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# Effects of Close-to-Nature Conversion on *Pinus massoniana* Plantations at Different Stand Developmental Stages

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## Abstract

Close-to-nature (CTN) forestry integrates multiple forest functions and emphasizes forest ecosystem conservation. Within this framework, forests are typically maintained as uneven-aged mixed stands with multiple vertical layers and are managed following the defined stand developmental stages, that is, the various phases of forest succession. This study aimed to evaluate the long-term effects of CTN management on the stand structure and growth of *Pinus massoniana* using data from 28 plots managed with the CTN approach and 58 plots of traditional monocultures in southern China. A comparison was performed between three vertical layers across five developmental stages of the CTN stands and the monoculture stands. The results showed that the tree species diversity improved in the CTN stands, with a decrease in the importance value of *P. massoniana*. The conversion did not change the diameter growth averaged over all species, but it did promote the radial growth of *P. massoniana* in the canopy layer. The stand growth, in terms of the basal area and the volume of the canopy trees, declined in the CTN stands during the final two stages, as harvesting took place, and the volume growth of *P. massoniana* also decreased in the CTN stands. However, the conversion seemed to improve the stand productivity of the subcanopy and regeneration layers, where higher relative dominance values of all species were observed, especially during the later stages. Overall, the CTN conversion tended to benefit the stand structure and improve the single tree growth of *P. massoniana* rather than the total stand growth.

## Keywords

silviculture, close-to-nature forestry, plantation, *Pinus massoniana*, mixed forest, monoculture, stand succession

## Introduction

With the increasing global demand for forest products, tropical natural forests have been placed under considerable pressure, and large areas of these forests are being degraded (Lamb, Erskine, & Parrotta, 2005). Consequently, the installation of new plantations cannot be avoided (Arbez, 2001). Traditionally, tropical plantations were mostly even-aged, mono-specific, or species-poor (Puettmann et al., 2015) and managed using the clearcutting system (Mason et al., 2003). These plantations only focused on wood products such as timber or pulp, based on the notion that homogenous products are cheaper to produce and manipulate (Puettmann et al., 2015). Such intensive timber plantations, over a long period of time and large areas, cause ecological problems in the tropics (Arbez, 2001), such as the loss of biological

diversity (Lamb et al., 2005) and forest resilience toward pest outbreaks (Nair, 2001). The identification of scientifically based improvements in tropical plantation forestry has become an urgent concern (Arbez, 2001).

A response to the even-aged, uniform, monoculture plantations, which were viewed as far-to-nature (O'hara, 2016), is so-called close-to-nature (CTN) or

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ecologically sound forestry (Bieling, 2004); many concepts and techniques of CTN forestry are designed based on conservation, and CTN forestry has become one of the approaches expected to meet the requirements of ecological conservation in subtropical and tropical forests (Meng, 2010).

CTN forestry is a management system that simultaneously integrates the production function and ecological service function of a forest at relatively small spatial scales (e.g., at the stand level; Bauhus, Puettmann, & Kühne, 2013). However, it is more defined by a set of general principles than a rigid, commonly agreed definition (Bauhus et al., 2013; Brang et al., 2014), although these principles can be weighted differently for different usages. These principles are as follows: (a) promoting natural and site-adapted tree species, (b) avoiding clear cutting, (c) developing ecologically stable forests (e.g., mixed-forest), (d) relying on forest natural processes and natural regeneration, (e) focusing on individual tree development, and (f) promoting mixed, uneven-aged and multilayered forests to maintain a high structural diversity (Bauhus et al., 2013; Brang et al., 2014). Under the principle of relying on natural processes, forests should be managed following their natural processes of succession (Bauhus et al., 2013; Duncker et al., 2012; Schütz, 2011) to take advantage of the natural processes (e.g., self-thinning). The phases of forest succession are defined as stand developmental stages, which are key to CTN management with respect to, for example, arranging silvicultural operations along multiple management cycles (Duncker et al., 2012) and evaluating the stand growth over time.

As the location of the world's most rapid expansion of forest plantations in recent decades, China has long been struggling with negative effects resulting from its enthusiasm for even-aged monocultures; these effects include forest instability, soil acidification, low stand yield, and poor timber quality (Jiang et al., 2015; Stone, 2009). Under these pressures, China launched its project of transferring the traditional monoculture management system to CTN forestry at the beginning of the 2000s in the subtropics. This conversion was started in monocultures of *Pinus massoniana*, a major coniferous species that is economically important in the subtropical to tropical regions of southeastern Asia, aiming to enhance the ecological status of the *P. massoniana* forests while maintaining or even improving the timber production to satisfy economic needs.

One cannot draw any conclusion about the fulfilment of these goals before an examination of the long-term effects of the conversion. However, the local empirical data accumulated so far (after a period of nearly a decade, at the longest) are not sufficient to represent long-term effects, as the effects are likely to shift over different stand developmental stages, the growth ratios

of different species may change considerably over time, and various biotic and physical factors may influence the successional process (Drössler et al., 2015).

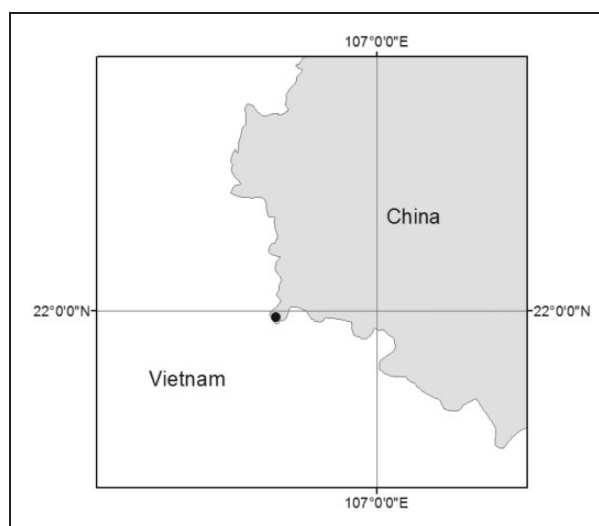
To enable the analysis of long-term effects, this study used a space-for-time substitution method to select 28 mixed stands comprising *P. massoniana* and various other species and 56 stands with an exclusive dominance of *P. massoniana*, which resemble forests managed under the CTN approach and traditional monoculture approach, respectively, along defined stand developmental stages. The long-term dynamics of forest growth and structure, in terms of the stand diversity, diameter at breast height (DBH) and DBH increment, importance value (IV), basal area (BA) and BA increment (BAI), relative dominance, and volume (V), were compared between these two types of stands in order to answer two questions that address the goals of the CTN conversion of *P. massoniana* plantations in subtropical China:

1. Will the CTN conversion improve the ecological status of the forests?
2. Will the CTN plantations achieve greater timber productivity and therefore be more economically successful than monocultures?

## Methods

### Study Area and the Local CTN Conversion Trial

The study area, at the Experimental Centre of Tropical Forestry (ECTF), Chinese Academy of Forestry, is located in the subtropics of southwestern China ( $21^{\circ}57'47''$ – $22^{\circ}19'27''$ N,  $106^{\circ}39'50''$ – $106^{\circ}59'30''$ E; Figure 1).



**Figure 1.** Location of the administration of the Experimental Centre of Tropical Forestry (ECTF), Chinese Academy of Forestry.

The annual rainfall in this region is 1,200 to 1,500 mm, with relative humidity of 80% to 84%. The mean annual temperature ranges between 20.5°C and 21.7°C, and the mean temperature of January (the coldest month) and July (the hottest month) is 11.4 to 13.5°C and 25.7 to 27.7°C, respectively. The historical maximum temperature is 40.3°C and the minimum temperature is -1.5°C. Topographically, the area is featured by low mountains, with an altitude of 430 to 680 m above sea level. The local soil is classified as red soil according to the Chinese soil classification, with a pH value of 4.8 to 5.5 (He et al., 2013).

Large areas of *P. massoniana* plantations, mainly monocultures, were installed with an initial density of 2,500 stems per hectare (ha) after the establishment of the ECTF in 1979, accounting for 63% of the total area of forested land, among which 90% was a monoculture (Lu et al., 2013).

