



**Full Length Article**

# Plant Diversity and Composition in Masson pine Monocultures and Mixtures

Na Lin<sup>1</sup>, Huiyan Xie<sup>1</sup>, Tao Ma<sup>1</sup>, Chunyong Li<sup>2</sup>, Demin Huang<sup>3</sup>, Mingxuan Zheng<sup>1</sup> and Shiqing Chen<sup>1\*</sup>

<sup>1</sup>Department of Forest Management, College of Forestry and Landscape Architecture, South China Agricultural University, Guangzhou, China

<sup>2</sup>Deqing Forest Farm of Guangdong Province, China

<sup>3</sup>Qingyuan Forestry Bureau, Guangdong, China

\*For correspondence: sqc@scau.edu.cn

Received 11 June 2020; Accepted 02 April 2021; Published 30 December 2022

## Abstract

We studied the interactions of the communities of *Pinus massoniana* plantations and mixed *P. massoniana*/broad-leaved forests, which are two of the successional stages of Masson pine plantations in South China, to determine the effect of plantations on species diversity and composition. Moreover, by analyzing the relationships between different forest strata in both forest types, we aimed to detect general interaction patterns of the Masson pine monocultures in South China that could either facilitate or counteract the conversion of Masson pine monocultures into mixed forests. Plant species richness and composition of the tree, shrub, and herb layers were determined in three 20 x 20 m plots in both *P. massoniana* plantations and mixed *P. massoniana*/broad-leaved forests to make comparisons. We found that *P. massoniana* plantations had a higher species richness in the understory layer, lower cover value for the tree layer, and lower species richness of the herb layer than mixed *P. massoniana*/broad-leaved forests. The different successional stages of the *P. massoniana* plantations had a different species composition as well, which indicate that the study area had a high potential to convert *P. massoniana* monocultures into more natural and stable mixed *P. massoniana*/broad-leaved forests. The results further demonstrate a positive overstory-understory diversity relationship in the early to middle stages of succession and emphasize the effectiveness of admixing tree species in Masson pine plantations for maintaining biodiversity in Chinese subtropical forests. The findings of this research can be used to guide forest management to enhance plant species diversity. © 2022 Friends Science Publishers

**Keywords:** *Pinus massoniana*; Masson pine; Succession; Monoculture; Structure; Richness; Diversity

**Abbreviations:** DBH – Diameter at breast height; DCA – Detrended correspondence analysis

## Introduction

Ancient forests are considered as the focus of conservation because of their complex structure and diverse floristic composition, but these mature forests are rapidly disappearing as a result of logging and conversion to agriculture (Schuldt *et al.* 2010). Therefore, the protection value of secondary forest is increasing. Successional processes in secondary forest may restore species composition and diversity to the level of original forest (Brockhoff *et al.* 2008). As we know, succession is one of the most studied processes in ecology, and it provides highly predictable. Few researchers have studied the influence of the preceding stages of succession on subsequent stages of succession to test the assumption that passing through one stage is essential before entering the next stage. The succession of the ecosystem processes of each successional stage may be affected by the diversity of

species present, but there are few studies showing that plant species diversity affects succession. Over time, changes in plant composition are influenced by the effectiveness of propagules (Bekker *et al.* 1997), changes in soil fertility (Marrs 1993), above- and below-ground herbivore activities (Olf and Ritchie 1998), the presence or absence of mutualistic symbionts (Clay and Holah 1999) and the relationships between plant species and related soil communities (Westover *et al.* 1997). The outcome of all these interactions, such as facilitation and competition (Cavard *et al.* 2011), determines which species successfully compete for the available resources at a certain stage of succession (Putten and Stoel 1998).

Species diversity and rarity are essential indicators of the value of natural habitats (Locky *et al.* 2005). Tree species diversity is related to ecosystem functions and services, of which productivity and decomposition are their key features (Hooper *et al.* 2012; Ammer 2019). Using

ground-sourced data from 777,126 permanent sample plots across 44 countries, Liang *et al.* (2016) showed that the reduce of species richness would lead to the decrease of forest productivity. In addition, Ruiz-Benito *et al.* (2014) used diversity gradient datasets of ~54,000 plots in Spain and showed that species diversity increases carbon stock and tree productivity. Wood production has also been found to be higher in Aleppo pine forests in mixed plots than in monospecific plots (Vilà *et al.* 2003). Similarly, Chamagne *et al.* (2017) showed that increases in tree diversity increased forest productivity and increases in tree growth rates without a cost. Plant diversity and composition have also been indirectly related to net nitrification through a positive relationship between species richness and nitrifier abundance (Laughlin *et al.* 2010).

Understanding plant biodiversity in different successional periods of subtropical Masson pine plantations is useful, particularly in the South China subtropical area where Masson pine is one of the most economically important and popular tree species grown in monocultures or in mixture with broad-leaved tree species. Biodiversity assessments provide opportunities for monitoring community changes over time, prioritizing areas of conservation concern and developing testable hypotheses relating patterns of geographic variation in species assemblages to selected environmental factors (Debinski and Humphrey 1997). Some studies have examined species-environment relationships to understand the determinants of community composition (Svenning and Skov 2002). These studies commonly showed a predominant effect of soil pH on plant diversity, including species richness and composition (Debinski and Humphrey 1997). In addition, researchers have shown that interactions between site-specific factors can reduce, facilitate (Connell and Slatyer 1977), or even divert successional sequences predicted by the general successional model. Barrufol *et al.* (2013) showed that successional older stands, which had a high plant diversity, also had a higher total stem basal area.

Successional processes govern the plant interactions that occur between plant species: interspecific interactions tend to change with stand development and among species (Cavard *et al.* 2011). In this study it was examined the positive and negative interactions in communities of *Pinus massoniana*, plantations and mixed *P. massoniana*/broad-leaved forests, which are the different successional stages of Masson pine plantations in South China, to verify the negative effect of plantations on species diversity and to assess dissimilarities in species composition. Moreover, by analyzing the relationships between different forest strata in both forest types, we aimed to detect general interaction patterns in the Masson pine monocultures in South China that could either facilitate or counteract the conversion of Masson pine monocultures into mixed forests. The findings of this research can be used to guide the management of these forests to enhance plant species diversity.

