stresses. For example, for a given tree species, the potential maximum height that is a key functional trait related to tree maturity, generally declines against increasing shade stress within forests (Poorter et al. 2008). This indicates partly that tree architecture is associated with the availability of radiation at a given position within a forest. There is now mounting evidence that, in response to light availability, tree architecture is highly variable for species positioned in different vertical layers within a given forest (Kohyama 1993; King 1998; Davies and Ashton 1999; Sterck et al. 2001; Kohyama et al. 2003; Poorter et al. 2003; Wright et al. 2005; Iida et al. 2011; McCulloh et al. 2012), and for species occurring in different successional stages (Shukla and Ramakrishnan 1986; Thomas1996b; Davies and Ashton 1999; Falster and Westoby 2005; England and Attiwill 2006; Selaya et al. 2008; Selaya and Anten 2010; McCulloh et al. 2011; Yan et al. 2013; Yang et al. 2013). Even though these empirical studies suggest that tree architecture varies either with forest succession or with vertical change of forest structure, the combined effects between forest succession and forest vertical change on tree architecture has been poorly studied. Moreover, most research has focused only on the across-species patterns of tree architecture without directly testing their relationship with light availability across species (Poorter et al. 2003; Wright et al. 2005; Iida et al. 2011). Currently, how forest succession, forest vertical structure and light availability affect tree architecture across successional forests remains unclear. Therefore, linking temporal and vertical (spatial) patterns of tree architecture simultaneously with changes in light conditions over forest succession is important for understanding the arrangement strategies among leaves, branches, stems, and tree crowns.

It is plausible that tree species could respond to forest succession by changing their architecture as light availability and species composition shift considerably with succession (Shukla and Ramakrishnan 1986; Selaya and Anten 2010). It is well understood that shade stress exacerbates and tree height increases through forest succession (Selaya et al. 2008; Yan et al. 2009). For light interception and development reasons, trees must grow tall into the canopy layer within a given forest and/or in late-successional forest, but only need the lower tree height in understory and/or in early-successional forest. As tree height changes with forest succession, other architectural traits should change as well. This is because tree architectural traits are affected each other by trade-offs between height extension and mechanical stability (Putz et al. 1983; Mizunaga and Umeki 2001; Poorter et al. 2010).

Tree architecture can be influenced by its vertical position in a given forest (Westoby et al. 2002; Poorter et al. 2006), while its pattern of change over forest succession could result from different light availabilities and developmental changes over forest succession. Within a given forest, a progressive decline of light level occurs when incoming radiation from above is intercepted by successive leaf layers in the forest canopy (Ashton 1958). To win the light competition, canopy trees as compared with understory plants are expected to have wider and thicker crowns that maximize light interception (Horn 1971; Givnish 1988). In order to capture light as much as possible, canopy trees are also expected to have a greater proportion of horizontal branches and leaf coverage relative to understory plants (Thomas 1996a; Davies and Ashton 1999; Sterck et al. 2001; Poorter et al. 2003, 2008; Clark 2010; Wright et al. 2010). Similarly, pioneer species in early-successional forests that are light demanding must grow rapidly and should thus have deep and narrow crowns to place preference on vertical growth, as compared with the same sized climax species in late-successional forests. In addition, in contrast to the light-demanding pioneer species, shade-tolerant climax species in late-successional forests are expected to develop their crown architecture by presenting a greater proportion of horizontal branches, leaf coverage and dispersed leaves in leaf convergence.

Temporal patterns of tree architectural changes may result from shifts in both light availability and forest development (forest age). Crown exposure index (CEI) is considered a repeatable and accurate index to assess light availability and plant light strategies indirectly (Poorter et al. 2006, 2010). Empirical studies reported that tree height, crown diameter and depth are associated with CEI in semi-evergreen moist tropical forests (Poorter et al. 2006, 2010). Currently, little is understood whether trees architecture correlates to this CEI during forest succession.

Evergreen broad-leaved forests (EBLFs) in the subtropical region in eastern China are notable for its diversity of community types with intact and semi-intact climax forests, as well as secondary shrubs, all found in close proximity in a diverse mosaic landscape (Yan et al. 2006), allowing us to explore the successional patterns of tree architecture. Secondary shrubs (early-successional stage) are mostly formed after the cessation of repeated clear cutting. After 20 years in the shrub stage due to very dense stem density, the succession proceeds to young evergreen broad-leaved forests (mid-successional forests) that can reach canopy closure. At late stage of succession, the

climax evergreen broad-leaved forests (late-successional stage) form approximately 120 years after the cessation of forest clear cutting (Yan et al. 2006). Along the successional series, canopy height, soil moisture content, soil nutrients all increase, but light availability within forests gradually decreases (Song and Wang 1995; Yan et al. 2009). The pioneer plant species are often a mixture of deciduous species and a few resprouting evergreen broad-leaved species that are light demanding and usually occur in the early stage of secondary forest succession. As the succession proceeds, pioneer species are gradually replaced by light-prone evergreen species. Eventually, shade-tolerant species dominate in climax forests (Yan et al. 2006).

In this study, we investigated vertical (canopy, sub-canopy, and understory species) and temporal (pioneer, mid-successional, and climax species) patterns of change in tree architecture and their relationship with woody plant CEI along three successional series in subtropical forests in eastern China. Specifically, we ask the following questions: (1) do canopy species have the greatest crown area and depth, stem basal diameter, leaf coverage and the proportion of clumped leaves and vertical branches, but the lowest proportions of dispersed leaves and horizontal branches, relative to sub-canopy and understory species? (2) Are tree height, crown area and depth, stem basal diameter, leaf coverage, and the proportions of dispersed leaves and leaned branches the largest, but the proportions of clumped leaves and vertical branches the smallest in climax species than in mid-successional and pioneer species? And (3) do tree height, crown area and depth, leaf coverage, and stem basal diameter positively correlate with CEI?

Materials and methods

Study sites and successional series

This study was conducted in the lower eastern extension of the Siming Mountain (29°41–50′N, 121°36–52′E), located on the Ningbo coastal area, Zhejiang province, in Eastern China. The area has the highest peak at 653 m above sea level with most other relief in the range of 70–300 m. The region has a typical monsoon climate with a hot, humid summer and a drier cold winter. Details of climatic and edaphic conditions were described in Yan et al. (2006, 2009).