The local CTN conversion trial was initiated at the beginning of the 2000s, with conversion strategies gradually established and refined over time. The strategies could differ among stands, depending on the stand starting status and the conversion objective, defined by the forest development type (Larsen, 2012), of a given stand. Therefore, there was not a prescribed common direction (e.g., stand age or height, thinning intensity of *P. massoniana*, mixing density) of implementing conversions. In general, the conversion strategies included three types: (a) using various combinations of *P. massoniana* and other species in the afforestation process after clear-cutting; for example, *P. massoniana* and *Erythrophleum fordii*, a local hardwood species, were simultaneously installed at a mixing density of 3:2 on the clearcutting site of *P. massoniana*, pursuing high-quality and high-value timber output among other ecological benefits; (b) replanting different tree species in the *P. massoniana* stands after thinning or partial harvesting, in which case the pine layers were usually older than 10 years (the canopy closure age) and could be older than 31 years (the harvesting age) when the replanting took place; for instance, *Mytilaria laevis*, a fast-growing species with a low timber value, was replanted to the understory of *P. massoniana* after thinning (with accumulated thinning intensity of approx. 30%–50%, varying among stands) to improve the site condition while promoting the growth of *P. massoniana*; and (c) the few mixed stands that exhibited CTN features (e.g., uneven-aged and multi-layered) prior to the conversion were also included in the system of CTN management; for instance, some *P. massoniana*–*Castanopsis* spp. mixed stands were developed from the late 1990s, among which the present density percentage of *Castanopsis* spp. was 75% to 86%. For Types (b) and (c), the time and manner of the admixture (e.g., thinning intensity of *P. massoniana* and initial mixing density) were usually poorly recorded, and

therefore, the stand current mixing proportion was used when needed.

### Data Extraction and Assignment of the Developmental Stages

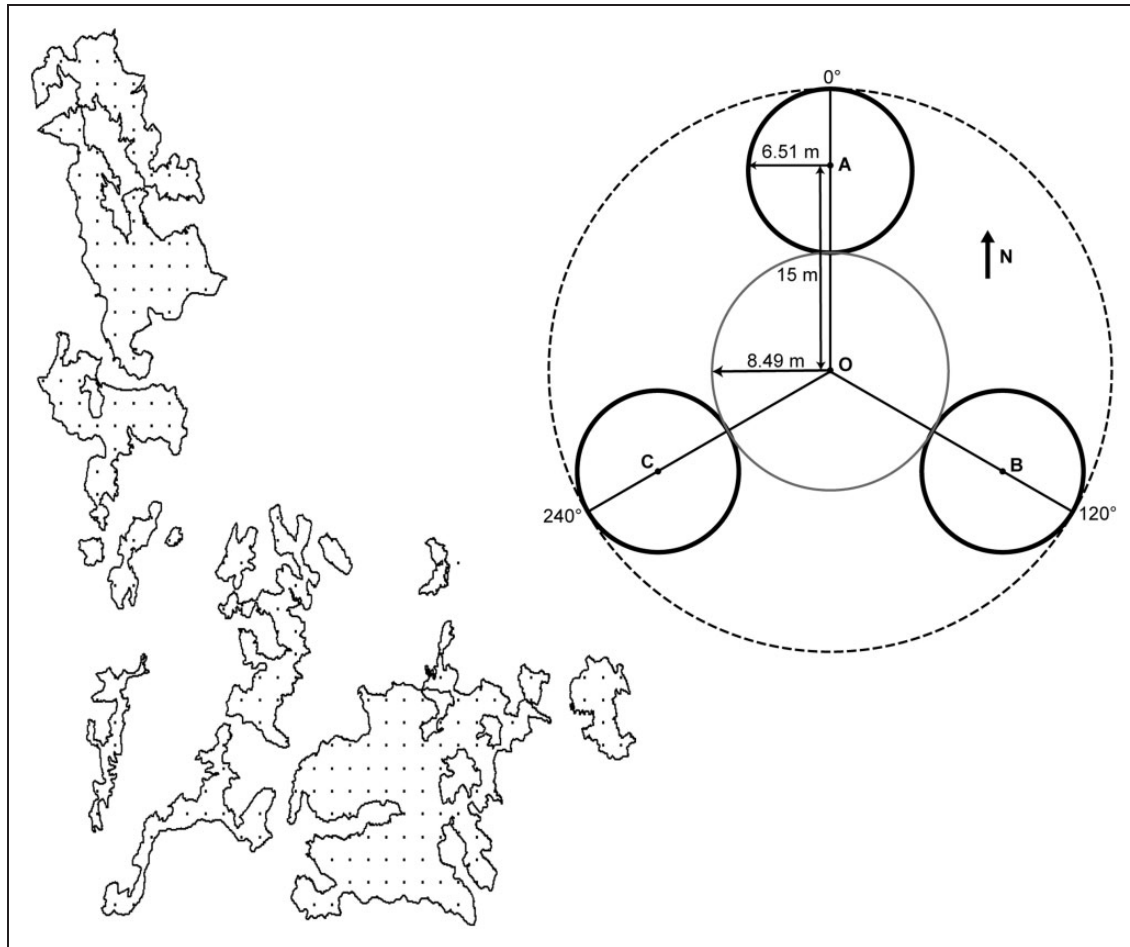
This study used space-for-time substitution to enable comparisons over the full process of stand development. This method utilizes contemporary spatial patterns to model temporal processes in order to project changes through time (Wogan & Wang, 2017). It is frequently used when analyzing changes in species composition, structure, and growth in forests over long time periods (Lorimer & Halpin, 2014), as direct observations on forest successional dynamics are extremely time-consuming. In this study, several currently coexisting stands were selected based on certain criteria to represent different stand development phases that only appear successively during forest succession, and the stands were compared to infer the long-term effects of the CTN conversion.

The inventory data used for the space-for-time substitution were compiled from 28 plots representing CTN stands and 58 plots representing traditional monoculture stands (Table 1, Online Appendix 1). The 28 CTN stands were mixed stands of *P. massoniana* and additional tree species, with the additional species accounting for 30% to 50% by BA percentage and 25% to 85% by density percentage; and the 58 monoculture stands were exclusively dominated by *P. massoniana* (accounting for 85%–100% by BA percentage; Table 1, Online Appendix 1). These plots belonged to 238 permanent monitoring plots systematically distributed across the ECTF, based on a grid of 1 km × 1 km (Figure 2). The 238 plots were used as the sample pool because the *P. massoniana* stands they included were diverse with respect to the stand development stages and were, therefore, most suitable choices for the space-for-time substitution among the inventory designs of the ECTF.

The extraction of the 28 CTN stands and 58 monoculture stands used for the analysis followed a two-step procedure. First, the respective developmental stages of all the mixed plots of *P. massoniana* in the 238 plots ( $n = 42$  plots) were determined following a classification proposed for the ECTF by Lu et al. (2014). This classification divided the successional process under the CTN regime at the ECTF into five developmental stages, that is, the forest establishment stage (Stage I), rapid height growth stage (Stage II), stem quality differentiation stage (Stage III), understory reinitiation stage (Stage IV), and complex growth stage (Stage V) (Lu et al., 2014; Online Appendix 2). In the field, the developmental stages of all the mixed plots ( $n = 42$ ) were separately assessed by three experienced technicians following the baseline proposed by Lu et al. (2014; Online Appendix 2). The assessments for each plot were cross-checked, and only the plots with

**Table 1.** Number of Sample Plots and Overview of the Canopy Layer Age, Stand Density, Stand Basal Area (BA), Stand Volume, Species Richness, Species Composition (by Basal Area Percentage), Mean Diameter at Breast Height (DBH), Tree Height for the Close-to-Nature Stands (CTNS), and the Monoculture Stands (MS) at Five Developmental Stages.