## Materials and Methods

### Study area

The study was conducted in the Dinghushan Biosphere Reserve in a subtropical area of South China (112° 30' 39" E – 112° 33' 41" E, 23° 09' 21" N – 23° 11' 30" N) with a subtropical moist monsoon climate (Fig. 1). The area is mountainous, has steep slopes, and has an elevation range of 100–700 m. The annual average temperature of the study area is 21.4°C with an annual mean maximum temperature of 28.0°C and an annual mean minimum temperature of 12.6°C and the mean precipitation of the study area is 1678 mm, with about 80% of the mean precipitation occurring in the wet season: April to September. The study area has ~78% forest cover and is located in the subtropical evergreen zone, mostly on sand-shale stone. The typical forest types at the study site are *P. massoniana* monocultures, mixed *P. massoniana*/broad-leaved forests, and monsoon evergreen broad-leaved forests. The dominant broad-leaved species in the study area include *Schima superba* and *Castanopsis chinensis*. *P. massoniana* is the dominant species in the coniferous forests.

### Data sampling

We established six 20 × 20 m plots in two forest types in the Dinghushan Biosphere Reserve. Three plots were located in *P. massoniana* monoculture, and the other three plots were placed in mixed *P. massoniana*/broad-leaved forest. The study plots were located at 200–300 m a.s.l. and had similar soil conditions. In late summer, in 2017, a vegetation survey was conducted in each plot. Species were recorded separately for the tree layer, which was comprised of woody plants and climbers with heights of >5 m, shrub layer, which was comprised of woody plants and climbers with a height of 0.5–5 m and herb layer, which included all herbaceous species and climbers/woody plants with a height <0.5 m. The moss layer was not considered. Cover values per species and vegetation layer were recorded directly in percent. The height was measured by Blume-Leiss Hymrometer (Parde 1955). The diameter at breast height (DBH) of the tree layer was quantified by measuring the diameter of all trees. The nomenclature of plant taxa followed the Flora of China (www.efloras.org). We collected soil using a soil corer with a diameter of 8 cm to investigate soil chemical characteristics. Ninety-six cores were bulked by mineral soil depths of 0–5, 5–10, 10–20, 20–40 and 40–60 cm to form 16 composite samples per depth (Table 1). The organic matter of the soil in the *P. massoniana* plantations and mixed *P. massoniana*/broad-leaved forests was 29.41 t·ha<sup>-1</sup> and 32.04 t·ha<sup>-1</sup>, respectively, and the soil pH of the two forests was 2.82 and 2.91, respectively (Table 1).

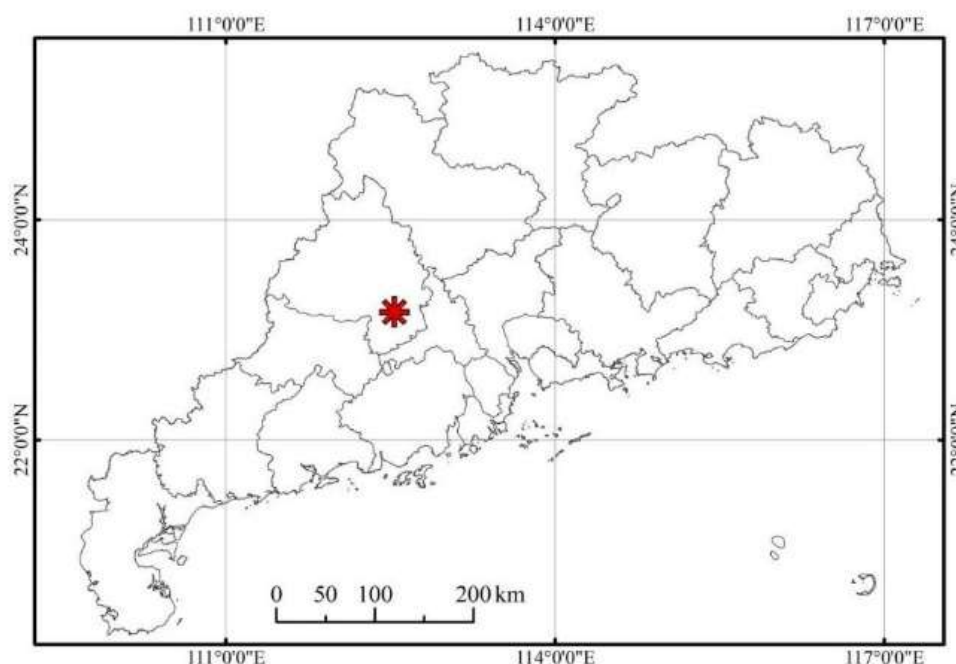
### Data analysis

The tree layer characteristics, species richness and abundance of the understory layer and its component shrub

**Table 1:** Primary soil chemical characteristics of the studied mixed and pure *Pinus massoniana* forests. Superscript letters indicate significant differences between the pure forest and the mixed forest at each depth ( $P < 0.05$ , pairwise Wilcoxon test)

