

Factors influencing the assembly of understory woody communities in *Pinus massoniana* plantations in Guangxi, China

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Research Article

Keywords: Functional traits, phylogeny, community assembly, *Pinus massoniana* plantations, tropic and subtropic Guangxi

Posted Date: September 6th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1977075/v1>

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Abstract

The study of community assembly, or the non-random process of species coming together, can reveal mechanisms that allow species to coexist and maintain their diversity. To investigate the community-building mechanisms behind the assembly of woody plant communities in *Pinus massoniana* plantations, we found plantations existing in three different climates (northern tropic, central subtropic, and southern subtropic) and at three different successional stages (young, middle-aged, and old-growth) in Guangxi, China. Using field community surveys and sampling, we collected, named, and analyzed a variety of woody plant species, and measured their functional using leaf thickness (LT), tissue density (LTD), area (LA), specific area (SLA), dry matter content (LDMC), nitrogen content per unit mass (LNC_{mass}), potassium content per unit mass (LKC_{mass}), and several other indicators. Using these communities' functional traits and computer models that generated their likely phylogeny, we were able to elucidate what forces may have driven the development of community-building mechanisms communities in their various climates and successional stages. We found: 1) The functional traits LT, LTD, SLA, LDMC, LNC_{mass} , and LKC_{mass} were likely phylogenetically conserved, while the other traits we measured likely were not. 2) When we based communities' structures on their functional traits, they were generally consistent their phylogenetic structure in southern and central subtropical plantations, middle-aged plantations in northern tropics and central subtropics, and old-growth plantations in northern tropics. In these communities, their assembly was driven by habitat filtering. 3) Communities in middle-aged and old-growth plantations in southern subtropical Guangxi had functional traits inconsistent with their phylogeny: while their functional traits indicated a tendency to aggregate, their phylogeny indicated a shift from aggregation to dispersion. In these communities, their assembly was driven by habitat filtering and similarity limitation. This information can then be used to enhance the function of ecosystem services and protect biodiversity of communities in *Pinus massoniana* plantations through tropic and subtropic China.

Introduction

Biodiversity within plant communities can reveal their ecological processes, such as evolutionary history, environmental screening, interspecific interactions, and stochastic processes. To this point, Diamond (1975) introduced "community assembly" to the field of biodiversity to refer to the non-random process of species coming together to form a community. As the study of community ecology has advanced, theories have arisen to explain the process and rules of community construction, such as "species pool," "dispersal limitation," "environmental filtering," and "niches" (Vellend, 2010; Götzenberger et al., 2012). While these theories are valuable, quantitative analyses, like studying the phylogenetic structure of communities, can similarly elucidate the process of community construction (Webb et al., 2002). Phylogenetic structure is an especially important tool to reveal how community biodiversity changes at different temporal and spatial scales (Jarzyna and Jetz, 2016). As such, analyzing a community's assembly and phylogenetic structure are crucial to maintaining and conserving biodiversity.

Plantation forests are an important resources within the global supply of vegetation, not only because they supply timber and timber-derived products, but also because they have secondary environmental benefits, such as sequestering carbon, increasing soil health, and providing habitat for wildlife(Shu et al., 2022; Ali et al., 2022). In China's forestry industry, which produces 20% of the world's timber supply, Guangxi produces 40% of timber, and *Pinus massoniana* is one of the three major species comprising their timber forests. *P. massoniana*

plantations are incredibly productive due to their drought resistance and adaptation to infertile conditions (Mo et al., 2002). However, in the long-term management of these plantation, *P. massoniana* have been maintained as the sole tree species, and natural ecosystem development has been intentionally stifled (Li et al., 2020). To this point, research on *P. massoniana* plantations has focused on the classical areas of species composition and community structure (Wu et al., 2020; Gao et al., 2018; Huang et al., 2018), diversity patterns at multiple scales (Zhang et al., 2020; Chen et al., 2019), and community succession (Chen et al., 2010). However, a gap exists in our understanding of the forces causing these species to assemble and adjust to varying conditions over their community succession.