Development stage	Stand type	No. of plots	Canopy layer mean age (age range)	Mean stand density				Mean stand volume ( $m^3 ha^{-1}$ )	Mean specie richness	Species composition	By relative BA (%)	By relative density (%)	Mean DBH (cm)	Mean height (m)
				<i>P. massoniana</i> density (stem $ha^{-1}$ )	Mean stand BA ( $m^2 ha^{-1}$ )	Mean stand volume ( $m^3 ha^{-1}$ )	Mean specie richness							
I	CTNS	5	5 ± 2 (4–8)	653 ± 487 (405 ± 286)	2.50 ± 2.20	11.00 ± 9.32	3 ± 1	<i>P. massoniana</i>	67 ± 7	63 ± 8	6.8 ± 1.2	5.5 ± 1.3		
	MS	8	6 ± 2 (3–8)	1,193 ± 576 (1,013 ± 475)	4.51 ± 3.10	15.21 ± 11.26	2 ± 1	<i>P. massoniana</i>	96 ± 5	94 ± 7	7.2 ± 1.0	7.0 ± 2.9		
II	CTNS	3	10 ± 2 (9–12)	1,083 ± 255 (558 ± 58)	8.78 ± 3.64	42.26 ± 20.02	2 ± 1	<i>P. massoniana</i>	62 ± 10	52 ± 7	7.3 ± 1.2	6.6 ± 0.6		
	MS	12	11 ± 1 (9–12)	1,126 ± 281 (1,028 ± 250)	14.13 ± 5.37	66.13 ± 29.71	3 ± 2	<i>P. massoniana</i>	96 ± 5	88 ± 13	12.2 ± 1.9	8.2 ± 1.3		
III	CTNS	4	25 ± 3 (21–28)	1,038 ± 461 (419 ± 213)	19.57 ± 8.67	144.04 ± 69.28	7 ± 4	<i>P. massoniana</i>	64 ± 8	41 ± 8	8.9 ± 3.6	8.7 ± 2.9		
	MS	16	22 ± 2 (21–26)	817 ± 322 (691 ± 381)	20.12 ± 9.70	132.77 ± 66.30	3 ± 2	<i>P. massoniana</i>	96 ± 5	83 ± 19	10.2 ± 3.0	10.0 ± 3.7		
IV	CTNS	7	32 ± 2 (29–35)	1,060 ± 270 (479 ± 129)	25.55 ± 7.65	185.06 ± 61.94	6 ± 4	<i>P. massoniana</i>	66 ± 4	47 ± 13	7.8 ± 2.3	7.5 ± 1.5		
	MS	13	31 ± 2 (30–35)	865 ± 232 (646 ± 129)	27.19 ± 7.27	199.10 ± 63.66	3 ± 2	<i>P. massoniana</i>	96 ± 3	78 ± 18	23.0 ± 2.5	16.0 ± 3.5		
V	CTNS	9	44 ± 5 (36–49)	792 ± 210 (261 ± 129)	32.57 ± 11.69	277.90 ± 124.90	6 ± 4	<i>P. massoniana</i>	66 ± 4	33 ± 16	10.5 ± 6.5	9.5 ± 3.2		
	MS	9	43 ± 4 (38–47)	739 ± 176 (478 ± 128)	35.03 ± 13.32	375.19 ± 173.17	5 ± 3	<i>P. massoniana</i>	95 ± 4	68 ± 24	23.0 ± 2.9	15.8 ± 1.9		
									5 ± 4	32 ± 24	7.9 ± 2.1	7.8 ± 1.2		
									5 ± 4	32 ± 24	34.3 ± 5.7	20.9 ± 3.5		
									5 ± 4	32 ± 24	12.9 ± 3.8	10.7 ± 3.5		
									5 ± 4	32 ± 24	28.9 ± 6.6	21.0 ± 3.8		
									5 ± 4	32 ± 24	9.3 ± 2.3	8.6 ± 1.6		



**Figure 2.** Distribution of the 238 permanent monitoring plots (dots) at the Experimental Centre of Tropical Forestry and the inventory design of each plot (circle,  $R = 21.51$  m, broken line.). A subplot (circle O,  $R = 8.49$  m, thin solid line) was established in the center of the plot to investigate soil conditions and understory litter; three subplots (circles A, B and C,  $R = 6.51$  m for each, thick solid line) were established with their centers positioned 15 m from the plot center at angles of  $0^\circ$  (true north),  $120^\circ$  and  $240^\circ$ , respectively, to examine the vegetation.

the same results were retained. Then, the canopy layer ages of the retained plots were determined by their management records. The plots assigned to different developmental stages but with the same canopy layer age were eliminated from further analyses. Thus, 28 of the 42 plots were successfully arranged into the five developmental stages and were termed CTN stands. Then, 58 monoculture plots with a canopy layer age belonging to one of the five age ranges were extracted and assigned to their respective stages; these plots were termed monoculture stands.

These plots were established in 2011 and were investigated every 2 years. Each plot consisted of three circular subplots (subplot A, B, and C in Figure 2). Each subplot had a radius of 6.51 m, and together, these subplots represented an investigation area of  $400 \text{ m}^2$ . In each subplot, tree species, DBH, and tree height were recorded for each individual. Tree height was measured using an optical

height meter (SUUNTO PM-5/1520 P, Finland) in 2011 and was only visually assessed in the subsequent inventories. Within each subplot, recruitments and shrubs were examined in a  $4 \text{ m} \times 4 \text{ m}$  square. The plot soil condition and undergrowth litter were investigated in a separate subplot located in the center of each plot (subplot O in Figure 2). The data used in this study were from 2011 and 2015. This study focused only on trees with  $\text{DBH} \geq 5 \text{ cm}$ ; individuals with  $\text{DBH} < 5 \text{ cm}$  were excluded from further analyses.

Over the selected 58 monoculture stands, *P. massoniana* accounted for 85% to 100% of the stand total BA (in 2011; Table 1, Online Appendix 1). Over the selected 28 CTN stands, 20 species, in addition to *P. massoniana*, were presented with a BA percentage of 5% to 50%, among which, nine species were installed artificially, with a density of 38 to  $675 \text{ stems ha}^{-1}$  (7%–48% of the total stand density), as the high value (timber value)

**Table 2.** The Nine Artificially Admixed Species, the Number of Plots in which They Were Recorded, the Admixing Proportion by Basal Area (BA) Percentage and Density Percentage, and the Admixing Density.

	Species	No. of plots	BA percentage	Density percentage	Density (stem ha <sup>-1</sup> )
1	<i>Castanopsis hystrix</i>	6	19–41	19–76	100–650
2	<i>Cunninghamia lanceolata</i>	6	11–50	20–42	100–675
3	<i>Acacia confusa</i>	2	10–30	23–46	325/450
4	<i>Castanopsis fabri</i>	2	7–11	21–26	225/250
5	<i>Michelia macclurei</i>	2	30–41	14–45	125/475
6	<i>Erythrophloeum fordii</i>	1	30	40	600
7	<i>Mytilaria laoensis</i>	1	30	48	675
8	<i>Eucalyptus urophylla</i>	1	14	20	275
9	<i>Dalbergia odorifera</i>	1	5	7	38

species (Table 2). The manner and time of the species mixture (e.g., thinning intensity of the original *P. massoniana* monoculture) were poorly recorded, especially for the older stands (stands belonging to developmental Stages III to V; Online Appendix 1). The other 11 species were regenerated naturally, because they were low in market value and not of traditional management interest.

### Division of the Stand Vertical Layers

The stands were analyzed in three vertical layers to address the difference of stand vertical structure between the CTN stands and the monocultures, as CTN forestry features a multilayered structure. Based on the tree height measurements in the year 2011, Layer A included trees with a height lower than 7.8 m, representing the regeneration layer; Layer B included trees with a height ranging from 7.8 m to 15.6 m, representing the subcanopy layer; and Layer C included trees with a height larger than 15.6 m, representing the canopy layer. The layer subdivision was based on a study conducted by Jiang et al. (2015) in which the dominant height (15.6 m) was calculated from the tree height inventory data of the 238 plots mentioned earlier by averaging the heights of the tallest 50 to 100 trees per hectare, and then the stand layers were divided by heights of 7.8 m and 15.6 m based on International Union of Forest Research Organizations criteria (Jiang et al., 2015).

### Data Analyses

The following parameters were calculated and compared between the three layers and five developmental stages of the CTN stands and the monoculture stands: stand diversity, IV of *P. massoniana*, mean DBH and DBH increment of all tree species and only *P. massoniana*, stand BA and BAI of all species, relative dominance ( $R_{do}$ ) of all species, and stand volume (V) of all species and only

*P. massoniana*. The diversity index, IV, DBH, BA,  $R_{do}$ , and V parameters were calculated with data from 2011, and the DBH increment and BAI parameters were calculated with data from 2011 to 2015 (4-year interval).

**Stand diversity.** Species diversity takes into account both species richness (the number of species present) and species evenness (the relative abundance of each species). The indices of tree species diversity for plots belonging to the same developmental stage were averaged to derive the stage-wise stand diversity of the CTN stands and the monoculture stands. The diversity of each plot was calculated using the Shannon–Wiener index ( $H'$ ), as follows

$$H' = \ln N - \frac{1}{N} \sum_{i=1}^m n_i \ln n_i$$

where  $n_i$  represents the stems of tree species  $i$  within a plot,  $m$  represents the total number of tree species, and  $N$  represents the total number of stems. The calculation was performed in R using the spaa package (Zhang & Ma, 2014). The diversity indices for different stages were compared between the CTN stands and monoculture stands.