Soil Depth (cm)	Organic Matter (t·ha <sup>-1</sup> )		C (t·ha <sup>-1</sup> )		N (t·ha <sup>-1</sup> )		PH	
	mix forest	pure forest	mix forest	pure forest	mix forest	pure forest	mix forest	pure forest
0-5	32.04 (2.9) <sup>a</sup>	29.41 (2.4) <sup>a</sup>	18.63 (1.7) <sup>a</sup>	1.71 (1.4) <sup>a</sup>	1.00 (0.1) <sup>a</sup>	0.93 (0.1) <sup>a</sup>	2.91 (0.0) <sup>a</sup>	2.82 (0.0) <sup>a</sup>
5-10	28.74 (7.6) <sup>a</sup>	21.70 (0.6) <sup>a</sup>	16.71 (4.4) <sup>a</sup>	12.62 (0.4) <sup>a</sup>	0.98 (0.2) <sup>a</sup>	0.74 (0.0) <sup>a</sup>	3.11 (0.0) <sup>a</sup>	3.04 (0.1) <sup>a</sup>
10-20	16.20 (2.7) <sup>a</sup>	10.83 (1.0) <sup>a</sup>	9.42 (1.6) <sup>a</sup>	6.29 (0.6) <sup>a</sup>	0.63 (0.1) <sup>a</sup>	0.47 (0.0) <sup>a</sup>	3.22 (0.0) <sup>a</sup>	3.28 (0.0) <sup>a</sup>
20-40	9.53 (1.2) <sup>a</sup>	7.88 (0.9) <sup>a</sup>	5.54 (0.7) <sup>a</sup>	4.58 (0.5) <sup>a</sup>	0.49 (0.0) <sup>a</sup>	0.41 (0.0) <sup>a</sup>	3.21 (0.0) <sup>a</sup>	3.17 (0.1) <sup>a</sup>
40-60	9.97 (4.3) <sup>a</sup>	6.25 (0.7) <sup>a</sup>	5.80 (2.5) <sup>a</sup>	3.64 (0.4) <sup>a</sup>	0.44 (0.1) <sup>a</sup>	0.38 (0.0) <sup>a</sup>	3.32 (0.0) <sup>b</sup>	2.81 (0.1) <sup>a</sup>

The data figures are means of six replicates

**Fig. 1:** Location of Dinghushan Biosphere Reserve in the City of Zhaoqing in the middle of Guangdong Province, South China

and herb layers were compared for the two forest types *P. massoniana* monoculture ( $n = 3$ ) and *P. massoniana*/broad-leaved forest ( $n = 3$ ) using Wilcoxon tests. It was further quantified the Shannon diversity index for the understory layers. Linear regressions were used to quantify the impact of different tree layer variables, including species richness, height, cover and DBH, on the understory, with cover and species richness of the understory and its component shrub and herb layer as dependent variables for each forest type. The same method was used to analyze the interactions between the shrub and herb layer variables and the impact of the tree layer on the number and cover of tree, shrub and herbaceous species, including graminoids, herbs, and ferns within the understory, according to the Flora of China.

Detrended correspondence analysis (DCA; Nesheim *et al.* 2010) was used to investigate the gradients of species composition among the six plots and to examine the

vegetation-environment relationships in the two different successional stages. DCA was used to analyze plant species composition of the shrub and herb layer and to quantify a potential difference between forest types. Ordinations were applied to square-root transformed cover values. The cover values of each species sampled in the shrub and herb layer were fitted to the ordination axes to investigate which species determined differences in species composition. Then, indicator species analysis was used to identify possible indicator species for *P. massoniana* and mixed *P. massoniana*/broad-leaved forests (Dufrière and Legendre 1997). Calculated an indicator value (*IV*) for each species in the shrub and herb layers of the two forest types as the proportional abundance of the species in the herb or shrub layer relative to its abundance in both layers multiplied by the proportional frequency of the species in each layer. The *IV* ranges between 0 (no indication) and 1 (perfect

indication), which means that a perfect indicator is always present in one of the plant layers. The significance of each indicator value was tested using Monte Carlo simulation with 1 000 iterations (McCune and Grace 2002). All calculations and statistical tests were performed using R, version 3.3.1 (QUOTE: R Development Core Team 2017).

## Results

### Characteristics of forest types

Within the six study plots, found 57 different plant species, and 48 of these species occurred in the herb and shrub layers of the understory. Only *Eucalyptus urophylla* × *E. grandis* and *S. superba* occurred exclusively in the tree layer in the *P. massoniana* plantations and *C. fissa* occurred exclusively in the mixed *P. massoniana*/broad-leaved forests (Table 2). In the *P. massoniana* plantations 56 species were recorded, and in the mixed *P. massoniana*/broad-leaved forest 57 species were recorded.

The investigated *P. massoniana* plantations were located at a slightly higher elevation than the mixed *P. massoniana*/broad-leaved forests (Table 3). The structure and diversity variables of the tree and understory layers showed no significant differences between forest types. Separating the understory into its components, the shrub layer of the *P. massoniana* plantations had a higher species richness and coverage than the mixed *P. massoniana*/broad-leaved forests, while the species richness and coverage of the herb layer was higher in the mixed *P. massoniana*/broad-leaved forest (Fig. 2).

### Interactions between vegetation layers

There was a positive relationship between the coverage of the tree layer and species richness of the understory layers in *P. massoniana* plantations (Table 4) and a negative relationship between species richness of the tree layer and species richness of the understory, shrub layer, and herb layer (Table 4). There was also a negative relationship between the cover of the tree layer and the species richness of the herb layer in the mixed *P. massoniana*/broad-leaved forests (Table 4).

There was no interaction between the shrub and herb layer variables (Table 5). However, there was a positive relationship between coverage and species richness of the shrub layer in the mixed *P. massoniana*/broad-leaved forest and a negative relationship between these variables in the *P. massoniana* forests.

### Vegetation structure

The DCA ordination revealed a clear difference in species composition between mixed *P. massoniana*/broad-leaved forests and *P. massoniana* plantations for both the shrub and herb layers along the second axis (Fig. 3 and 4). *S. superba*,

*Desmos chinensis*, *Schefflera heptaphylla*, *C. fissa*, and *Sapium discolor* were characteristic of the shrub layer in mixed *P. massoniana*/broad-leaved forests. Correlations between species cover values and the ordination axes revealed two groups of species communities that were correlated with the second axis and characterized either mixed *P. massoniana*/broad-leaved forests or *P. massoniana* plantations in the shrub layer (Fig. 3). In the overstory, *Ficus simplicissima*, *Ixora chinensis*, and *Evodia lepta* were associated with *P. massoniana* plantations, whereas *Litsea rotundifolia* was associated with mixed *P. massoniana*/broad-leaved forests. In the herb layer, more species were associated with mixed *P. massoniana*/broad-leaved forests, which had higher herb layer cover and species richness than *P. massoniana* plantations (Fig. 4).