The zonal vegetation in this region is subtropical EB-LFs. The vegetation of the region has been severely disturbed in the past with only small tracks of intact or semi-intact EBLFs left around several Buddhist temples. Outside of these sites, virtually all vegetations are secondary. In this study, we established a series of sites representing three

successional stages in each of Beilun, Nanshan and Tiantong, sites were selected around each of the three temples. In each site, secondary shrub (early-), young EBLFs (mid-), and climax EBLFs (late-successional stage) were chosen as representative of the early-, mid- and late-successional stages, based on both forest age and species composition. The three forest stands used at each site to represent successional status were located on similar slope positions, had the same historical vegetation and the soils were developed from the same quartzitic parent material (Yan et al. 2009). Forest age was determined by firstly referring to documents from the local governmental forestry department, and then confirmed by counting tree rings from tree cores collected from 3 to 4 of the largest trees in each successional stage. A tree core sample was collected per tree at breast height (1.3 m) with a 5-mm-diameter increment borer. These cores were then air-dried, mounted, and sanded with 150–600 grit sandpaper. For each tree core sample, the number of tree rings was determined using the WinDendro tree-ring image analysis software [Version 2003a, Regent Instruments (Sainte-Foy, Quebec, Canada)]. Then the mean value of the documentary and the number of tree rings from 3 to 4 tree cores in each successional stage was used to represent the age of the forest.

For each successional stage in each of the three sites, one plot was established in a stand where forest age and species composition were representative of its successional stage. With this sampling protocol, a plot was randomly located in the interior of the stand (>5 ha), at least 100 m away from the stand edge to avoid the edge effect. A total of nine plots were established across the three sites. In this region, 10×10 and 20×20 m were the smallest reasonable area to be considered as a community for secondary shrubs and subtropical forests, respectively (Song and Wang 1995). Therefore, 10×10 m plots were set up for secondary shrubs, and 20×20 m for both young and climax forests. The vegetation in the secondary shrub plots was made up of two vertical layers: canopy (4 < height < 8 m) and understory plants (<4 m). In the young and climax forests, there were three vertical layers: canopy (height >8 m), sub-canopy (4 < height < 8 m), and understory plants (height <4 m). Other community characteristics are listed in Table 1.

Measurements of tree architecture and crown exposure index

In each plot, all woody plants were measured for architecture and crown exposure index in July and August 2008. For each individual plant, height, the height of the lowest branch, and the height of the lowest leaf were measured with a telescope pole for heights up to 15 m, and with a Vertex meter (Vertex-IV, Haglöf Haglof, Dalarna,

Table 1 Description of successional series in the lower eastern extension of the Siming Mountain, Ningbo coastal area, Zhejiang province in eastern China

Site	Successional stage	Forest age (years)	Dominant species	Stem density (N m⁻²)	Top height (m)	Number of vertical layers (N)	Proportion of branches by orientation (%)						Proportion of leaf convergence (%)			
							Understory plants (height <4 m)			Canopy and sub-canopy trees[a] (height >4 m)			Understory plants (height <4 m)		Canopy and sub-canopy trees[a] (height >4 m)	
							Vertical	Horizontal	Leaned	Vertical	Horizontal	leaned	Clumped	Dispersed	Clumped	Dispersed
Beilun	Early	16	*Lithocarpus glaber*	1.09	5.3	2	0.52	0.42	0.06	0.33	0.63	0.04	0.68	0.32	0.63	0.37
	Mid	49	*Schima superba*	0.42	16.6	3	0.42	0.44	0.14	0.41	0.57	0.02	0.65	0.35	0.63	0.37
	Late	91	*Schima superba* and *Castanopsis fargesii*	0.17	13.3	3	0.25	0.50	0.25	0.48	0.31	0.21	0.52	0.48	0.52	0.48
Nanshan	Early	15	*Lithocarpus glaber* and *Castanopsis sclerophylla*	2.2	7.5	2	0.53	0.43	0.04	0.50	0.38	0.13	0.34	0.66	0.67	0.33
	Mid	42	*Schima superba*	0.27	16.4	3	0.50	0.45	0.05	0.38	0.41	0.21	0.52	0.48	0.43	0.57
	Late	89	*Schima superba* and *Castanopsis fargesii*	0.55	18.9	3	0.43	0.44	0.13	0.50	0.33	0.17	0.40	0.60	0.22	0.78
Tiantong	Early	18	*Lithocarpus glaber* and *Schima superba*	1.17	5.7	2	0.43	0.35	0.22	0.44	0.22	0.33	0.98	0.02	0.94	0.06
	Mid	52	*Schima superba*	0.64	24.4	3	0.38	0.36	0.26	0.35	0.33	0.33	0.85	0.15	0.98	0.02
	Late	120	*Schima superba* and *Castanopsis fargesii*	0.59	23.3	3	0.22	0.39	0.39	0.04	0.16	0.80	0.55	0.45	0.76	0.24

Studied site, successional stage and forest age, dominant species, stem density, number of vertical layers, branch orientation, leaf convergence, and the top height of the forest stand are given

[a] As mid- and late-successional stages, the data of the canopy and sub-canopy were combined for the mid- and late-successional stages, to keep consistent vertical patterns across successional stages

Sweden) for heights >15 m. At the same time, we measured stem basal diameter (based on diameter measured at 5 cm from the ground for saplings, and 20 cm from the ground for trees) using a diameter tape. Crown width was determined as the average diameter of the east–west and north–south cross sections of the crown using a meter stick. Then crown area was estimated with Eq. 1 below, and crown depth was calculated by subtracting the height of the lowest leaf from the crown height (Eq. 2).

$$\text{Crown area} = D_{\text{East−West}} \times D_{\text{South−North}} \tag{1}$$

$$\text{Crown depth} = \text{Hight} − \text{Lowest leaf height} \tag{2}$$

After this, leaf coverage, leaf convergence, stretch direction of branch and CEI of tree crown were estimated by two independent observers, and then the average value was used to reduce individual bias. The leaf coverage of the crown was estimated in 10 % cover classes. The leaf convergence of the crown was classified into two groups, i.e., clumped and dispersed. The clumped group has trees with a monolayer if the leaves were (densely) stacked in a single layer in the upper part of the crown. The dispersed group has trees with a multilayer, and the leaves are stacked in several more widely spaced layers, shading over each other (Poorter et al. 2006). The orientation of branch was classified as being mainly vertical, mainly horizontal, or leaned. We determined the branch orientation by focusing on the average angle between the branch and the main trunk. Branches with the average angle less than 30° is considered vertical, 30 and 60° is considered leaned, and greater than 60° is considered horizontal. Lastly, the crown exposure index (CEI) was determined on a five-point scale for each individual tree: 1 = no direct light received in the crown area, 2 = lateral light received in the crown area, 3 = partial overhead light received in the crown area, 4 = more than 90 % of the crown area receives direct overhead light, and 5 = emergent crown with direct light from all direction (Dawkins and Field 1958; Poorter et al. 2006).