Woody plant communities in plantations play a key role in regulating the structure of forest communities because they maintain biodiversity and stand production (He and Fu, 2002; Chen et al., 2013). As such, to improve the quality and efficiency of ecosystem services of communities developing in *P. massoniana* plantations, research is needed on the factors driving the assembly of these communities as the pure plantations transform in to diverse ecosystems. It is theorized that plants' functional traits are what allow communities to adapt and assemble to varying climates and habitats (Ma et al., 2018). Plant functional traits are the morphological, physiological, and phenological characteristics of a plant that determine its ability to acquire, use, and preserve resources, which influence their survival, growth, and reproduction (Violle et al., 2007). Because leaves allow plants to access and use resources in varying habitats and climates, they are often used way to represent measurable functional traits of plants. Within a given plant community, different species of plants tend to have leaves with similar functional traits, allowing leaves to be used in ecological studies to unravel "strategies" species use to adapt to changing environments, and to understand mechanisms that allowed them to assemble their community (Cornelissen, et al., 2003). In summary, the functional traits of plants can be used to predict community and ecosystem function, understand patterns of functional diversity, and evaluate mechanisms that allow species to coexist within different climates and habitats.

This study illuminated mechanisms that drove species use to assemble and maintain their communities by investigating characteristics of woody plant communities in *P. massoniana* plantations at different successional stages and in different climates. Specifically, we measured the functional traits of leaves collected from these communities and used models to predict their phylogenetic structure so that we could answer the following questions: 1) Do mechanisms of community assembly of the woody plants in *P. massoniana* plantations change when they exist in different climates and in plantations at different successional stages? 2) Is there agreement between what we learn about community assembly based on their functional traits and based on their modeled phylogenetic structure?

Materials And Methods

Study Area and Sampling Design

Guangxi, China, lies on a low latitude and spans three types of climatic zones: northern tropical, southern subtropical, and central subtropical. The study sites were selected from the Paiyangshan forest farm in the northern tropics, the Zhenlong forest farm in the southern subtropics, and the Huashan forest farm in the central subtropics of Guangxi. Huashan forest farm is located in central Huanjiang Maonan Autonomous County in northwest Guangxi, with geographical coordinates 108°06'-108°38' E, 25°05'-25°31' N. It is a low

mountainous landscape with an altitude of 300-600 m above sea level. Furthermore, its mid-subtropical monsoon climate causes an average annual precipitation of 1402.1 mm and average annual temperature of 19.8 °C. Zhenlong forest farm is located in northern Hengxian County, in south-central Guangxi, with geographical coordinates of 109°08'-109°19' E, 23°02'-23°08' N. It is also a low mountainous terrain with an altitude of 400-700 m above sea level. Furthermore, its southern subtropical monsoon climate causes an average annual precipitation of 1477.8 mm and an average annual temperature of 21.5 °C and. Finally, Paiyangshan forest farm is located in Ningming County in southwest Guangxi, with geographical coordinates of 106°30'-107°15' E, 21°15'-22°30' N. It is also a low mountainous terrain with an altitude of 200-800 m. Its northern tropical monsoon climate causes an average annual precipitation of 1475 mm and an average annual temperature of 21.8 °C. These conditions are summarized in Table 1 and Figure 1.

The community survey method was used to select seven types of *P. massoniana* plantations in Huashan forest farm, Zhenlong forest farm, and Paiyangshan forest farm to find similar stand conditions but different geographical conditions for this study. In this method, the characteristics and structure of the investigated communities are counted by surveying small-area sections that are representative of species and structures in the sample plot. Details for the sample plots are shown in Table 1. For each type, we established three 20 m×20 m sample plots, and four 10 m×10 m subplots in each sample plot, all of which are managed by the Guangxi Forestry Research Institute of China for long-term monitoring (Fan and Yang, 2012). Woody plants ≥1 cm in diameter at breast height were surveyed in each sample plot and their height, species name, diameter at breast height were recorded. These sites were planted in the early stages of *P. massoniana* plantation development, and they were maintained for three consecutive years. Field community surveys and sampling were carried out in July and August each year. Unidentified plant specimen were collected and sent to Guangxi Institute of Botany to be identified. Species nomenclature was adopted from the Flora of China (<http://frps.eflora.cn>) and the Flora of China database (<http://foc.eflora.cn/>).