Results of the ordination were largely in accordance with the assignment of species based on their occurrence frequency and IV. Of the 32 species in the shrub layer, *C. fissa* was identified as a significant indicator of *P. massoniana*/broad-leaved forests and *Mallotus paniculatus*, *Embelia ribes*, and *Melastoma candidum* were concentrated in *P. massoniana* plantations. Of the 40 species present in the herb layer, the indicators for *P. massoniana*/broad-leaved forests were *Dicranopteris pedata*, *Mussaenda pubescens* and *Blechnum orientale*, and the indicators for *P. massoniana* plantations were *Melicope pteleifolia* and *M. paniculatus* (Table 6). We also found that with the increase of succession age, the species number and coverage of shrub layer decreased: *M. paniculatus*, *E. ribes*, *M. candidum*, *Clerodendrum fortunatum* and *Alchornea trewioides* were indicators for young stages. In the herb layer, we found that the number and coverage of herbaceous species increased with the age of succession: *D. dichotoma*, *M. pubescens*, and *B. orientale* were indicators for old stages.

Alchtrew, *A. trewioides*; Castfiss, *C. fissa*; Clerfort, *C. fortunatum*; Cratcoch, *Cratoxylum cochinchinense*; Desmchin, *D. chinensis*; Emberibe, *E. ribes*; Ficusimp, *F. simplicissima*; Ixorchin, *I. chinensis*; Jatrinte, *Jatropha integerrima*; Litsglut, *L. glutinosa*; Litsrotu, *L. rotundifolia*; Mallpani, *M. paniculatus*; Melacand, *M. candidum*; Evodlept, *E. lepta*; Psycasia, *Psychotria asiatica*; Rhodtome, *Rhodomyrtus tomentosa*; Sapidisc, *S. discolor*; Schehept, *S. heptaphylla*; Scheocto, *S. octophylla*; Schisupe, *S. superba*; Smilchin, *Smilax china*; and Toxisucc, *Toxicodendron succedaneum*.

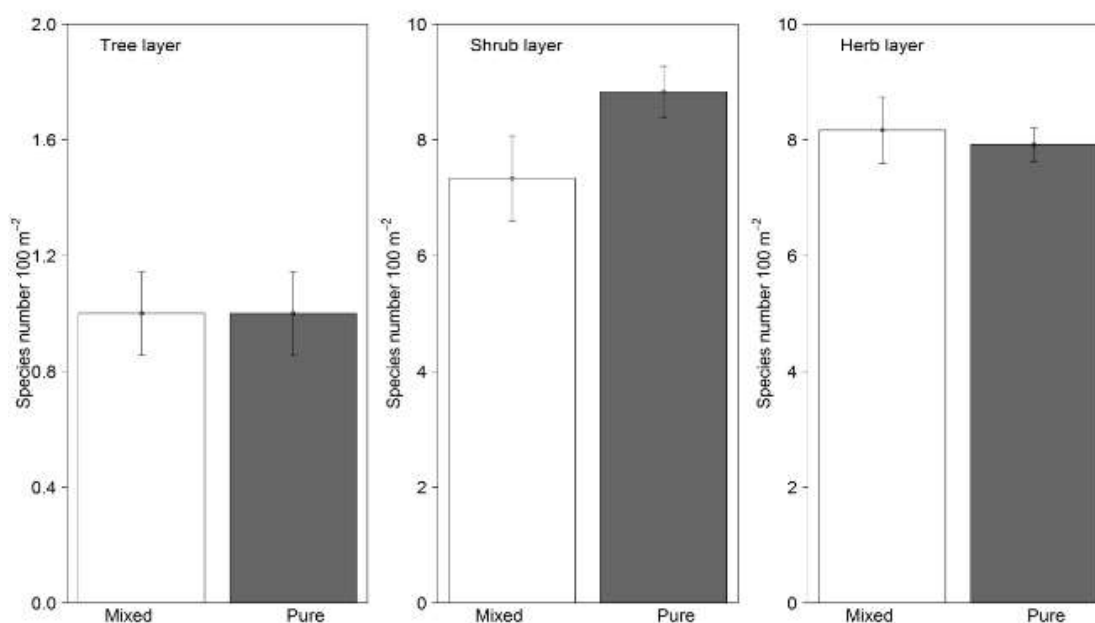
The abbreviation in herb layer: Aspltric (*Asplenium trichomanes*), Blecorie (*B. orientale*), Desmchin (*D. chinensis*), Dianensi (*Dianella ensifolia*), Dicrpeda (*D. pedata*), Emberibe (*E. ribes*), Eurygrof (*Eurya groffii*), Gardjasm (*Gardenia jasminoides*), Ixorchin (*I. chinensis*), Litsrotu (*L. rotundifolia*), Lygoflex (*Lygodium flexuosum*), Melaaffi (*M. affine*), Meliptel (*M. pteleifolia*), Miscflor (*Miscanthus floridulus*), Musspube (*M. pubescens*), Oplicomp (*Oplismenus compositus*), Panibrev (*Panicum brevifolium*), Polychin (*Polygonum chinense*), Psycasia (*P. asiatica*), Psycserp (*P. serpens*), Rhodtome (*R. tomentosa*).