Data analysis

We analyzed changes of tree architectural traits by using both absolute values (i.e., measured data) and standardized values (i.e., values corrected with tree stem basal diameter) to confirm whether trees at different stages were taller, or had wider or narrower crowns for a given diameter. In this study, the architectural traits were measured for all individual trees, instead of sampling a portion of individuals for a given species in the plot. In this case, the community-weighted means of the architectural traits can be calculated by averaging trait values for all individuals across species in a given community. Therefore, we scaled up the

architectural traits from individuals to each of canopy trees, sub-canopy trees and understory plants in a given successional stage by arithmetically averaging trait values for all individuals in the vertical layer of the forest.

One-way ANOVA was used to determine the effects of forest succession and vertical structure, respectively on each architectural trait, except leaf convergence and branch stretch direction due to the qualitative nature of those properties. If the variance of architectural traits was homogeneous among the treatments (i.e., each of forest succession and vertical structure), least-squares mean separation with Duncan's correction was used to test differences among climax, mid-successional and pioneer species, as well as among canopy, sub-canopy and understory species. Alternatively, if the variance was heterogeneous, Tamhane's T3 test was used. In the case of the early-successional stage, a t test was used since only two vertical layers were available.

In order to test whether tree architectural traits correlate to CEI across the three vertical layers in a given successional stage, each of the architectural traits was combined in each vertical layer for each of the three replicated forests for each successional stages. Then we used linear regression to analyze the relationship between CEI and each of tree height, crown area and depth, leaf coverage, and stem basal diameter at each of three successional forests. After this, each architectural trait was combined for the three successional stages, to determine whether relationships between CEI and architectural traits were changed if the successional effect was ignored. Further, the relationships between CEI and architectural traits for species in each of three different vertical layers across successional stages were examined using a linear regression to test whether tree architectural traits were related to light availability induced by forest succession, when the effect of the vertical change in the forest was ignored. Finally, two-way ANOVA was used to determine whether there were significant "forest age" effects on each response (each architectural trait) over the five CEI levels. Forest age and CEI were independent variables that were considered fixed effects. All statistical tests were conducted using SPSS 11.5.

Results

Tree architecture among canopy, sub-canopy and understory species

Across the three successional stages, tree architectural traits were affected by the forest vertical structure (Table 7). Tree height, crown area and depth, stem basal diameter and leaf coverage were consistently the highest in

canopy and sub-canopy trees and the lowest in understory plants across three successional stages (Fig. 1). When the traits were corrected with stem diameter, standardized values of tree height, crown area and depth were also the highest in canopy and sub-canopy trees and the lowest in understory plants (Tables 2, 10). In addition, there were no significant differences in standardized tree height, crown area and depth between canopy and understory plants for pioneer species (Table 2). Similarly, the standard deviations of tree architectural traits were also the largest in canopy trees, intermediate in sub-canopy trees, and the lowest in understory plants (Table 8).

There was no consistent pattern in leaf convergence between understory plants and the upper layer trees (including canopy and sub-canopy trees) amongst the three successional series (Table 1). When the data from the three
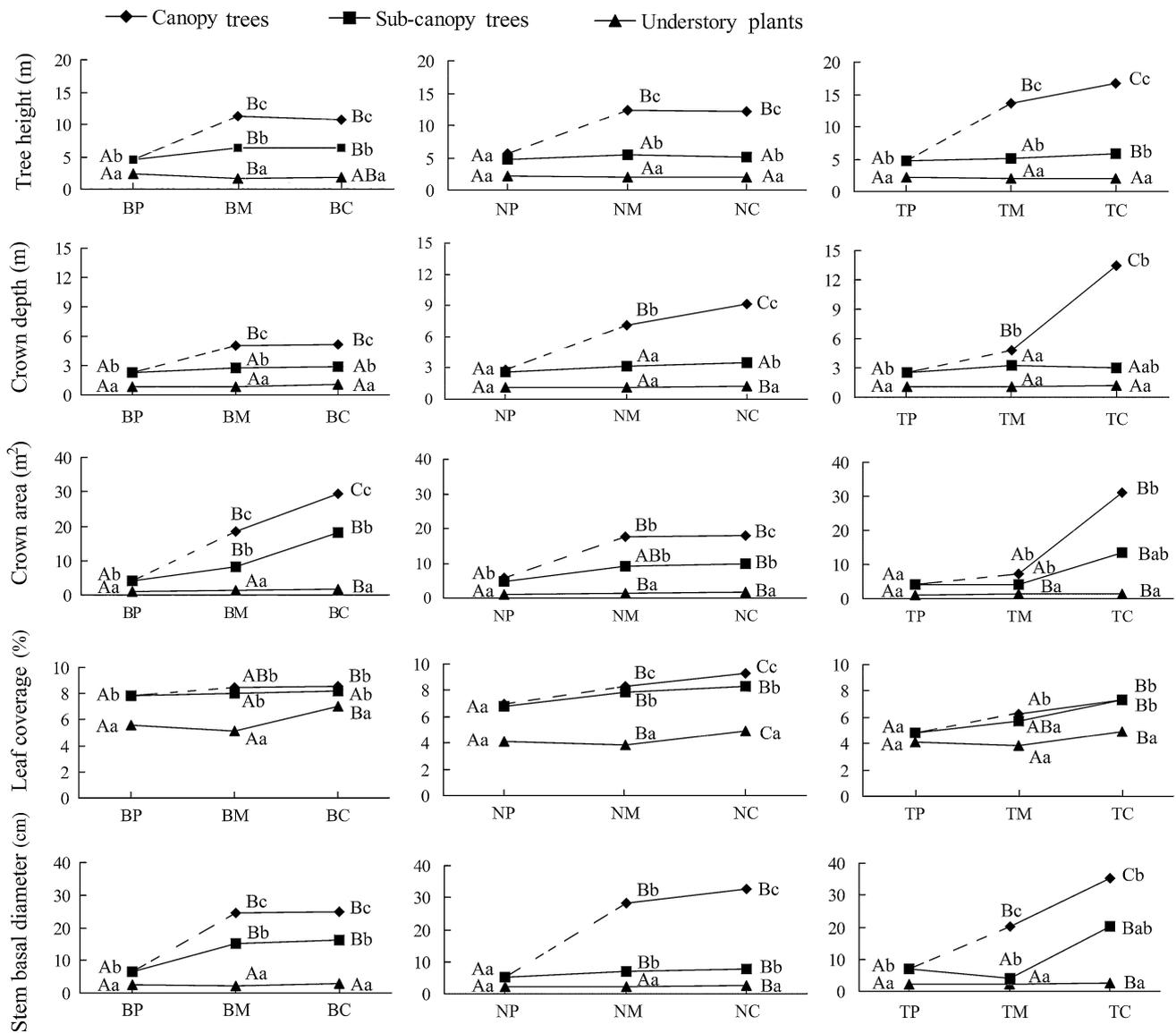
Fig. 1 Temporal pattern of tree height, crown area and depth, leaf coverage, and stem basal diameter among three vertical layers along the successional series in three sites. Species in different vertical layers include canopy trees (height is large than 8 m in the mid and late stages, while large than 4 m in the early stage), sub-canopy trees (in the mid and late stages, height is lesser than 8 m and large than 4 m, while there is no sub-canopy trees in the early stage), and understory plants (height <4 m for three stages). *Different letters in each line* with capital indicate significant differences between successional stages. *Different letters in each line* with *lowercase* indicate significant differences between species in different vertical layers in each of three successional stages. *Dashed line* linking the early and mid stages for sub-canopy trees show the potential shift pattern only. *Letter of B, N and T in the x-axis* is the corresponding successional series in each of Beilun, Nanshan and Tiantong sites, respectively. *P, M and C* represent pioneer, mid-successional and climax species in each of the early-, mid- and late- stage of succession