**IV of *P. massoniana*.** The IV was calculated as the average of the relative density ( $R_{de}$ ) and relative dominance ( $R_{do}$ ; Cottam & Curtis, 1956; Zhang et al., 2007). In each plot, the  $R_{de}$  of *P. massoniana* in a certain layer was calculated as the number of *P. massoniana* stems in that layer divided by the total number of stems within the plot, and the  $R_{do}$  was calculated as the total BA of *P. massoniana* in that layer divided by the total plot BA. Then, the average IV of *P. massoniana* in each layer at each developmental stage was calculated as follows

$$IV_p^q = \frac{\sum_{i=1}^n IV_i^q}{n}$$

where  $IV_p^q$  represents the average IV in Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ ),  $IV_i^q$  represents the IV of *P. massoniana* in Layer  $q$  of Plot  $i$ , and  $n$  represents the number of plots belonging to Stage  $p$  and representing Layer  $q$ . The IVs for different layers and stages were compared between the CTN stands and monoculture stands.

**Mean DBH of all species and of only *P. massoniana*.** In each plot, the mean DBH (cm) of all tree species was calculated for each layer. Then, the mean values belonging to the same layer and the same developmental stage were further averaged to derive the mean DBH growth for each layer at each stage. The mean DBH growth of *P. massoniana* for each layer at each stage was calculated following the same procedure. The DBH growth of all species and of *P. massoniana* was compared between the CTN stands and monoculture stands.

**Annual DBH increment of all species and of only *P. massoniana*.** The mean DBH increment (cm stem<sup>-1</sup> year<sup>-1</sup>) of all species was calculated for each layer at each stage using inventory data from 2011 to 2015 (4-year interval) as follows

$$DBHI_p^q = \frac{\sum_{j=1}^n \sum_{i=1}^m (DBH_{ij}^t - DBH_{ij}^0)}{t \cdot m \cdot n}$$

where  $DBHI_p^q$  represents the annual DBH increment averaged over Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ ),  $DBH_{ij}^t$  represents the DBH (cm) of a single tree  $i$  in Plot  $j$  in 2015,  $DBH_{ij}^0$  represents the DBH of the same tree (tree  $i$ ) in 2011,  $m$  represents the stem number of Layer  $q$  in Plot  $j$ ,  $n$  represents the plot number belonging to Stage  $p$  and representing a Layer  $q$ , and  $t$  represents the time interval (years) between the two inventories ( $t = 4$ ). The mean DBH increment of *P. massoniana* for each layer at each stage was calculated following the same procedure. The increment values were compared between the CTN stands and monoculture stands.

**Stand BA and BAI of all species.** The BA growth (m<sup>2</sup> ha<sup>-1</sup>) of all species in each layer at each stage was calculated as follows

$$BA_p^q = \frac{25\pi \sum_{j=1}^n \left( \sum_{i=1}^m DBH_{ij}^2 \right)}{1000 \cdot n}$$

where  $BA_p^q$  represents the average BA per unit area (ha) of Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ ),  $DBH_{ij}$  represents the DBH (cm) of a single tree  $i$  in Layer  $q$  of Plot  $j$ ,  $m$  represents the stem number in Layer  $q$  of Plot  $j$ , and  $n$  represents the number of plots

belonging to Stage  $p$  and representing Layer  $q$ . The plot-level BA (400 m<sup>2</sup>) was multiplied by 25 to scale to the hectare level (10,000 m<sup>2</sup>). The BA growth of different layers and stages was compared between the CTN stands and monoculture stands.

The annual BAI (m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) of all species was calculated for each layer at each stage using inventory data from 2011 to 2015 (4-year interval) as follows

$$BAI_p^q = \frac{BA_p^{t+1} - BA_p^t}{t}$$

where  $BAI_p^q$  represents the average BAI per unit area (ha) over Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ ),  $BA_p^{t+1}$  represents the average BA per ha of Layer  $q$  at Stage  $p$  in 2015,  $BA_p^t$  represents the average BA per ha of Layer  $q$  at Stage  $p$  in 2011, and  $t$  represents the time interval (years) between the two inventories ( $t = 4$ ). The BAI values were compared between the CTN stands and monoculture stands.

**Relative dominance ( $R_{do}$ ) of all species.** The  $R_{do}$  was calculated as the relative BA of each layer to the stand total BA at each stage, to reflect the relative BA growth dynamics over different layers and stages. The average  $R_{do}$  for each layer at each stage was calculated as follows

$$R_{do}p^q = \frac{\sum_{j=1}^n \left( \sum_{i=1}^m DBH_{ij}^2 / \sum_{i=1}^{m'} DBH_{ij}^2 \right)}{n}$$

where  $R_{do}p^q$  represents the mean  $R_{do}$  for Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ ),  $DBH_{ij}$  represents the DBH (cm) of a single tree  $i$  in Layer  $q$  of Plot  $j$ ,  $m$  represents the stem number of Layer  $q$  in Plot  $j$ ,  $m'$  represents the total stem number in Plot  $j$ , and  $n$  represents the number of plots belonging to Stage  $p$  and representing a Layer  $q$ . The  $R_{do}$  values were compared between the CTN stands and monoculture stands.

**Stand volume growth of all species and of only *P. massoniana*.** The volume growth (m<sup>3</sup> ha<sup>-1</sup>) for each layer at each developmental stage was calculated as follows

$$V_p^q = \frac{25\pi \sum_{j=1}^n \left( \sum_{i=1}^m V_{ij} \right)}{4000 \cdot n}$$

where  $V_p^q$  represents the average stand volume per unit area (ha) of Layer  $q$  ( $q = A, B, C$ ) at Stage  $p$  ( $p = I, II, \dots, V$ );  $V_{ij}$  represents the volume of a single tree  $i$  in Layer  $q$  of Plot  $j$ ,  $m$  represents the stem number in Layer  $q$  of Plot  $j$ , and  $n$  represents the number of plots belonging to Stage  $p$  and representing Layer  $q$ . The volume growth at a plot level (400 m<sup>2</sup>) was multiplied by 25 to scale to the hectare



level.  $V_{ij}$  was calculated using various single-tree binary volume equations for different tree species, provided by the ECTF

$$V = 0.714265437 \times 10^{-4} \times D^{1.867010} H^{0.9014632} \quad (P. \textit{massoniana})$$

$$V = 0.65671 \times 10^{-4} \times D^{1.769412} H^{1.069769} \quad (\textit{Cunninghamia lanceolata})$$

$$V = 0.034785 - 6.75245 \times 10^{-3} D + 2.73652 \times 10^{-4} D^2 + 5.02044 \times 10^{-4} DH + 1.54609 \times 10^{-5} D^2 H - 3.35291 \times 10^{-3} H \quad (\textit{Eucalyptus urophylla})$$

$$V = 0.667054 \times 10^{-4} \times D^{1.84795450} H^{0.96657509}$$

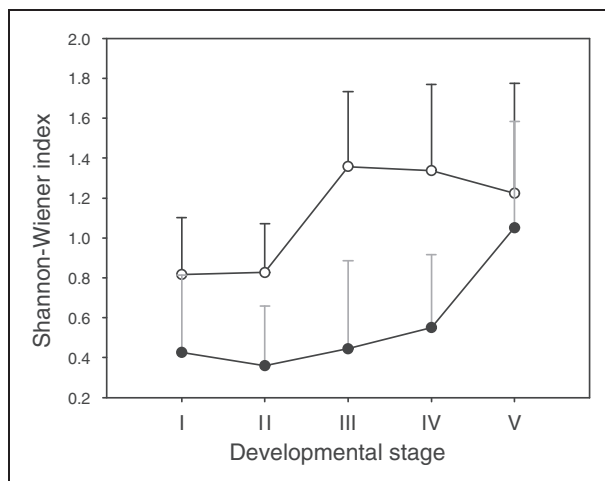
(other broadleaved species)

where  $V$ ,  $D$ , and  $H$  represent the single-tree volume ( $\text{m}^3$ ), DBH (cm), and height (m), respectively. The volumes growth of different layers and stages was compared between the CTN stands and monoculture stands.