**Table 2:** Tree species abundance in *P. massoniana* plantations and mixed *P. massoniana*/broad-leaved forests

	<i>P. massoniana</i> forest	Mixed <i>P. massoniana</i> /broad-leaved forest
<i>C. fissa</i>	-	39
<i>E. urophylla</i> × <i>E. grandis</i>	5	-
<i>L. cubeba</i>	1	1
<i>M. paniculatus</i>	1	12
<i>M. pteleifolia</i>	2	2
<i>P. massoniana</i>	37	36
<i>S. superba</i>	7	-

**Table 3:** The mean values ± standard error of the characteristics of *P. massoniana* plantations and mixed *P. massoniana*/broad-leaved forests. There were no significant differences in values between forest types ( $P < 0.05$  using the pairwise Wilcoxon test)

	<i>P. massoniana</i> forest	Mixed <i>P. massoniana</i> /broad-leaved forest
Stand Age	50 - 60 years	70 - 80 years
Altitude [m asl]	200 - 300	220 - 300
Tree layer variables		
DBH [cm]	24.8 ± 1.6	16.9 ± 1.1
Tree height [m]	10.1 ± 0.5	8.8 ± 0.4
Cover [%]	85.3 ± 9.7	141.2 ± 3.82
Species richness/100 m <sup>2</sup>	1.0 ± 0.1	1.0 ± 0.1
Understory variables		
Total Understory		
Cover [%]	148.43 ± 5.47	147.62 ± 4.73
Species richness/100 m <sup>2</sup>	7.1 ± 0.4	6.8 ± 0.4
Shannon-Index	4.5 ± 1.7	2.8 ± 0.0
Shrub layer		
Cover [%]	80.3 ± 5.3	53.6 ± 13.9
Species richness/100 m <sup>2</sup>	8.8 ± 0.4	7.3 ± 0.7
Shannon-Index	2.3 ± 0.1	2.2 ± 0.0
Herb layer		
Cover [%]	142.27 ± 4.63	142.37 ± 4.07
Species richness/100 m <sup>2</sup>	7.9 ± 0.3	8.2 ± 0.6
Shannon-Index	2.4 ± 0.1	2.4 ± 0.1

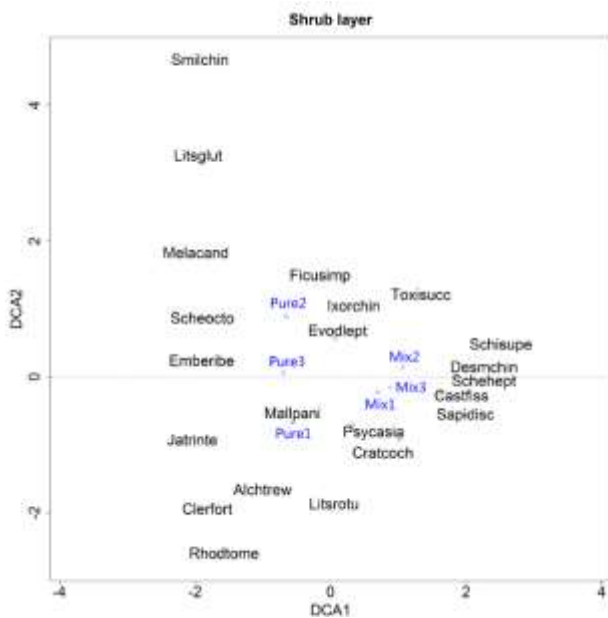
**Fig. 2:** The mean number of species per subplot for the three plant layers in each plot: tree layer (n = 3), shrub layer (n = 6), and herb layer (n = 6). There were no significant differences between the numbers of species in the three layers using a pairwise Wilcoxon test

**Table 4:** Relationships between species richness or cover and different tree layer variables for the understory, shrub layer and herb layer. Significance levels are: \* $P < 0.1$ , \*\* $P < 0.05$

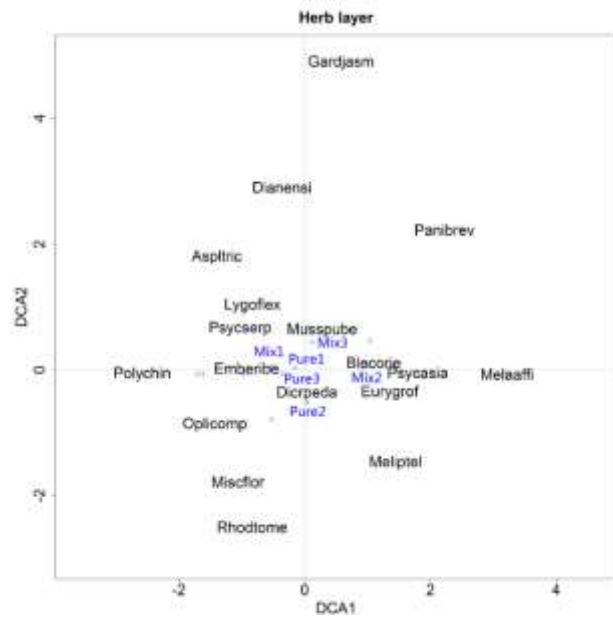
A)	Understory				Shrub layer				Herb layer			
	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$
Tree layer variables												
Cover [%]	0.175	0.923	-0.117	0.000	1.547	0.395	2.565	0.739	0.238	0.982	-0.353	0.000
DBH(cm)	0.009	0.000	-0.017	0.000	-0.088	0.000	-0.091	0.699	0.003	0.000	-0.010	0.000
Height [m]	0.002	0.000	0.005	0.898	0.035	0.700	0.000	0.000	0.003	0.000*	0.005	0.991**
Richness	0.009	0.256	-0.009	0.067	0.109	0.969	0.021	0.000	0.013	0.752	-0.011	0.614
B) Richness	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$
Tree layer variables												
Cover [%]	-5.321	0.861	14.320	0.000	-7.712	0.815	36.650	0.430	-2.206	0.000	35.790	0.000
DBH(cm)	0.050	0.000	-0.819	0.967*	-0.492	0.000	-1.528	0.917	0.534	0.308	-2.048	0.967*
Height [m]	-0.086	0.143	0.070	0.000	-0.046	0.000	0.050	0.000	-0.107	0.952*	0.175	0.000
Richness	-0.321	0.929	0.000	0.000	-0.346	0.039	0.214	0.000	-0.242	0.210	0.000	0.000

**Table 5:** Relationships between species richness and cover of the shrub layer and herb layer. There were no significant values