Table 2 One-way ANOVA and *t* test among different vertical layers and successional stages for standardized height, crown depth, and crown area

Site	Vertical layer	Standardized height × (10²)			Standardized crown depth × (10²)			Standardized crown area × (10⁴)		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Beilun	Understory plants	1.02 ± 0.11^{Aa}	0.48 ± 0.02^{Bb}	0.47 ± 0.02^{Bb}	0.36 ± 0.03^{Ab}	0.21 ± 0.02^{Bb}	0.22 ± 0.02^{Bb}	0.40 ± 0.03^{Aa}	0.52 ± 0.03^{Bb}	0.57 ± 0.06^{Bb}
	Sub-canopy trees	–	0.46 ± 0.02^{Aab}	0.44 ± 0.06^{Ab}	–	0.21 ± 0.04^{Ab}	0.18 ± 0.03^{Ab}	–	0.57 ± 0.07^{Ab}	1.10 ± 0.23^{Ba}
	Canopy trees	0.89 ± 0.05^{Aa}	0.84 ± 0.03^{Aa}	0.67 ± 0.05^{Ba}	0.47 ± 0.10^{Aa}	0.39 ± 0.02^{Ba}	0.41 ± 0.04^{Ba}	0.54 ± 0.11^{Aa}	0.73 ± 0.06^{Ba}	1.22 ± 0.11^{Ca}
Nanshan	Understory plants	1.14 ± 0.04^{Aa}	0.46 ± 0.03^{Bb}	0.43 ± 0.04^{Bb}	0.53 ± 0.02^{Aa}	0.27 ± 0.03^{Bb}	0.32 ± 0.04^{Bb}	0.52 ± 0.02^{Aa}	0.61 ± 0.11^{Ba}	0.56 ± 0.07^{Bb}
	Sub-canopy trees	–	0.36 ± 0.05^{Ab}	0.91 ± 0.26^{Ba}	–	0.24 ± 0.04^{Ab}	0.37 ± 0.11^{Aab}	–	0.69 ± 0.22^{Aa}	1.97 ± 1.02^{Ba}
	Canopy trees	1.17 ± 0.17^{Aa}	0.96 ± 0.03^{Bb}	0.83 ± 0.03^{Ba}	0.60 ± 0.08^{Aa}	0.41 ± 0.02^{Ba}	0.44 ± 0.03^{Ba}	0.89 ± 008^{Aa}	0.84 ± 0.06^{Aa}	0.79 ± 0.04^{Ab}
Tiantong	Understory plants	0.87 ± 0.04^{Aa}	0.72 ± 0.03^{Bb}	0.51 ± 0.04^{Cb}	0.48 ± 0.09^{Aa}	0.25 ± 0.02^{Ab}	0.42 ± 0.04^{Aa}	0.43 ± 0.05^{Aa}	0.33 ± 0.04^{Ac}	0.55 ± 0.02^{Bb}
	Sub-canopy trees	–	1.15 ± 0.24^{Aa}	0.40 ± 007^{Bb}	–	0.78 ± 0.19^{Aa}	0.21 ± 0.08^{Bb}	–	0.64 ± 0.37^{Ab}	0.71 ± 0.24^{Bab}
	Canopy trees	1.20 ± 0.12^{Aa}	1.03 ± 0.03^{Aa}	0.94 ± 0.02^{Ba}	0.58 ± 0.03^{Aa}	0.55 ± 0.02^{Ba}	0.57 ± 0.02^{ABa}	0.48 ± 0.07^{Aa}	0.80 ± 0.03^{Ba}	0.83 ± 0.10^{Ba}

Standardization was done by dividing tree height (m) and crown depth (m) by stem basal diameter (cm), and dividing crown area (m²) by stem basal area (cm²). The *t* test was used to determine differences of standardized architectural traits between mid-successional and climax species, due to the lack of sub-canopy trees in the early-successional stage (mean ± SE). Different capital letters indicate significant differences between successional stages and different lowercase letters indicate significant differences between vertical layers (*p* < 0.05)

"–" indicates that data are not available in sub-canopy layer for the early succession stage

successional series were combined, there were obvious patterns of changes in leaf convergence between canopy trees and understory plants. For pioneer species, the proportion of clumped leaves was greater in canopy trees than in understory plants, whereas a reversed pattern was found for dispersed leaves (Table 3). In contrast, for both mid-successional and climax species, the proportions in each of clumped and dispersed leaves were almost similar between canopy trees and understory plants (Table 3).

The distribution pattern of the orientation of branches between canopy trees and understory plants was also successional stage specific. The proportion of the vertical branches was greater in understory plants than in canopy and sub-canopy trees for pioneer and mid-successional species, but pattern was opposite in climax species (Table 3).

The proportion of horizontal branches was similar between understory plants and canopy trees for pioneer and mid-successional species, but was higher in understory plants than in canopy and in sub-canopy trees for climax species (Table 3). In contrast, the proportion of the leaned branches was lower in understory plants than in canopy trees across successional species (Table 3).