Table 1. Sample plots of *P. massoniana* plantations

Climate	Plot Location	Forest Age	Year Planted	Aspect	Slope position	Altitude (m)	Longitude	Latitude
Northern tropical	Paiyangshan forest farm	middle-aged	2005	SW	Mid	426	107°09'E	22°01'N
Northern tropical	Paiyangshan forest farm	old-growth	1958	NE	Mid to Upper	425	107°12'E	22°01'N
Southern subtropical	Zhenlong forest farm	young	2012	NW	Mid	313	109°16'E	23°01'N
Southern subtropical	Zhenlong forest farm	middle-aged	1999	SE	Mid to Upper	378	109°10'E	23°03'N
Southern subtropical	Zhenlong forest farm	old-growth	1960	SE	Upper	326	109°09'E	23°02'N
Central subtropical	Huashan forest farm	young	2009	N	Mid to Upper	314	108°18'E	25°07'N
Central subtropical	Huashan forest farm	Middle-aged	2000	SE	Mid	315	108°18'E	25°06'N

Measuring Functional Traits

To quantify the functional traits of these species, we measured leaf area (LA, cm²), leaf thickness (LT, mm), saturated fresh weight (FW, g), dry leaf weight (DW, g), specific leaf area (SLA, cm²·g⁻¹), leaf dry matter content (LDMC, g/g), leaf tissue density (LTD, kg/m³), leaf carbon content (LCC_{mass}, mg·g⁻¹), leaf nitrogen content (LNC_{mass}, mg·g⁻¹), phosphorus content per unit mass of leaf (LPC_{mass}, mg·g⁻¹), potassium content per unit mass of leaf (LKC_{mass}, mg·g⁻¹), carbon to nitrogen ratio (C/N), and nitrogen to phosphorus ratio (N/P). To collect these measurements, we removed petioles from each species we collected to separate the leaves from the branches, washed the separated leaves gently under running water to remove soil and impurities, and then dried them. The LA of the woody plants was measured using a leaf area meter. We measured the LT using digital calipers at three random measurement points, taking care to avoid the main leaf veins, and averaged these values to calculate leaf thickness. The leaves were then placed in a light-proof environment, soaked in ice water at a temperature of 5 °C for 24 h, removed, gently blotted with clean filter paper, flattened, and weighed on an electronic balance (accuracy: 0.0001 g) to obtain their FW. Next, leaf samples were placed in paper bags, and put in an oven at 75 °C to dry for at least 48 h until a constant weight was reached. After that, they were removed and quickly weighed for their DW. SLA, LDMC, and LTD were calculated using the following equations:

$$\text{LDMC g/g} = \text{DW g} / \text{FW g} \quad (2-1)$$

$$\text{SLA cm}^2/\text{g} = \text{LA cm}^2 / \text{DW g} \quad (2-2)$$

$$\text{LTD kg/m}^3 = 1/ \text{SLA cm}^2/\text{g} \times \text{LT mm} \times 10^4 \quad (2-3)$$

For each species, three more healthy, mature plants were selected, and their complete leaves were collected from different locations on the branch, and the petioles were removed, dried to a constant weight, crushed, and sieved through 80 mesh to examine their nutrient content using an elemental analyzer. This instrument measured the LCC and LNC per unit mass of leaf. Next, plant samples were digested with H₂SO₄-H₂O₂, and the molybdenum antimony colorimetric method was used to measure the LPC_{mass}. LKC_{mass} was measured by atomic absorption spectrometry, and finally C/N and N/P were calculated.