Shrub layer	Cover				Species richness			
	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$
Shrub layer variables								
Cover [%]					-2744	0000	15460	0926
Species richness	-0144	0000	0062	0926				
Herb layer variables								
Cover [%]	6856	0565	-0240	0000	-3112	0688	6357	0000
Species richness	-0301	0446	0041	0494	0192	0000	0714	0786
Herb layer								
	$\beta$ (pure)	$R^2_{adj}$	$\beta$ (mix)	$R^2_{adj}$	$\beta$ (pure)	R2	$\beta$ (mix)	$R^2_{adj}$
Shrub layer variables								
Cover [%]	0114	0565	-0022	0000	-2406	0446	1802	0494
Species richness	-0027	0688	0002	0000	0081	0000	1250	0786
Herb layer variables								
Cover [%]					-11110	0000	30500	0000
Species richness	-0023	0000	0006	0000				



**Fig. 3:** Detrended correspondence analysis (DCA)-ordination of vegetation survey data of the shrub layer in the six plots assigned to the two forest types: mixed *P. massoniana*/broad-leaved forest (Mix1, Mix2, and Mix3) and *P. massoniana* plantations (Pure1, Pure2, and Pure3). Single species cover values were correlated with the ordination axes and displayed in the diagram when correlation was significant at  $P < 0.01$



**Fig. 4:** Detrended correspondence analysis (DCA)-ordination of vegetation survey data of the herb layer in the six plots assigned to the two forest types: mixed *P. massoniana*/broad-leaved forest (Mix1, Mix2, and Mix3) and *P. massoniana* plantations (Pure1, Pure2, and Pure3). Single species cover values were correlated with the ordination axes and displayed in the diagram when correlation was significant at  $P < 0.01$

**Table 6:** The indicator values (IVs) for species in the shrub layer and herb layer. \*\*\* $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ 

		Species	IV	P
Shrub layer	<i>P. massoniana</i> /broad-leaved forests	<i>C. fissa</i>	0.816	0.002**
		<i>P. asiatica</i>	0.805	0.029*
	<i>P. massoniana</i> plantations	<i>M. paniculatus</i>	0.868	0.005**
		<i>E. ribes</i>	0.764	0.005**
		<i>M. candidum</i>	0.764	0.003**
		<i>C. fortunatum</i>	0.645	0.034*
		<i>A. trewioides</i>	0.610	0.046*
Herb layer	<i>P. massoniana</i> /broad-leaved forests	<i>D. dichotoma</i>	1	0.001***
		<i>M. pubescens</i>	0.917	0.001***
		<i>B. orientale</i>	0.913	0.001***
	<i>P. massoniana</i> plantations	<i>M. lepta</i>	0.98	0.001***
		<i>M. paniculatus</i>	0.957	0.001***
		<i>M. candidum</i>	0.764	0.004**
		<i>A. trewioides</i>	0.633	0.032*

## Discussion

There was a higher species richness of the understory layer in pure forests (8.8 species/100 m<sup>2</sup>) than in mixed forests (7.3 species/100 m<sup>2</sup>), which is contrary to our expectations that mixed forests are usually more suitable habitats for forest species. Duan *et al.* (2010) who compared the vegetation community in six plantations in South China and found that mixed forests absorbed more species than monoculture forests. Song and Yang (2001) showed that species diversity was much higher in *Larix gmelini*-*Betula platyphylla* forest than in *Larix gmelini* forest in the Daxing'an Mountains. In addition, Bruelheide *et al.* (2011) tested five successional stages of subtropical broad-leaved forests in southeastern China and found that species richness raised with successional stage. While in present study the *C. fortunatum*, *E. ribes*, *M. candidum* and *S. octophylla* were the leading species and only occurred in the Masson pine monocultures, which likely corresponds to the lower soil organic matter and soil pH in the plantations (Table 1). Another factor explaining the high diversity in Masson pine monocultures in the study area was the proximity of further natural secondary forests, providing an important seed source (Wang *et al.* 2010; Heinrichs and Pauchard 2015). The high coverage of the tree layer also resulted in the lower species diversity of the understory in the *P. massoniana*/broad-leaved forests, which was 141.2% compare with 85% in the Masson pine plantations (Both *et al.* 2011).

In the *P. massoniana* plantations and mixed *P. massoniana*/broad-leaved forests, the understory should become more similar in their species composition of seedlings during the course of succession. However, our result showed that species composition differed largely between the two forest types, which indicated that tree canopy structure affected the understory composition as demonstrated by Wang *et al.* (2014) and Ou *et al.* (2015) in other regions of China. The primary difference between the two forest types was the higher species richness of the shrub layer in *P. massoniana* plantations. Legendre *et al.* (2009) found that the altitude and terrain convexity have a great

influence on species composition and richness. In the study area, the altitude of the three *P. massoniana* plantation plots was lower than that of the three mixed *P. massoniana*/broad-leaved forest plots.

In the mixed *P. massoniana*/broad-leaved forest plots, two species were important indicators of the shrub layer and three species were significant indicators of the herb layer, while in the *P. massoniana* plantations there were five and four species, respectively (Table 6). Our finding of an increase in species richness and cover with successional age is in contract with the findings of Both *et al.* (2011), who showed that a decrease in the number and cover of herbaceous species with successional age. However, such declines in number and cover were found for the shrub layer woody species *M. paniculatus*, *C. fissa*, which were early-successional pioneer species and indicators for plantations. This result was accordant with the succession of the plantation to the mixed *P. massoniana*/broad-leaved forest, in which the tree layer was composed of *M. paniculatus*, *C. fissa*, and *P. massoniana*, suggesting that seed rain and the seed bank play significant role in providing seeds for plant recruitment in the understory (Wang *et al.* 2014).