Tree architecture among pioneer, mid-successional and climax species

Tree architectural traits were affected by forest succession (Table 9). There were similar temporal trends of tree architecture for plants positioned among the three vertical layers (Fig. 1). Generally, climax species displayed the highest values of tree height, crown area and depth, leaf coverage and stem basal diameter, relative to mid-successional and pioneer species (Fig. 1). Standard deviations of tree architectural traits did not significantly differ for species differing in successional status (Table 8). However, in some cases, there were no significant differences between species in adjacent pairs of successional series in their architectural traits (Fig. 1). Interestingly, after standardizing the actual traits with stem diameter, there were significant differences in standardized values of tree height, crown area and depth between species adjacent pairs of successional series (Tables 2, 10). Specifically, standardized values of tree height and crown depth were lower significantly in climax species than in mid-successional and pioneer species (Tables 2, 10). In contrast, standardized values of crown area were statistically greater in climax than in pioneer species (Tables 2, 10).

For both canopy and understory plants, the proportion of clumped leaves was the lowest in climax species, intermediate in mid-successional species, and the highest in pioneer species (Table 3). The proportion of vertical branches was the largest in pioneer species, intermediate in

Table 3 Proportions of branches by orientation and leaf convergence between canopy trees and understory plants when the three stands in each successional stage were combined

Successional stage	Vertical layer	Proportion of branch stretch direction (%)			Proportion of leaf convergence (%)	
		Vertical	Horizontal	Leaned	Clumped	Dispersed
Early	Understory plants (height <4 m)	0.49	0.40	0.11	0.67	0.33
	Canopy trees (height >4 m)	0.43	0.40	0.17	0.75	0.25
Mid	Understory plants (height <4 m)	0.43	0.42	0.15	0.67	0.33
	Canopy and sub-canopy trees (height >4 m)	0.38	0.44	0.18	0.68	0.32
Late	Understory plants (height <4 m)	0.30	0.44	0.26	0.49	0.51
	Canopy and sub-canopy trees (height >4 m)	0.34	0.26	0.39	0.49	0.50

As there were two vertical layers for the early-successional stage, but three layers for the mid- and late-successional stages, the data of the canopy and sub-canopy were combined for the mid- and late-successional stages, to keep consistent vertical patterns across successional stages

mid-successional species, and the lowest in climax species for both canopy trees and understory plants (Table 3). However, the proportion of leaned branches was the greatest in climax species, intermediate in mid-successional species, and the lowest in pioneer species (Table 3). With respect to the proportion of horizontal branches, it showed a contrasting pattern between canopy trees and understory plants across the succession. Specifically, understory plants showed the largest proportion of horizontal branches in climax species, the intermediate in mid-successional species, and the smallest in pioneer species. Instantly, canopy trees displayed the largest proportion of horizontal branches in mid-successional species, intermediate in pioneer species, and the smallest in climax species (Table 3).

Relationships between tree architectural traits and CEI and forest age

Tree height, crown area and depth, leaf coverage, and basal area were positively correlated with CEI in each of three

successional stages (Table 4) and when three successional stages were combined (Fig. 2). Moreover, across successional stages, CEI was positively correlated with each of tree height, crown area and depth, leaf coverage, and stem basal diameter for both canopy trees and understory plants, while for sub-canopy trees CEI was positively correlated with leaf coverage only (Table 5). Two-way ANOVA showed that forest age, CEI and the interaction between forest age and CEI significantly affected tree architectural traits (Table 6).

Discussion

Tree architecture in relation to forest vertical structure

The progressively increased tree height, crown area and depth, stem basal diameter and leaf coverage from understory plants to canopy trees in each of the three successional stages (Fig. 1) provides evidence for the vertical differentiation of tree architecture across successional

Table 4 Linear regression of crown exposure index (CEI) against architectural traits when the three stands in each successional stage were combined

Succession stage	Height				Crown depth				Crown area			
	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p
Early	0.77	0.23	0.42	<0.01	0.38	0.06	0.29	<0.01	1.03	−1.55	0.35	<0.01
Mid	2.23	−2.44	0.48	<0.01	0.99	−0.97	0.35	<0.01	2.80	−4.14	0.27	<0.01
Late	1.68	−1.48	0.31	<0.01	1.15	−1.27	0.23	<0.01	3.72	−5.93	0.20	<0.01

Succession stage	Leaf coverage				Stem basal diameter			
	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p
Early	1.10	1.57	0.38	<0.01	1.33	−1.16	0.34	<0.01
Mid	0.92	2.55	0.27	<0.01	4.64	−6.78	0.43	<0.01
Late	0.73	3.74	0.19	<0.01	4.34	−6.33	0.29	<0.01