## Results

### Tree Species Diversity and IV of *P. massoniana*

The stand diversity indices were compared between the five developmental stages of the various stands (Figure 3). In the CTN stands, the indices ranged between 0.816 (Stage I) and 1.358 (Stage III) over time; these indices were higher than their respective values in the monoculture stands, and the diversity decreased slightly over



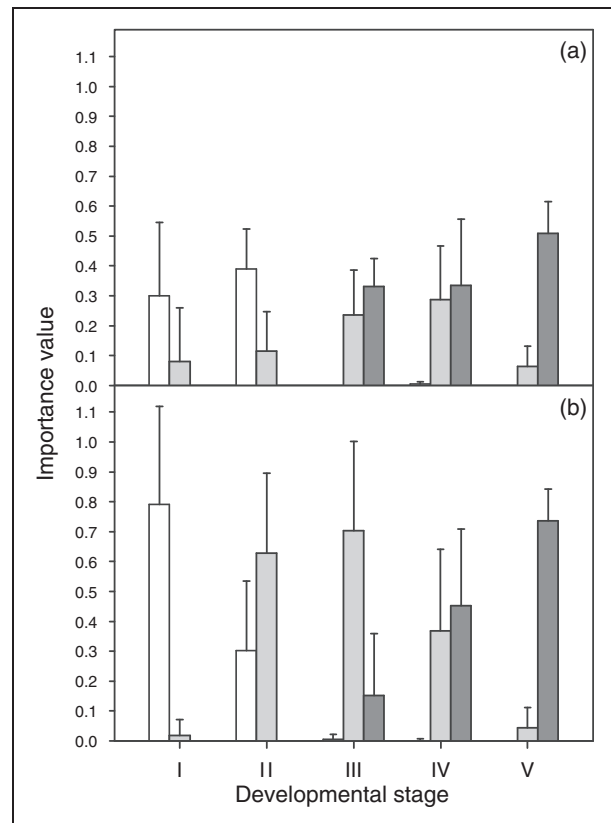
**Figure 3.** Comparison of tree species diversity in the close-to-nature stands (open circles) and the monoculture stands (filled circles) during five developmental stages based on the Shannon–Wiener index (mean  $\pm$  SD).

Stages IV and V. In the monoculture stands, the diversity indices ranged between 0.360 (Stage II) and 1.051 (Stage V), and increased at Stage V.

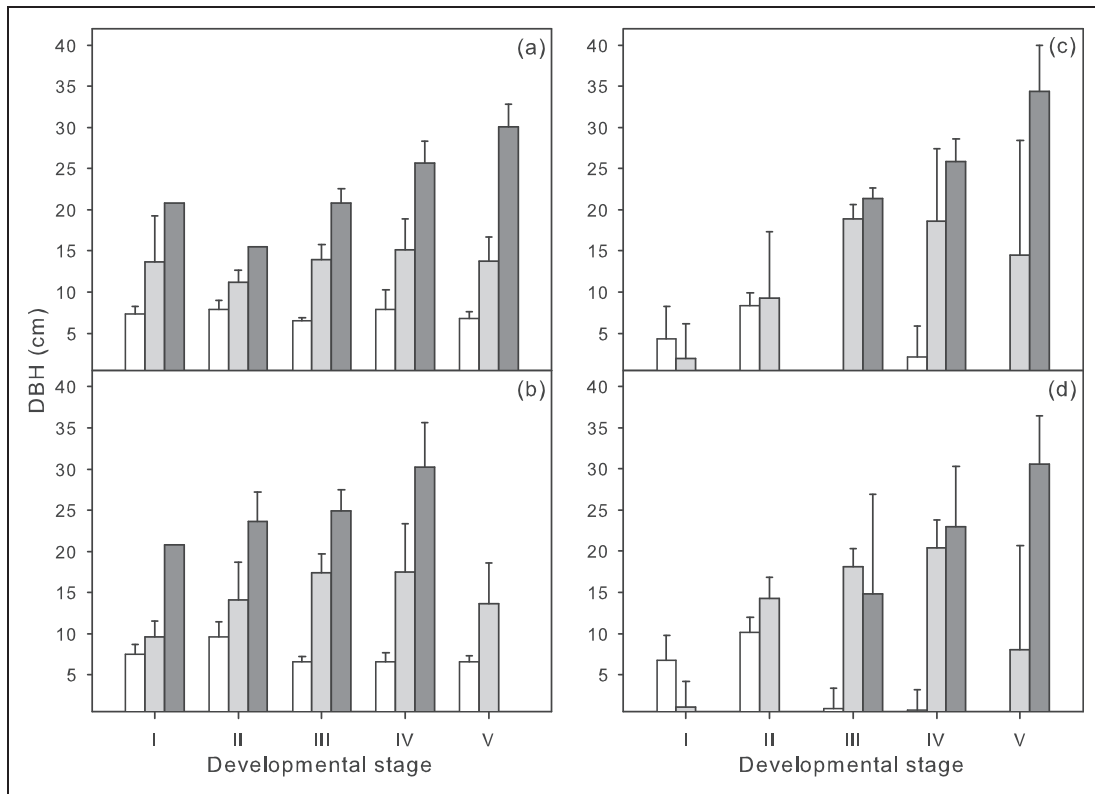
The IVs of *P. massoniana* in the CTN stands were generally lower than their respective values in the monoculture stands (Figure 4). A comparison between the different layers indicated that the IVs of *P. massoniana* were the highest at Stage I (0.79) in Layer A, Stages II (0.63) and III (0.70) in Layer B, and Stages IV (0.45) and V (0.73) in Layer C in the monoculture stands, whereas in the CTN stands, the IVs were the highest in Stages I (0.30) and II (0.39) in Layer A and from Stages III to V (0.33, 0.34 and 0.51) in Layer C.

### Mean DBH of all Tree Species and of Only *P. massoniana*

The average DBH of all species and of *P. massoniana* in each layer at each stage was calculated for all stands (Figure 5). For all species, the differences in DBH growth in Layer A were very small between stands: The average DBH ranged between 6.56 cm and 9.61 cm in the



**Figure 4.** Importance values (mean  $\pm$  SD) of *Pinus massoniana* in three stand vertical layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages in (a) the close-to-nature stands and (b) the monoculture stands.



**Figure 5.** Diameter at breast height (DBH, mean  $\pm$  SD, cm) in three vertical stand layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages for (a) all tree species in the close-to-nature stands, (b) all tree species in the monoculture stands, (c) *P. massoniana* in the close-to-nature stands and (d) *P. massoniana* in the monoculture stands.

monoculture stands and between 6.49 cm and 7.92 cm in the CTN stands. The DBH growth in Layer B was higher in the monoculture stands than in the CTN stands over Stages II to IV (14.14–17.50 cm and 11.20–15.09 cm, respectively), and at Stage V, the values dropped to almost the same level (13.67 cm and 13.78 cm). In Layer C, the DBH growth at Stage V was the highest in both stands (30.11 cm and 30.23 cm for the CTN stands and monoculture stands, respectively), while over Stages II to IV, the DBH growth of the monoculture stands (20.80–24.88 cm) was higher than or equal to that of the CTN stands (15.5–25.65 cm).

The differences in *P. massoniana* DBH growth in Layers A and B were rather small between stands, with CTN stands exhibiting higher values at the final stage in each layer. In Layer C, diameter growth was higher from Stages III to V in the CTN stands (21.35–34.42 cm) compared with the monoculture stands and was eventually higher than the respective value for all species at Stage V.

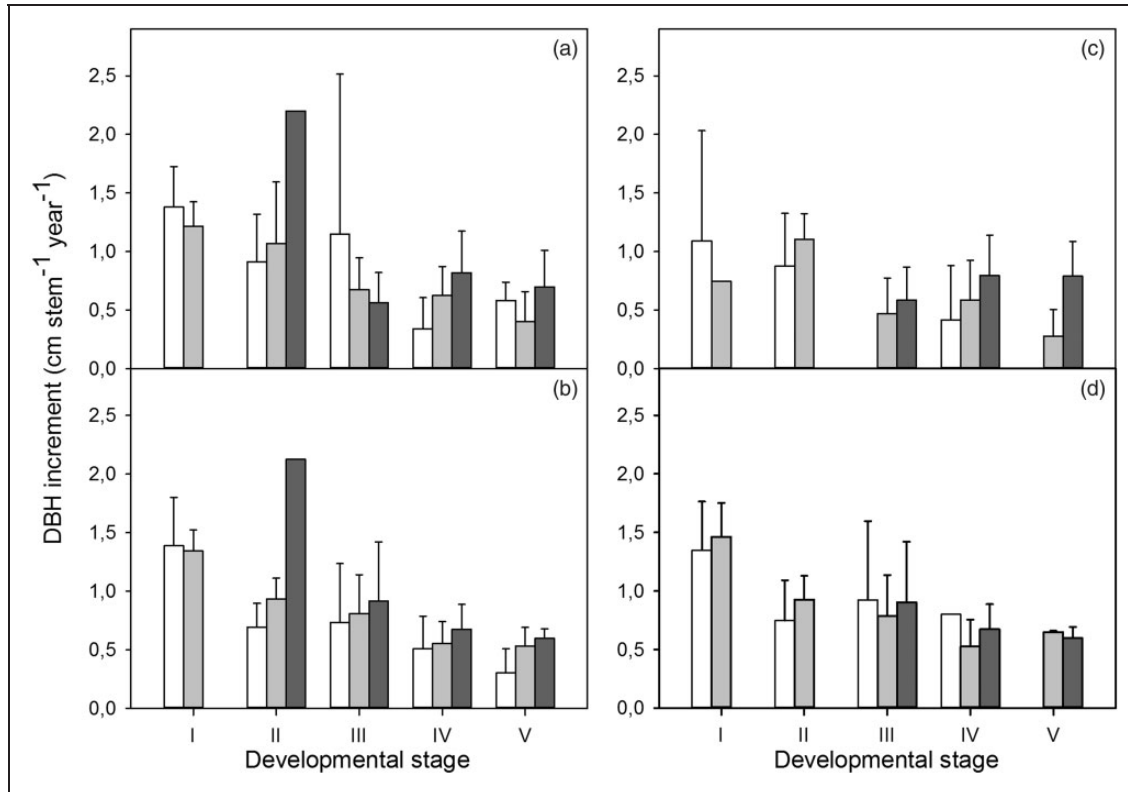
#### Annual DBH Increment of all Species and of Only *P. massoniana*