Forests are structurally complex, especially the understory vegetation layers, which often account for the majority of species richness. Furthermore, variations in diversity in the overstory layer may affect understory diversity due to trees having a species-specific impact on resource availability and edaphic conditions, which influence the understory (Ampoorter *et al.* 2014). Several studies have shown a positive relationship between the species diversity of different strata (Beatty 2003; Gilliam 2007; Márialigeti *et al.* 2016; Zhang *et al.* 2017), in which the diversity of the tree layer positively affects the diversity of the understory through influencing the diversity of tree saplings and creating heterogeneous environmental conditions. Yet, in our study, increasing tree species richness reduced the species richness of the understory, shrub layer, and herb layer in *P. massoniana* plantations (Table 4B). This may be because monocultures have a significant impact on resources, while mixtures usually share the same tree species or species with

similar influences on the environment (Ampoorter *et al.* 2014). Another explanation is an increase in specialist herbivore loads, which can reduce plant diversity (Schuldt *et al.* 2010). In the *P. massoniana* plantations there was higher shrub layer species richness than in the mixed *P. massoniana*/broad-leaved forests, which is in contrast to findings by Both *et al.* (2011) who showed that there was lighter available in young successional forests thereby increasing shrub layer diversity. However, in the mixed *P. massoniana*/broad-leaved forests in this study, there was a higher coverage (423.75%) than in the *P. massoniana* plantations (256%) and the dense cover of the tree layer in the mixed *P. massoniana*/broad-leaved forests reduced the species richness of the herb layer (Table 4A), indicating a potential limitation for the admixture of tree species when tree cover is too dense. This is because herbaceous species prefer open areas with sufficient light (Schnitzer *et al.* 2008; Márialigeti *et al.* 2016), which is evidently influenced by canopy openness.

## Conclusion

Present study shows that *P. massoniana* plantations have a different species composition to that of mixed forests and they can be characterized as a very early-successional community. Results also demonstrate a high potential to convert Masson pine monocultures into more natural and stable mixed stands with broad-leaved forest species, especially when other tree species are already present in the tree layer. The positive relationship between tree species richness in the overstory and tree species diversity in the understory was probably because of suitable soil conditions. Our results further indicate a positive overstory-understory diversity relationship in the early to mid-successional stages and underline the effectiveness of admixing tree species in Masson pine plantations to maintain biodiversity in Chinese subtropical forests. Our findings can be used to manage forests to enhance species richness in these forests. In our future research, we measure the plant diversity and composition continuously, in order to get more accurate information of the plant development.

## Acknowledgments

We acknowledge Dr. Xiaodong Liu for his help in setting up the experiment plots. Authors thank the Dinghushan Biosphere Reserve for permission to undertake the fieldwork in the City Zhaoqing, Guangdong Province. This work was supported by funding from the Natural Science Foundation of Guangdong Basic and Applied Basic Research Foundation, through the research projects 2021A1515011092, as well the support from Qingyuan Forestry Bureau and Deqing Forestry Farm. The authors would like to thank all staff in the Yangmei, Jinji, Yingde, and Xiaolong forest farms. We also thank the editor and reviewers for their constructive comments on the manuscript.

## Author Contributions

Na Lin: Conducted data analysis and writing; Huiyan Xie: conducted the soil sampling and analysis; Tao Ma: conducted the vegetation survey; Chunyong Li conducted the tree survey; Demei Huang: conducted the vegetation survey. Mingxuan Zheng: conducted the vegetation survey; Shiqing Chen: Conceptualization, Methodology.

## Conflicts of Interest

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

## Funding Source

This research was funded by Natural Science Foundation of Guangdong Basic and Applied Basic Research, grant number "2021A1515011092" and "Qingyuan Forestry Bureau"

## References

- Ammer C (2019). Diversity and forest productivity in a changing climate. *New Phytol* 221:50–66
- Ampoorter E, L Baeten, J Koricheva, M Vanhellemont, V Verheyen (2014). Do diverse overstoreys induce diverse understoreys? Lessons learnt from an experimental – observational platform in Finland. *For Ecol Manage* 318:206–215
- Barrufol M, B Schmid, H Bruelheide, XL Chi, A Hector, KP Ma, S Michalski, ZY Tang, PA Niklaus (2013). Biodiversity promotes tree growth during succession in subtropical forest. *PLoS One* 8:1–9
- Beatty SW (2003). Habitat heterogeneity and maintenance of species in understory communities. In: *The Herbaceous Layer in Forests of Eastern North America*, pp:177–198. Gilliam FS, MR Roberts (Eds). Oxford University Press, New York, USA
- Bekker RM, JP Bakker, K Thompson (1997). Dispersal of plant species in time and space: Can nature development rely on soil seed banks and dispersal? In: *Species Dispersal and Land Use Processes*, pp:247–255. Cooper A, J Power (Eds). International Association of Landscape Ecology, Aberdeen, UK
- Both S, T Fang, M Böhnke, H Bruelheide, C Geißler, P Kühn, T Scholten, S Trogisch, A Erfmeier (2011). Lack of tree layer control on herb layer characteristics in a subtropical forest. *J Veg Sci* 22:1120–1131
- Brocknerhoff EG, H Jactel, JA Parrotta, CP Quine, J Sayer (2008). Plantation forests and biodiversity: Oxymoron or opportunity? *Biodivers Conserv* 17:925–951
- Bruelheide H, M Böhnke, S Both, T Fang, T Assmann, M Baruffol, J Bauhus, F Buscot, XY Chen, BY Ding, W Durka, A Erfmeier, M Fischer, C Geißler, D Guo, LD Guo, W Härdtle, JS He, A Hector, W Kröber, P Kühn, AC Lang, K Nadrowski, K Pei, M Scherer-Lorenzen, X Shi, T Scholten, A Schuldt, S Trogisch, GV Oheimb, E Welk, C Wirth, YT Wu, X Yang, X Zeng, S Zhang, H Zhou, KP Ma, B Schmid (2011). Community assembly during secondary succession in a Chinese subtropical forest. *Ecol Monogr* 81:25–41
- Cavard X, Y Bergeron, HYH Chen, D Paré, J Laganière, B Brassard (2011). Competition and facilitation between tree species change with stand development. *Oikos* 120:1683–1695
- Chamagne J, M Tanadini, D Frank, R Matula, CET Paine, CD Philipson, M Svátek, LA Turnbull, D Volářík, A Hector (2017). Forest diversity promotes individual tree growth in central European forest stands. *J Appl Ecol* 54:71–79
- Clay K, J Holah (1999). Fungal endophyte symbiosis and plant diversity in successional fields. *Science* 285:1742–1744