Fig. 2 Linear regression of crown exposure index (CEI) against tree height, crown area and depth, leaf coverage, and stem basal diameter in the case of data was combined across three successional series and three successional stages. Each *box plot* indicates the median (*horizontal line*), the first and third quartiles (*box*), the range that excludes outliers (i.e., 1.5 interquartile range; whiskers), and the outliers (*points*) for each architectural trait over five CEI levels
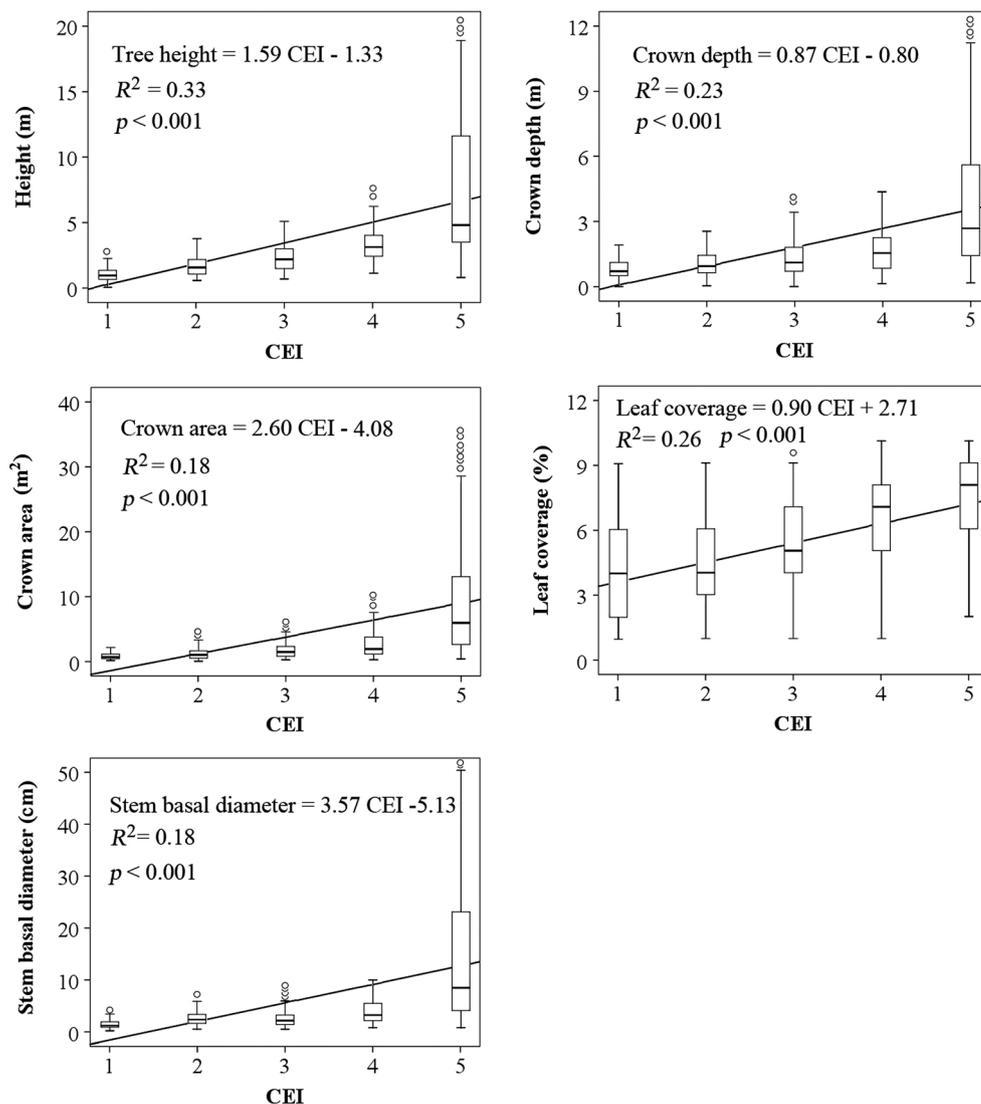
series. It is understandable that tree architecture could be influenced by the vertical position of its crown in a given forest. Spatial arrangement of tree architecture in a forest may be caused by the distribution of light availability among vertical layers (Turner 2001). In this study, it is supported by the significant relationships between CEI and tree height, crown area and depth, leaf coverage, and basal area across successional stages (Table 4). In a given forest, light intensity declines from canopy to understory as incoming radiation are intercepted by forest canopy (Ashton 1958). For intercepting a large amount of light, canopy trees having wider and thicker crowns are more effective as compared to understory plants (Horn 1971; Givnish 1988). However, the deployment patterns of leaves and branches are specific to canopy and understory plants depending on the light condition within a given forest (Poorter et al. 2003, 2008; Clark 2010; Thomas 1996a; Davies and Ashton 1999; Sterck et al. 2001; Wright et al. 2010). In this

study, the proportions of vertical branches and dispersed leaves were greater in understory than in canopy trees in pioneer and mid-successional species, indicating understory plants with a large proportion of dispersed leaves attached on many vertical branches might benefit much more in intercepting light for rapid growth where a forest gap exists (Poorter et al. 2003; Falster and Westoby 2003, 2005).

In contrast, the greater proportion of vertical branches and the lower proportion of horizontal branches in canopy trees than in understory plants in climax forests (Table 3) reflect strong competitions for space among canopy trees in late-successional forests where the canopy becomes closed. When succession proceeds to the late stage, due to congestion of tree crowns, canopy trees are particularly adapted to competition for light, typically through strong apical dominance at the expense of reduced lateral growth (Aarssen 1995; Sterck et al. 2001; Kohyama et al. 2003;

Table 5 Linear regression of crown exposure index (CEI) against architectural traits among three vertical layers when nine plots were combined

Vertical layer	Height				Crown depth				Crown area			
	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p
Understory plants	0.37	1.14	0.19	<0.01	0.15	0.68	0.08	<0.01	0.47	0.20	0.12	<0.01
Sub-canopy trees	0.74	2.19	0.03	<0.01	4.50	0.98	0.01	<0.01	4.53	−10.74	0.16	<0.01
Canopy trees	3.74	−8.00	0.10	<0.01	1.59	−2.44	0.10	<0.01	6.26	−18.01	0.14	<0.01

Vertical layer	Leaf coverage				Stem basal diameter			
	Slope	Intercept	R^2	p	Slope	Intercept	R^2	p
Understory plants	0.64	3.23	0.14	<0.01	0.65	0.82	0.18	<0.01
Sub-canopy trees	0.64	5.14	0.15	<0.01	4.71	−8.92	0.01	<0.01
Canopy trees	1.14	2.24	0.14	<0.01	10.83	−31.97	0.09	<0.01

Poorter et al. 2003; Iida et al. 2011). Instead of producing a large number of horizontal branches, canopy trees may be better served by producing larger proportion of vertical and leaned branches—these may serve well in shading competitors (Falster and Westoby 2003, 2005). Understory plants, on the other hand, may benefit more from having a relatively large proportion of horizontal branches per unit crown size, thus enhancing the capacity to adjust shoot placement in response to changes in light availability (Thomas 1996b; Davies and Ashton 1999; Sterck et al. 2001; Wright et al. 2005; Iida et al. 2011).

The vertical variation in tree height, crown area and depth, and stem basal diameter also depends on plant ontogeny. In order to justify effects of plant ontogeny on tree architecture, we standardized tree height, and crown area and depth by dividing stem basal diameter. Predicatively, among vertical layers, the standardized tree height and crown area and depth were significantly the highest in canopy trees, intermediate in sub-canopy trees, and the lowest in understory plants (Tables 2, 10).

Temporal changes of tree architecture through forest succession

Tree architecture is a set of plant traits that directly or indirectly reflect plants' ability to cope with environmental stress. With forest succession, the number of forest vertical strata increases, thus leading to a gradual decrease of light intensity in the same vertical layer within a forest (Shukla and Ramakrishnan 1986). In this context, to cope with a shaded environment, shade-tolerant climax species are thus characterized by greater crown area, leaf coverage, stem basal diameter, and larger proportions of dispersed leaves and horizontal orientation of branches, than those pioneer species. This is due to that climax species are generally slow growing, and thus have broader crown to place preference on horizontal growth (Givnish 1988; Poorter

et al. 2006). In this study, such temporal patterns of tree architecture changes can be justified further when we corrected the actual traits with stem basal diameter. The result demonstrates that, relative to mid-successional and pioneer species, climax species had greater crown area, and lower tree height and crown depth (Tables 2, 10). It is reasonable that, pioneer plants that are light-demanding species must grow rapidly, and should thus have narrow and deeper tree crown with large proportions of clumped leaves and vertical branches (Poorter et al. 2006). Evidently, this is supported by the positive relationships between CEI and tree height, stem basal diameter, crown area and depth, and leaf coverage among successional species in the same forest vertical layer (Table 5).