Constructing the Phylogenetic Tree

We compared the species we collected from the *P. massoniana* plantations to those listed in Flora of China, and recorded their Latin scientific names. After verifying our findings, we listed the collected specimen in a comma-separated (csv) format with three columns: species (e.g. *Acacia_berlandieri*), genus (e.g. *Acacia*), and family (e.g. *Fabaceae*). We found the phylogenetic relationships of the woody plants based on the global plant phylogenetic tree established by Jin and Qian (2019). Finally, a phylogenetic tree was used to perform correlation operations (Fig. 1).

Examining the phylogenetic signals

We used *Blomberg' K* to examine the phylogenetic signal for functional traits (Blomberg et al., 2003). *Blomberg' K* is a continuous value extending from 0 to infinity. If *K* = 1, species functional traits evolved in a stochastic fashion along Brownian motion. If *K* < 1, there is less similarity between related species than would be expected

by chance. If $K > 1$, there is more similarity between related species than would be expected by chance. As such, these values can be used to determine the likelihood that these species developed functional traits as a community. We compared the observed K values with random K values that we generated by rearranging species at the end of the phylogenetic tree 999 times. If the observed K value is greater than the value generated by the random model more than 950 times ($P < 0.05$), this indicates there is a significant phylogenetic signal for functional traits (O'Brien, 2014).

Calculating the kinship index

The Net relatedness index (NRI) and the Nearest taxon index (NTI) were used as indicators to quantify how closely species were phylogenetically related (Webb et al, 2002). The phylogenetic diversity indices NTI and NRI are calculated using the mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD), respectively, of all species in the sample. Both metrics are based on the null model approach. NTI and NRI are calculated as:

$$\text{NRI} = -1 \times \left[\frac{\text{MPD}_{\text{obs}} - \text{mean}(\text{MPD}_{\text{rand}})}{\text{sd}(\text{MPD}_{\text{rand}})} \right] \quad (2-4)$$

$$\text{NTI} = -1 \times \left[\frac{\text{MNTD}_{\text{obs}} - \text{mean}(\text{MNTD}_{\text{rand}})}{\text{sd}(\text{MNTD}_{\text{rand}})} \right] \quad (2-5)$$

where MPD_{rand} and $\text{MNTD}_{\text{rand}}$ represent the MPD and MNTD of a random community ($n=999$), MPD_{obs} and MNTD_{obs} are calculated from the actual community, $\text{mean}(\text{MPD}_{\text{rand}})$ and $\text{mean}(\text{MNTD}_{\text{rand}})$ are the means; and $\text{sd}(\text{MPD}_{\text{rand}})$ and $\text{sd}(\text{MNTD}_{\text{rand}})$ are the standard deviations. In contrast to NRI, NTI is calculated using the same formula, except that MPD is replaced by MNTD.

Functional trait structure was calculated using mean pairwise trait distance ($\text{trait}(\text{MPD})$) and nearest trait distance ($\text{trait}(\text{MNTD})$). After comparing $\text{trait}(\text{MPD})$ and $\text{trait}(\text{MNTD})$ to the pattern generated by the null model, these values were expressed in terms of standardized community mean pairwise trait distances ($\text{trait SES}(\text{MPD})$) and nearest trait distances ($\text{trait SES}(\text{MNTD})$). The index is calculated similarly to the community phylogenetic structure, using the following equations:

$$\text{trait SES}(\text{MPD}) = -1 \times \left[\frac{\text{MPD}_{\text{obs}} - \text{mean}(\text{MPD}_{\text{rand}})}{\text{sd}(\text{MPD}_{\text{rand}})} \right] \quad (2-6)$$

$$\text{trait SES}(\text{MNTD}) = -1 \times \left[\frac{\text{MNTD}_{\text{obs}} - \text{mean}(\text{MNTD}_{\text{rand}})}{\text{sd}(\text{MNTD}_{\text{rand}})} \right] \quad (2-7)$$

where MPD_{rand} and $\text{MNTD}_{\text{rand}}$ represent the expected MPD and MNTD of a random community ($n=999$), MPD_{obs} and MNTD_{obs} are the values calculated from the actual community, $\text{mean}(\text{MPD}_{\text{rand}})$ and $\text{mean}(\text{MNTD}_{\text{rand}})$ are their means, and $\text{sd}(\text{MPD}_{\text{rand}})$ and $\text{sd}(\text{MNTD}_{\text{rand}})$ are standard deviations. Compared to $\text{trait SES}(\text{MPD})$, $\text{trait SES}(\text{MNTD})$ is calculated using the same formula, except that MPD is replaced by MNTD.