The average single-tree annual DBH increment of all species and of only *P. massoniana* in each layer at each stage

were calculated for all stands (Figure 6). Overall, the DBH increment did not appear to be substantially different among the stands. In Layer C, the DBH increments of the CTN stands were slightly higher than those of the monoculture stands at the final two stages; for all species, the CTN and monoculture stand values, respectively, were 0.82 cm stem<sup>-1</sup> year<sup>-1</sup> and 0.67 cm stem<sup>-1</sup> year<sup>-1</sup> at Stage IV, and 0.70 cm stem<sup>-1</sup> year<sup>-1</sup> and 0.60 cm stem<sup>-1</sup> year<sup>-1</sup> at Stage V; for *P. massoniana* solely, the respective values were 0.80 cm stem<sup>-1</sup> year<sup>-1</sup> and 0.67 cm stem<sup>-1</sup> year<sup>-1</sup> at Stage IV, and 0.79 cm stem<sup>-1</sup> year<sup>-1</sup> and 0.60 cm stem<sup>-1</sup> year<sup>-1</sup> at Stage V.

#### Stand BA and BAI of all Tree Species

The average BA growth in each layer at each developmental stage was calculated for all stands (Figure 7). Within each stand, the BA growth of Layer A was higher than the respective values of the other layers at Stage I. In the monoculture stands, the BA growth of Layer B was higher than the respective values measured in other layers at Stages II and III, while in the CTN stands, the BA of Layer B was only higher at Stage II. The BA growth of Layer C presented the highest values at Stages IV (17.14 m<sup>2</sup> ha<sup>-1</sup>) and V (33.30 m<sup>2</sup> ha<sup>-1</sup>)



**Figure 6.** Annual diameter at breast height (DBH) increment (mean  $\pm$  SD,  $\text{cm stem}^{-1} \text{ year}^{-1}$ ) in three stand layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages for (a) all tree species in the close-to-nature stands, (b) all tree species in the monoculture stands, (c) *P. massoniana* in the close-to-nature stands and (d) *P. massoniana* in the monoculture stands.

among all layers and stages in the monoculture stands and from Stages III to V ( $11.37\text{--}28.38 \text{ m}^2 \text{ ha}^{-1}$ ) in the CTN stands. A comparison between the stands indicated that the BA of Layer A was higher at Stages III, IV, and V, that of Layer B was higher at Stages I, IV, and V, and that of Layer C was higher at Stages II and III in the CTN stands compared with the monoculture stands.

Overall, the BAI of the monoculture stands was similar to that of the CTN stands (Figure 8). In the two lower layers, the BAI of the CTN stands was only larger at Stages II and III in Layer A (by  $0.38 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  and  $0.15 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ , respectively), and at Stages I and IV in Layer B (by  $0.24 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  and  $0.14 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ , respectively); in Layer C, the BAI of the CTN stands varied from  $0.17 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  to  $1.12 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  from Stage II to Stage V, and the values were sometimes slightly lower than the respective monoculture stand values ( $0.32\text{--}1.28 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ ).

### Relative Dominance ( $R_{do}$ ) of all Tree Species

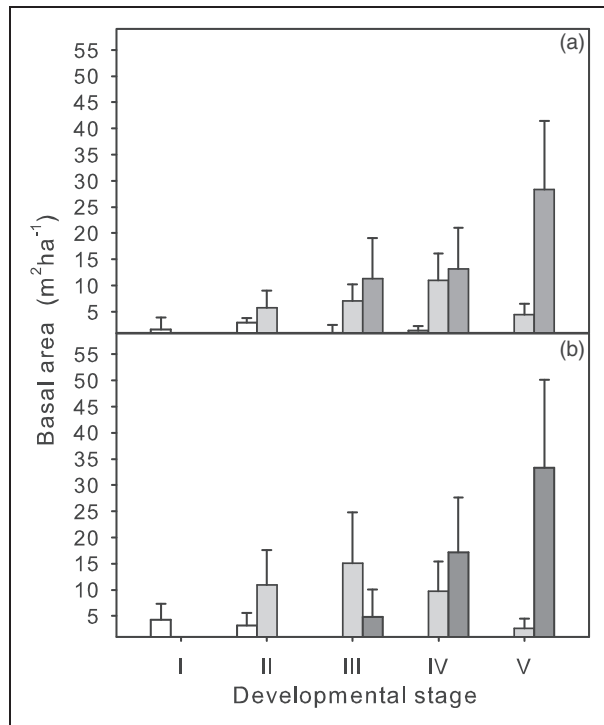
Compared with the monoculture stands, the  $R_{do}$  of Layer A in the CTN stands was increased by 0.09, 0.04, 0.04, and 0.03 over Stages II to V, and that of Layer B was increased by 0.07 and 0.08 at Stages IV and V,

respectively. In Layer C, the  $R_{do}$  values of the CTN stands were generally lower than those of the monoculture stands (Figure 9). At Stage I, the  $R_{do}$  values of Layer A were the highest among all layers in both stands. In addition, the  $R_{do}$  values of Layer B were the highest at Stage II in the CTN stands and at Stages II and III in the monoculture stands. Furthermore, the  $R_{do}$  values of Layer C were the highest from Stages III to V in the CTN stands and from Stages IV to V in the monoculture stands (Figure 9).

### Stand Volume Growth of all Species and of Only *P. massoniana*

The volume growth patterns of different layers at different stages were similar to their respective BA growth dynamics: The stages with greater BA growth also presented greater volume growth (Figure 10). The highest volume growth in the monoculture stands was observed in Layer C at Stages IV ( $146.13 \text{ m}^3 \text{ ha}^{-1}$ ) and V ( $323.09 \text{ m}^3 \text{ ha}^{-1}$ ). In the CTN stands, the highest volume growth occurred in Layer C from Stages III to V ( $93.05\text{--}256.59 \text{ m}^3 \text{ ha}^{-1}$ ).

Concerning growth in single height layers, the volume growth in the CTN stands was higher at Stages IV



**Figure 7.** Basal area growth (mean  $\pm$  SD,  $\text{m}^2 \text{ha}^{-1}$ ) for all tree species in three stand layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages in (a) the close-to-nature stands and (b) the monoculture stands.

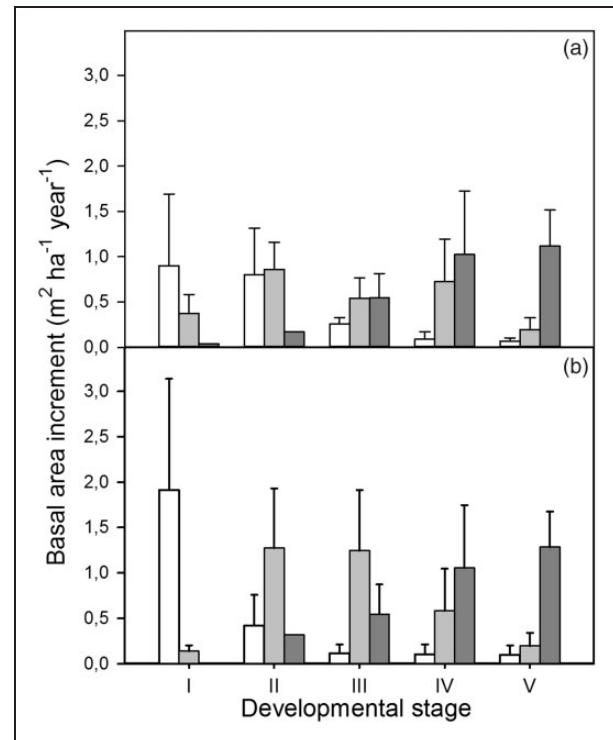
( $68.59 \text{ m}^3 \text{ha}^{-1}$ ) and V ( $28.58 \text{ m}^3 \text{ha}^{-1}$ ) (in Layer B) and at Stage III ( $93.05 \text{ m}^3 \text{ha}^{-1}$ ; in Layer C) compared with the respective values in the monoculture stands (Figure 10).