In addition to shading stress, successional change of tree architecture might also be affected by forest age. In this study, the significant positive relationship between tree architectural traits and forest age suggests that temporal change of tree architecture was associated with the forest development. This is further supported by the results of the two-way ANOVA. It showed that forest age and CEI interactively influence the tree architecture (Table 6). Indeed, light intensity within a forest decreases inherently with forest age, due to the increasing extent of canopy closure and the increased vertical layering. This thus suggests that change of tree architecture over forest succession is also a result of forest development.

It is important to note that there may have species effects on the pattern of change in tree architecture through forest succession. Variation in tree architecture of recurrent species among successional stages can be used to indicate relationship between tree architecture and light availability, by excluding confounding effects that result from plant phylogenetics. Recurrent species are defined here as species that appear in more than one successional stage. In another study, we examined how the tree architecture varies among recurrent species in different successional

Table 6 Results of two-way ANOVA for variability of tree architectural traits induced by crown exposure index (CEI) and forest age

Factors	df	Height		Crown depth		Crown area		Leaf coverage		Stem basal diameter	
		F	p	F	p	F	p	F	p	F	p
Forest age	2	30.60	<0.001	23.21	<0.001	26.68	<0.001	26.54	<0.001	38.01	<0.001
CEI	4	235.90	<0.001	139.71	<0.001	98.27	<0.001	122.58	<0.001	181.13	<0.001
Forest age × CEI	8	19.31	<0.001	14.02	<0.001	10.10	<0.001	2.07	<0.05	17.52	<0.001

F values and *p* values are presented

stages (Yang et al. 2013). The results showed that tree height, crown area and depth, stem basal diameter and leaf coverage of recurrent species increased gradually through forest succession. There were linear relationships between CEI and tree architectural traits ($p < 0.001$). These combined results demonstrated that light acclimatization, rather than species differences, was one of the main factors driving variations in tree architecture in the studied forests (Yang et al. 2013).

Temporal changes of tree architecture with variations in light conditions over forest succession might be associated with plant adaptive trade-offs between height extension and mechanical stability. For light interception and development reasons, climax canopy trees must grow taller than those pioneer canopy trees. As a result, tree crown should also change in response to vertical growth during forest succession. For example, climax species have greater crown area, leaf coverage, and larger proportions of dispersed leaves and horizontal branches, relative to pioneer and mid-successional species (Fig. 1; Tables 2, 3). This suggests that tree species must follow trade-offs between benefit and cost in biomass allocation, with which trees must modulate its architecture timely to balance the investment in light capture versus the cost in mechanical growth (Sterck et al. 2001; Poorter et al. 2003; King et al. 2005; Selaya et al. 2008; Olson et al. 2009; Anten and Schieving 2010). Specifically, pioneer trees with a relatively rapid growth rate, typically through strong apical dominance, may have a greater potential to take advantage of light availability, and could thus dominate the canopy layer, but it constrains mechanical support by producing relatively low stem wood density, slender shoots, narrow tree crown (Falster and Westoby 2003; Poorter et al. 2003; Price and Enquist 2007) and short leaf life span (Selaya and Anten 2010). Climax tree species, on the other hand, gains a relatively greater potential to produce horizontal shoots opportunistically and consequently form a broad tree crown, at the expense of reduced vertical growth, to take advantage of light patches available through the canopy of larger neighboring species (Rubinstein and Nagao 1976; Olejniczak 2001; Price and Enquist 2007; Selaya et al. 2008).

Temporal patterns of tree architectural changes during forest succession might also be related to life history trade-offs between efficiency and safety in hydraulic transportation. According to the hydraulic limitation hypothesis, the ability of hydraulic transport limits or shapes tree architecture (Ryan and Yoder 1997; Koch et al. 2004; Niklas and Spatz 2004; Woodruff et al. 2004; England and Attiwill 2006; Steppe et al. 2012). Theoretically, with increasing tree height, plants must have relatively large stem conduits to ensure soil water transport to tree crown. However, in this process, negative pressure produced by transpiration pull would increase the tension within stem conduits, thus constraint the enlargement of conduit size. As such, the potential maximum tree height could certainly be limited (Niklas and Spatz 2004; Savage et al. 2010; Steppe et al. 2012). In this hydraulic process, to alleviate constraints of water transport pressure to elevated height, plants must regulate its architecture, such as crown structure, branch orientation, and deployment pattern between branches and leaves, to balance the efficiency and safety in hydraulic transportation. Generally, pioneer species are particularly adapted to competition for water transportation, typically through constrictive crowns, a larger proportion of vertical branches, a lower number of branches and short petioles, because trees with a set of these architectural traits can have great force within stem conduits, by which water could be uplifted to a greater height (Sterck et al. 2001; Kohyama et al. 2003; Poorter et al. 2003; Price and Enquist 2007; Anten and Schieving 2010; Savage et al. 2010; McCulloh et al. 2012). In contrast, climax trees with a wide tree crown and large proportions of dispersed leaves and horizontal branches have limit vertical water transport efficiency, but can obtain stable growth and hence (possibly) future mechanical safety (Kohyama et al. 2003; Poorter et al. 2003; Iida et al. 2011; McCulloh et al. 2011).

In conclusion, tree architecture varies with changes in both forest vertical structure and successional status. The large variability of tree architectural traits in relation to CEI and forest age reflects a strong control of light availability that affects biomass allocation strategies of trees. Our study demonstrated that light induced shift in tree architecture may result in species coexistence through

divergence of vertical space, as well as species replacement through forest succession. Here, we report these interesting patterns and speculate about their underlying mechanisms. Direct testing of the importance of these mechanisms would come from experimental approaches that assess whether or not canopy and pioneer trees representing higher vertical growth have inherently higher efficiencies in light capture than those shaded understory or climax trees, and vice versa (Selaya and Anten 2010).

Author contribution statement Yan ER, Wang XH and Da LJ designed the experiments; Yang XD carried out data analysis; Yang XD, Yan ER and Chang SX wrote the manuscript.

Appendix

See Appendix Tables 7, 8, 9, 10.