When both NRI and NTI or trait SES(MPD) and trait SES(MNTD) are positive, they indicate that species aggregated within a community to develop their phylogenetic or functional trait together; if both are negative, the species diverged from a communities to develop their phylogenetic or functional trait structure; if both are zero, the phylogenetic or functional trait structure of the species is in a random state (Lili et al., 2017). When the NRI and NTI or trait SES (MPD) and trait SES (MNTD) are greater than 1.96 or less than -1.96, then aggregation and divergence, respectively, are significant (Zhao et al., 2020).

Data Analysis

Phylogenetic trees were constructed using the V. PhyloMaker package. *Blomberg's K* values, NRI indices, NTI indices, trait SES(MPD) and trait SES(MNTD) were calculated using the Picante package. Data were collated using Excel 2022 software, statistical analyses were completed via R(4.1.2) software, and plots were generated using Origin 2019.

Results

Phylogenetic signals of functional traits

We collected 96 woody plant species from communities in different climates and successional stages of *P. massoniana* plantations. To investigate whether these species' leaf functional traits evolved together, as an assembled community, across all climates and successional stages, we used the *Blomberg's K* test for phylogenetic signal on the values calculated for leaf functional traits (Table 2). The *K* values of the leave's functional traits ranged from 0.054 to 0.196. Because these *K* values were < 1 , there is less similarity between related species than would be expected by chance. However, when the functional traits were compared to the randomly generated phylogenetic tree, LT, LTD, SLA, LDMC, LNC_{mass} , and LKC_{mass} had significant ($P < 0.05$) phylogenetic signals for conserved traits. These results indicate that using a Brownian motion model of evolution, these species' functional traits had weak phylogenetic signals and were unlikely to have developed together as a community. In addition, the *K* values of LT, LTD, SLA, LDMC, LNC_{mass} , and LKC_{mass} were close to 0, indicating that the evolutionary process of the traits was stochastic and not well-conserved. For the remaining functional traits—LA, LCC_{mass} , LPC_{mass} —the phylogenetic signal was not significant, which indicates a non-conservative trait. This implies the association between species and the evolutionary history of the species are weak.

Table 2. Phylogenetic signatures of functional leaf traits in woody plants found in *P. massoniana* plantations grown in different climates

Traits	<i>Blombergs' K</i>	<i>P</i>
LT	0.114	0.041
LTD	0.137	0.014
LA	0.095	0.141
SLA	0.145	0.007
LDMC	0.161	0.014
LCC _{mass}	0.102	0.349
LNC _{mass}	0.196	0.002
LPC _{mass}	0.054	0.755
LKC _{mass}	0.185	0.009

Note: $P \geq 0.05$ is an insignificant difference; $0.01 \leq P < 0.05$ is a significant difference; $P < 0.01$ is a highly significant difference.

Community structure based on functional traits

Young *P. massoniana* plantations in southern and central subtropical Guangxi

We evaluated functional traits of woody plant communities in young *P. massoniana* plantations in southern and central subtropical Guangxi (Fig. 1-a). For communities collected from plantations in young successional stages, those in southern subtropics had mean trait SES(MPD) and trait SES(MNTD) values of 0.80 and 0.39, respectively, and 0.86 and 0.80 in central subtropics. Because these values were greater than 0, the functional traits indicate that communities had a tendency to aggregate. Further, because the values of functional traits increased from the southern to the central subtropics, it is possible that community structures in young *P. massoniana* plantations increase with latitude.