In the monoculture stands, the volume growth of *P. massoniana* accounted for the majority (49.7%–98.6%) of the total stand volume growth in 10 of the total 15 combinations of different layers and stages, while in the CTN stands, *P. massoniana* accounted for the majority (55.7%–90.9%) of the total stand volume growth in 7 of the 15 combinations (Figure 10). Furthermore, *P. massoniana* volume growth, calculated relative to the volume growth of all species at each layer in each stage, was 2.9% to 73.5% lower in the CTN stands than in the monoculture stands (Figure 10).

## Discussion

### Long-Term Dynamics of Stand Structure and Growth

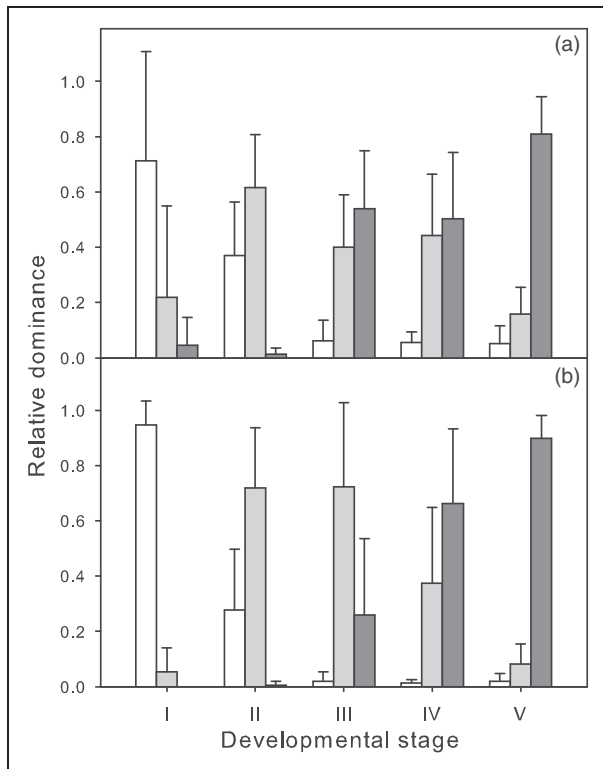
Tree species diversity was higher in the CTN stands than in the monoculture stands at each developmental stage, indicating that the conversion resulted in higher stand diversity over time. Thinning of dominant *P. massoniana* trees followed by replanting of native species, a typical operation in the local conversion approach, has been



**Figure 8.** Basal area increment (mean  $\pm$  SD,  $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$ ) for all tree species in three stand layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages in (a) the close-to-nature stands and (b) the monoculture stands.

proven to be efficient in increasing species diversity in plantations, even over a relatively short period (Luo et al., 2013). Similarly, in temperate forests in Europe, the large-scale conversion of even-aged coniferous stands into continuous cover mixed stands (typically conifer-beech-mixed stands) has been acknowledged as a means of improving forest biodiversity (Budde, Schmidt, & Weckesser, 2011). Natural regeneration, which is rich in spatial and compositional variability, is favored in the CTN conversion following various retention approaches (Swanson et al., 2010), and a greater diversity of species is therefore maintained on forest land. By contrast, in conventional management, “stand initiation” normally occurs through rapid and dense reforestation shortly after clearcutting, leading to limited stand conditions with simplified early stage functionality (Faaborg, 2002; Swanson et al., 2010) and eventually, lower stand diversity. In this study, we considered the increased diversity index at Stage V of the MS was due to the increased species richness, as shown in Table 1.

The decreased stand diversity during Stages IV to V after conversion was considered as a CTN feature, as lower diversity is sometimes observed in the later stages of natural succession (J. F. Gao & Zhang, 2005; X. Gao, Huang, Wan, & Chen, 1997). This pattern might be due to the numbers of species that previously dominated or



**Figure 9.** Relative dominance (mean  $\pm$  SD) of all species in three vertical stand layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages in (a) the close-to-nature stands and (b) the monoculture stands.

co-dominated being reduced in the climax community (J. F. Gao & Zhang, 2005).

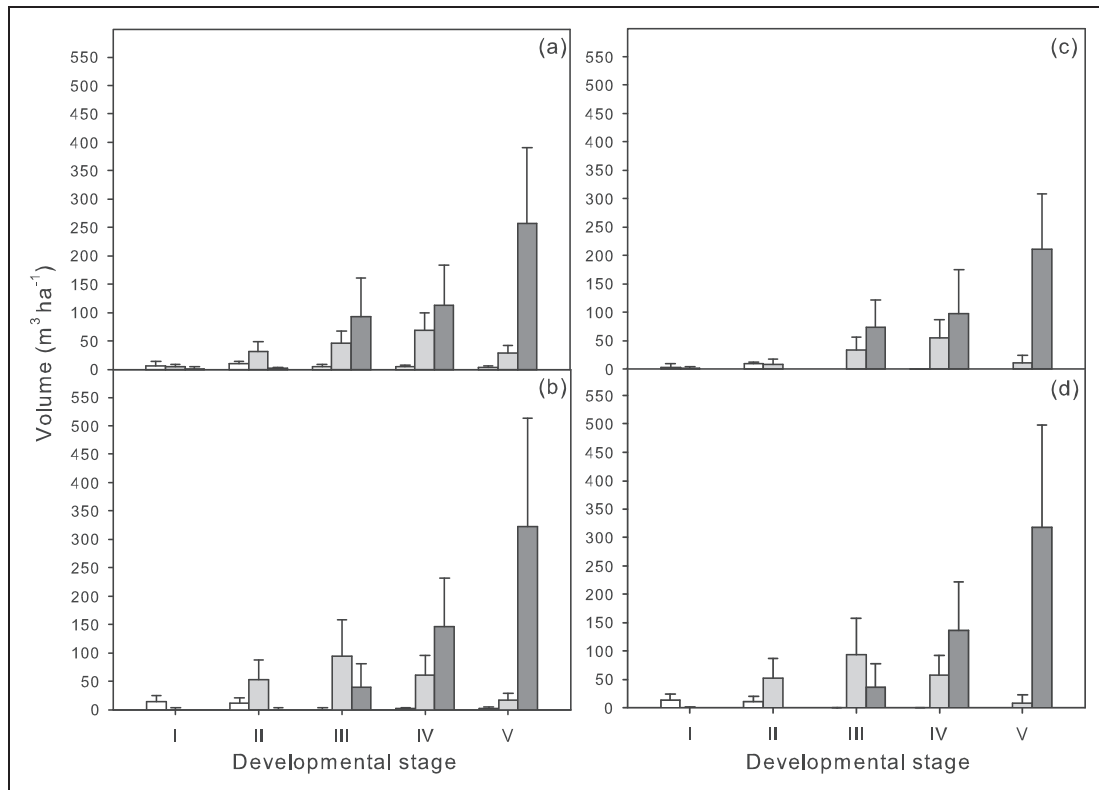
Along with the increased species diversity, the IVs of *P. massoniana* in the CTN stands were mostly decreased, likely due to the density of *P. massoniana* was lower in the CTN stands than in the monocultures (Table 1). The decreased importance of *P. massoniana* in the CTN stands also indicated that this species was no longer the only one being valued during the stand development.

In the CTN stands, the accelerated height growth of *P. massoniana* resulted in this species entering the canopy layer at an earlier stage than in the monocultures, as suggested by the pattern where the IVs of *P. massoniana* in the canopy layer (Layer C) started to become greater than those in the other two layers already at Stage III; in comparison, this occurred at Stage IV in the monoculture stands. The intensive inter- and innerspecies competition for light during the second developmental stage (“rapid height growth stage”) in the CTN forests might have benefitted the height growth, which was first visible at Stage III. An increase in height growth of *P. massoniana* during its earlier successional stages (20 years old) has also been observed in other mixed-species plantations in the same region as this study (Luo et al., 2013;

Zhu et al., 2014). However, this tree height development advantage might disappear over time, as this study showed the mean height of *P. massoniana* was similar between the CTN stands and the monoculture stands at the later developmental stages, where the mean canopy layer age was older than 30 years ( $16.0 \pm 3.5$  m and  $15.8 \pm 1.9$  m for the CTN and monoculture stands at Stage IV, respectively; and  $20.9 \pm 3.5$  m and  $21.0 \pm 3.8$  m for the CTN and monoculture stands at Stage V, respectively; Table 1). We, therefore, call for the inclusion of a time effect in the height growth comparison among different management regimes, as the height-growth rate can change over time, and differences in the mean height growth may occur only for a short period (Gutsell & Johnson, 2002).