Table 7 Results of one-way ANOVA and *t* test for variability of tree architectural traits induced by forest vertical differentiation among three successional series

Site	Succession stage	Height		Crown depth		Crown area		Leaf coverage		Stem basal diameter	
		F	p	F	p	F	p	F	p	F	p
Beilun	Early	43.89	<0.01	28.83	<0.01	27.62	<0.01	7.27	0.01	6.47	0.01
	Mid	734.80	<0.01	607.16	<0.01	131.49	<0.01	44.26	<0.01	607.16	<0.01
	Late	302.51	<0.01	67.10	<0.01	42.55	<0.01	16.99	<0.01	67.10	<0.01
Nanshan	Early	1.08	0.30	18.53	<0.01	20.55	<0.01	1.49	0.22	18.52	<0.01
	Mid	398.01	<0.01	158.37	<0.01	39.71	<0.01	36.38	<0.01	158.37	<0.01
	Late	592.43	<0.01	275.02	<0.01	102.67	<0.01	31.16	<0.01	275.02	<0.01
Tiantong	Early	6.44	0.01	51.73	<0.01	87.45	<0.01	0.55	0.46	51.73	<0.01
	Mid	1126.71	<0.01	819.32	<0.01	82.42	<0.01	28.87	<0.01	819.32	<0.01
	Late	723.83	<0.01	447.81	<0.01	134.21	<0.01	6.08	0.003	447.81	<0.01

F values and *p* values are presented. ANOVA was not conducted to early stage of succession, because sub-canopy trees were not existed in the early succession stage. Hence, *t* test was used to determine differences of tree architectural traits between canopy trees and understory plants

Table 8 Standard deviation (*SD*) of tree architectural traits among different vertical layers along three successional series

Site	Vertical layer	Height			Crown depth			Crown area			Leaf coverage			Stem basal diameter		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Beilun	Understory plants	1.00	0.77	0.89	0.70	0.53	0.59	1.06	1.19	1.63	2.28	2.17	1.1	1.63	1.40	1.41
	Sub-canopy trees	–	1.32	1.22	–	1.20	1.36	–	4.64	13.10	–	0.85	0.83	–	3.52	3.99
	Canopy trees	0.30	2.19	1.46	0.75	2.41	1.44	2.42	11.03	13.2	1.36	0.68	0.51	2.81	6.25	9.53
Nanshan	Understory plants	0.81	0.85	0.75	0.59	0.63	0.60	1.51	1.95	2.00	1.68	1.84	2.07	1.34	1.79	2.33
	Sub-canopy trees	–	1.13	1.05	–	1.13	1.34	–	6.72	8.94	–	1.31	0.95	–	4.21	4.29
	Canopy trees	2.81	2.36	3.16	0.95	3.15	3.41	5.78	13.94	12.49	1.84	1.02	0.57	6.95	9.84	14.85
Tiantong	Understory plants	0.79	0.83	0.87	0.62	0.62	0.63	0.76	0.93	1.03	2.02	1.83	2.05	1.33	0.10	1.85
	Sub-canopy trees	–	1.38	1.18	–	1.02	1.78	–	1.83	6.93	–	1.03	2.43	–	6.08	14.51
	Canopy trees	0.47	2.51	4.49	1.18	2.73	4.26	3.32	5.37	22.36	1.87	2.0	1.57	3.76	5.17	12.10

"–" indicates no values because sub-canopy trees were not existed in the early succession stage

Trees

Table 9 Results of one-way ANOVA and t test for variability of tree architectural traits induced by forest succession for species differing in vertical layers in three sites

Site	Vertical layer	Height F	Height p	Crown depth F	Crown depth p	Crown area F	Crown area p	Leaf coverage F	Leaf coverage p	Stem basal diameter F	Stem basal diameter p
Beilun	Understory plants	9.63	<0.05	1.71	0.18	3.10	0.05	7.51	<0.05	2.12	0.12
	Sub-canopy trees	26.28	<0.05	1.91	0.16	16.45	<0.05	0.43	0.65	43.96	<0.05
	Canopy trees	152.37	<0.05	23.87	<0.05	40.17	<0.05	4.82	<0.05	66.19	<0.05
Nanshan	Understory plants	1.79	0.17	3.76	<0.05	8.02	<0.05	32.22	<0.05	19.24	<0.05
	Sub-canopy trees	2.61	0.08	3.02	0.06	3.47	<0.05	20.05	<0.05	20.02	<0.05
	Canopy trees	41.01	<0.05	32.48	<0.05	9.74	<0.05	18.33	<0.05	28.93	<0.05
Tiantong	Understory plants	2.78	0.06	1.02	0.36	7.79	<0.05	11.18	<0.05	3.88	<0.05
	Sub-canopy trees	4.17	<0.05	0.93	0.41	3.24	<0.05	4.83	<0.05	7.80	<0.05
	Canopy trees	88.27	<0.05	72.36	<0.05	29.43	<0.05	1.73	0.19	58.94	<0.05

F values and p values are presented. ANOVA was not conducted to sub-canopy trees, because sub-canopy trees were not existed in the early succession stage. Hence, t test was used to determine differences of tree architectural traits between mid- and late-successional stages

Table 10 Results of one-way ANOVA and t test for variability of standardized architectural traits (height, crown area and depth)

Site	Succession stage	Standardized height F	p	Standardized depth F	p	Standardized crown area F	p	Site	Vertical layer	Standardized height F	p	Standardized depth F	p	Standardized crown area F	p
Beilun	Early	0.15	0.70	3.42	0.05	3.35	0.07	Beilun	Understory plants	9.72	<0.001	0.43	0.65	5.47	0.005
	Mid	27.11	<0.001	10.33	<0.001	4.89	0.009		Sub-canopy trees	1.04	0.32	1.87	0.19	21.55	<0.001
	Late	8.81	0.001	11.85	<0.001	11.96	<0.001		Canopy trees	12.56	<0.001	7.08	0.002	9.41	<0.001
Nanshan	Early	3.00	0.08	0.03	0.42	0.08	0.78	Nanshan	Understory plants	19.5	<0.001	5.22	0.00	3.81	0.02
	Mid	39.99	<0.001	7.82	0.001	0.68	0.51		Sub-canopy trees	1.64	0.21	1.56	0.23	1.82	0.19
	Late	5.76	0.004	3.83	0.05	10.20	<0.001		Canopy trees	17.41	<0.001	10.76	<0.001	4.31	0.02
Tiantong	Early	0.65	0.42	0.22	0.64	0.51	0.48	Tiantong	Understory plants	17.5	<0.001	0.37	0.69	8.63	<0.001
	Mid	16.49	<0.001	26.84	<0.001	12.20	<0.001		Sub-canopy trees	3.94	0.09	7.81	0.03	5.68	0.05
	Late	21.57	<0.001	6.19	0.002	5.86	0.003		Canopy trees	7.22	0.001	7.24	0.001	16.36	<0.001

Left parts showed the effects of forest succession. Right parts indicated the effects of forest vertical structure. F values and p values are presented. For sub-canopy species and pioneer species, t test was used

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