- Connell JH, RO Slatyer (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *Amer Nat* 111:1119–1144
- Debinski DM, PS Humphrey (1997). An integrated approach to biological diversity assessment. *Nat Area J* 17:355–365
- Duan W, H Ren, S Fu, J Wang, J Zhang, L Yang, C Huang (2010). Community comparison and determinant analysis of understory vegetation in six plantations in South China. *Restor Ecol* 18:206–214
- Dufrêne M, P Legendre (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Gilliam FS (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57:845–858
- Heinrichs S, A Pauchard (2015). Struggling to maintain native plant diversity in a peri-urban reserve surrounded by a highly anthropogenic matrix. *Biodivers Conserv* 24:2769–2788
- Hooper DU, EC Adair, BJ Cardinale, JE Byrnes, BA Hungate, KL Matulich, A Gonzalez, JE Duffy, L Gamfeldt, MI O'Connor (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108
- Laughlin DC, SC Hart, JP Kaye, MM Moore (2010). Evidence for indirect effects of plant diversity and composition on net nitrification. *Plant Soil* 330:435–445
- Legendre P, X Mi, H Ren, K Ma, M Yu, IF Sun, F He (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663–674
- Liang J, TW Crowther, N Picard, S Wiser, M Zhou, C Alberti, E-D Schulze, AD McGuire, F Bozzato, H Pretzsch, S de-Miguel, A Paquette, B Hérault, M Scherer-Lorenzen, CB Barrett, HB Glick, GM Hengeveld, G-J Nabuurs, S Pfautsch, H Viana, AC Vibrans, C Ammer, P Schall, D Verbyla, N Tchebakova, M Fischer, JV Watson, HYH Chen, XD Lei, M-J Schelhaas, HC Lu, D Gianelle, EI Parfenova, C Salas, E Lee, B Lee, HS Kim, H Bruelheide, DA Coomes, D Piotta, T Sunderland, B Schmid, S Gourlet-Fleury, B Sonké, R Tavani, J Zhu, S Brandl, J Vayreda, F Kitahara, EB Searle, VJ Neldner, MR Ngugi, C Baraloto, L Frizzera, R Balazy, J Oleksyn, T Zawila-Niedzwiecki, O Bouriadu, F Bussotti, L Finér, B Jaroszewicz, T Jucker, F Valladares, AM Jadodzinski, PL Peri, C Gonmadje, W Marthy, T O'Brien, EH Martin, AR Marshall, F Rovero, R Bitariho, PA Niklaus, P Alvarez-Loayza, N Chamuya, R Valencia, F Mortier, Wortel, NL Engone-Obiang, LV Ferreira, DE Odeke, RM Vasquez, SL Lewis, PB Reich (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science* 354:1–41
- Locky DA, SE Bayley, DH Vitt (2005). The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba Canada. *Wetlands* 25:564–582
- Márialigeti S, F Tinya, A Bidló, P Ódor (2016). Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary. *Plant Ecol* 217:549–563
- Marrs RH (1993). Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. *Adv Ecol Res* 24:241–300
- McCune B, JB Grace (2002) *Analysis of Ecological Communities*. Duke University, Durham, North Carolina, USA
- Nesheim I, R Halvorsen, I Nordal (2010). Plant composition in the Maya Biosphere Reserve: Natural and anthropogenic influences. *Plant Ecol* 208:93–122
- Oloff H, ME Ritchie (1998). Effects of herbivores on grassland plant diversity. *Trends Ecol Evol* 13:261–265
- Ou Z-Y, JZ Cao, WH Shen, YB Tan, QF He, YH Peng (2015). Understory Flora in Relation to Canopy Structure, Soil Nutrients, and Gap Light Regime: A case study in Southern China. *Pol J Environ Stud* 24:2559–2568
- Parde J (1955). A practical and efficient hypsometer: The Blume-Leiss. *Rev Franc* 7:207–210
- Putten WHVD, VD Stoel (1998). Effects of plant parasitic nematodes on spatio-temporal variation in natural vegetation. *Appl Soil Ecol* 10:253–262
- R Development Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>
- Ruiz-Benito P, L Gómez-Aparicio, A Paquette, C Messier, J Kattge, MA Zavala (2014). Diversity increases carbon storage and tree productivity in Spanish forests. *Glob Ecol Biogeogr* 23:311–322
- Schnitzer SA, J Mascaró, WP Carson (2008). Treefall gaps and the maintenance of plant species diversity in tropical forests. In: *Tropical Forest Community Ecology Oxford (UK)*, pp:196–209. Carson W, S Schnitzer (Eds). Wiley-Blackwell, New York, USA
- Schuld A, M Baruffol, M Böhnke, H Bruelheide, W Härdtle, AC Lang, K Nadrowski, G von Oheimb, W Voigt, H Zhou, T Assmann (2010). Tree diversity promotes insect herbivory in subtropical forests of southeast China. *J Ecol* 98:917–926
- Song GL, GT Yang (2001). Comparison of species diversity between *Larix gmelini* pure forest and *Larix gmelini*-*Betula platyphylla* mixed forest in Daxing'an mountains. *J For Res* 12:136–138
- Svenning JC, F Skov (2002). Mesoscale distribution of understorey plants in temperate forest (Kalo, Denmark): The importance of environment and dispersal. *Plant Ecol* 160:169–185
- Vilà M, J Vayreda, C Gracia, JJ Ibáñez (2003). Does tree diversity increase wood production in pine forests. *Oecologia* 135:299–303
- Wang J, D Li, H Ren, L Yang (2010). Seed supply and the regeneration potential for plantations and shrubland in southern China. *For Ecol Manage* 259:2390–2398
- Wang SX, H Guo, XA Wang, WY Fan, RY Duan (2014). Multiple-scale assessment of understory herb species diversity in pine plantations after long-term restoration. *Nord J Bot* 32:680–688
- Westover KM, AC Kennedy, SE Kelley (1997). Patterns of rhizosphere microbial community structure associated with co-occurring plant species. *J Ecol* 85:863–873
- Zhang Y, HYH Chen, AR Taylor (2017). Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. *Funct Ecol* 31:419–426