Tree size and allometric characteristics can change between pure and mixed stands (Dieler & Pretzsch, 2013; Zingg, 1994). However, the diameter growth of all species, in terms of single-tree mean DBH and DBH increment, did not vary considerably between the stands, which is in line with observations showing no significant differences in diameter allometric growth between pure and mixed stands (Drössler et al., 2015; Rouhi-Moghaddam, Hosseini, Ebrahimi, Tabari, & Rahmani, 2008). The potential reasons for this observation include the priority of photosynthetic energy allocation to height over diameter growth in species competing for light (Kramer & Kozlowski, 1960) and the combined influence of variations in site conditions and management options (e.g., planting density and thinning intensity). Explanation of this pattern calls for close scrutiny of growth–environment interactions, which are not addressed in this study. The diameter and its growth ratio of *P. massoniana* in the canopy layer (Layer C) increased in the CTN stands, suggesting that the cultivation of large-diameter trees of this species was facilitated, which was compatible with the principle of focusing on individual tree development in the CTN forestry (Bauhus et al., 2013; Brang et al., 2014). The increased diameter growth of the *P. massoniana* canopy trees could be explained by the reduced intraspecies competition, indicated by the lower density of this species compared with the monoculture stands (Table 1).

Overall, stand productivity, measured as stand mean volume, BA, and BAI of the canopy layer (Layer C), was not enhanced in the CTN stands, where the growth of all species was lower compared with the monoculture stands during the major harvesting period (Stages IV and V), and the volume growth of *P. massoniana* generally declined in the CTN stands. However, increased stem productivity has been widely observed in multispecies plantations (Erskine, Lamb, & Bristow, 2006; Jandla et al., 2007; Khanna, 1997; Piotta, Viques, Montagnini, & Khanna, 2004). Such an inconsistency suggests that the mixing effect depends on the tree species composition



**Figure 10.** Volume growth (mean  $\pm$  SD,  $\text{m}^3 \text{ year}^{-1}$ ) in three stand vertical layers (Layer A: white bars; Layer B: gray bars; Layer C: dark gray bars) during five developmental stages for (a) all tree species in the close-to-nature stands, (b) all tree species in the monoculture stands, (c) *P. massoniana* in the close-to-nature stands, and (d) *P. massoniana* in the monoculture stands.

(Drössler et al., 2015). For example, a mixture of *P. massoniana* and *Castanopsis hystrix* improved the growth of the latter species but negatively affected the growth of *P. massoniana* (He et al., 2013; Qin et al., 2011). In both stands, the harvestable stem in the canopy layer was considerably higher than in the two other layers, confirming that it was usually the dominant trees, that is, those with a large diameter, that were the most productive in a certain stand.

The conversion did appear to improve the stand productivity of the lower layers (Layers A and B), revealed by the higher values of relative dominance from Stages II to V of Layer A and IV to V of Layer B, compared with the respective values in the monoculture stands. The cumulative increase in stand growth relative to the regenerations and the subcanopy trees indicated a somewhat higher sustained capacity of timber output.

### Statistical Limitations Due to the Experimental Data and Methodology

One should be aware of several constraints concerning the data and methodology used in this study. Due to the paucity of long-term monitoring data, this study simplified 85 stands into two treatments (CTN forests and

monocultures), without considering the differences in management interventions (e.g., species combination, stand density, and thinning intensity) and without sufficient replications. In addition, using the chronosequence generated by the space-for-time substitution as an equivalent to true observations of stand dynamics could also be problematic; among the stands chosen to represent the later developmental stages, the understory species enrichment occurred recently, resulting in discontinuity, to some extent, in the canopy layer. More specifically, for example, the average tree height of the admixed species at Stage V in the CTN stands was lower than the current standard for canopy layer height (15.6 m; Table 1); ideally, abundant individuals from the enrichment species should enter the canopy layer at this stage (Lu et al., 2014). With these limitations, the results of this study were not able to distinguish the CTN conversion effects from the effects of other factors.

Nevertheless, considering the fact that, at least at the local scale, the majority of conversion cases started by transferring existing monocultures with various stand conditions and management histories that were not replicated, and considering that this heterogeneity would likely persist for a long time, the comparison of the defined CTN stands and monocultures presented in this

study should provide meaningful results addressing general or quantitative trends in the CTN conversion at a local to regional scale.

### Local CTN Conversion Goal Fulfilment

At the local scale, the common idea of the CTN conversion was to improve the ecological status of the forests while maintaining a high level of economic production, although the stand-scale goal might differ under different CTN management designs. Our analyses indicated an improved ecological status of the CTN forests, as the stands managed under the CTN regime tended (a) to be more complex with respect to tree species composition over time, as indicated by the consistently higher species diversity and (b) to have a higher sustainability with respect to stand productivity, as suggested by the higher cumulative stand growth in the layers beneath the canopy layer.

Concerning the timber production, however, the CTN conversion decreased the stand stem harvest biomass, although it appeared to have a good potential to cultivate large-diameter *P. massoniana* individuals, as evaluated based on their accelerated height growth during the early successional stage and their increased diameter growth in the canopy layer. However, the results of this study were insufficient to draw any conclusion concerning the overall economic efficiency of local CTN conversions. A few reflections concerning this issue are as follows:

1. Under the CTN method, trees remained in the stands longer and developed better, as CTN forestry preferred to cultivate large diameter timber, and the harvest was based on prescribed DBH rather than tree age. Thus, the per unit ( $\text{m}^3$ ) timber value could be substantially improved. At the study area, *P. massoniana* was traditionally harvested at age 31, with an average DBH of 23 cm (Table 1), and the corresponding timber price was usually  $725 \text{ CNY m}^{-3}$  (approx.  $115 \text{ USD m}^{-3}$ ; Deng, 2015), while in the CTN stands, the average DBH of *P. massoniana* reached 34 cm at the final development stage (Table 1), and the corresponding timber price was higher than  $840 \text{ CNY m}^{-3}$  (approx.  $133 \text{ USD m}^{-3}$ ). Nevertheless, again, this study was not able to determine whether the economic loss associating with the reduced stem harvest could be compensated by the increased value of those large-diameter trees.
2. Different species mixtures might substantially change the market value of the forest, as the timber value varied greatly among the local broadleaved species. The price for the normal species was approximately  $500 \text{ RMB m}^{-3}$  (approx.  $79 \text{ USD m}^{-3}$ ), whereas the price for the large-diameter timber (26 cm and above) of a few rare

hardwood species (e.g., *E. fordii*, *Dalbergia odorifera*) could be  $5,000$  to  $10,000 \text{ RMB m}^{-3}$  (approx.  $794$ – $1,588 \text{ USD m}^{-3}$ ) (Deng, 2015). Such a contrast might make any economic output assessment only available at the stand level. Moreover, the current output assessment might be valid only for one management cycle (from stand developmental Stages I to V) at a given stand, as the management goal and strategy might change in the following cycles; without management intervention, *P. massoniana*, an early-successional shade-intolerant species, might be excluded over the forest succession, which would change the forest species composition and structure at the stand level.

3. The economic efficiency of CTN management could be partly achieved by using natural processes and natural regenerations (Larsen, 2012; Schütz, 1999); this, however, was not the case in this study. The natural regeneration of the desired species, currently in the studied stands, was far from sufficient (maximum  $125 \text{ stem ha}^{-1}$ ), although it might be further promoted by single tree-based selective logging, which, over time, creates canopy gaps that facilitate natural regeneration.

Overall, we argue that CTN forestry in the current context benefits the ecological function of local forests (e.g., through improved tree species diversity), as opposed to timber production and the associated economic efficiency.

### Implications for Conservation

This study discussed the effects of implementing CTN forestry as an alternative to traditional monoculture in subtropical regions on the tree/stand full life-span or complete management process level. The results from this study contribute to the comprehension of CTN management with respect to Chinese implementation and can provide insight for forest managers and stakeholders seeking a balance between the utilization and conservation of forest resources. The CTN conversion maintained a higher level of species biodiversity over time and also improved the stand sustainability through the enrichment of the stand vertical structure. The essence of this type of conversion is to introduce indigenous species into fast-growing pioneer species (*P. massoniana* in this study) stands to enable the stands to develop into a climax community and to thus ultimately establish more sustainable forestry systems. This study also reveals the potential trade-offs between the ecological benefits and the economic efficiency associated with timber outputs in CTN forestry systems, although economic success with such systems may be achieved in the long run, as a result of well-maintained forest structure, function, and reduced management input.

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## Supplemental Material

Supplementary material for this article is available online.

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