Middle-aged *P. massoniana* plantations in Guangxi in different climates

We evaluated functional traits in woody plant communities collected from middle-aged *P. massoniana* plantations across all three climates in Guangxi (Fig. 1-b). For communities collected from plantations in middle-aged successional stages, those in northern tropics had mean trait SES(MPD) and trait SES(MNTD) values of 1.47 and 1.40, respectively, 2.52 and 1.38 in southern subtropics, and 1.66 and 0.36 in the central subtropics. The trait SES(MPD) increased and then decreased with increasing latitude, while the trait SES(MNTD) decreased with increasing latitude. The mean trait SES(MPD) value of communities in the south subtropical zone was greater than 1.96, indicating significant aggregation. However, its mean trait SES(MNTD) value was less than 0, which indicates dispersion. Thus, the functional trait-based community structure of this stand was probably influenced by both aggregation and dispersion. The functional trait structure of woody plants in the rest of the community showed a tendency to aggregate. In summary, when the community structure is described based on functional traits for middle-aged *P. massoniana* plantations in different climates in Guangxi, there is little relationship between traits and latitude.

Old-growth P. massoniana plantations in northern tropical and southern subtropical Guangxi

We evaluated functional traits in woody plant communities collected from old-growth *P. massoniana* plantations in northern tropical and southern subtropical Guangxi (Fig. 1-c). For communities collected from plantations in old-growth successional stages, those northern tropical plantations had mean trait SES(MPD) and trait SES(MNTD) values of 0.60 and 0.88, respectively, and 2.63 and 2.09 in southern subtropics. All of these values were greater than 0, indicating a general tendency for communities to aggregate based on functional traits. Because these values were greater than 1.96 in the southern subtropical plantation, there is likely significant aggregation. Further, because the values of functional traits increased from the northern tropics to the southern subtropics, it is possible that community structures in old-growth *P. massoniana* plantations significantly increase with latitude.

Phylogenetic structure of woody plant communities

Young P. massoniana plantations in south subtropical and central subtropical Guangxi

In evaluating the phylogenetic structure of woody plant communities in young *P. massoniana* plantations in Guangxi (Fig. 2-a), the mean values of NRI and NTI in the south subtropics were 0.61 and 1.07, respectively, while those in central subtropics were 1.00 and 0.50. Because the values are greater than 0, the community phylogenetic structure showed a tendency to aggregate. Further, because NRI increased from southern to central subtropics, the phylogenetic structure of these communities may increase with latitude; whereas NTI decreased, and may decrease with latitude.

Middle-aged P. massoniana plantations in different climates in Guangxi

In evaluating the phylogenetic structure of woody plant communities in middle-aged *P. massoniana* plantations in Guangxi (Fig. 2-b), the mean values of NRI and NTI in the northern tropics were 1.07 and 0.95, respectively, 1.22 and 0.43 in the central subtropics, and 0.26 and -0.31 in the southern subtropics. The mean NRI values were significantly higher in the northern tropics and the central subtropics than in the southern subtropics, initially decreasing with increasing latitude, and then increasing with latitude. Alternatively, NTI decreased from the northern, to central, to southern topics, indicating an inverse relationship between NTI and latitude.

old-growth P. massoniana plantations in northern tropical and southern subtropical Guangxi

In evaluating the phylogenetic structure of woody plant communities in old-growth forests of *P. massoniana* in Guangxi (Fig. 2-c), the mean values of NRI and NTI in the northern tropics were 0.17 and 1.54, respectively, and 0.15 and -1.06 in the southern subtropics. These values were greater than 0 in northern Guangxi, indicating that their community phylogenetic structure has a tendency to aggregate. Conversely, the southern subtropical old-growth community had a positive NRI value, indicating aggregation, and a negative NTI values, indicating random or divergent phylogeny. Thus, the phylogenetic structure of the woody plant communities in the *P. massoniana* old-growth forests in Guangxi tended to decrease with increasing latitude.

Discussion

Phylogenetic signatures of functional leaf traits

Functional traits in this study were represented through measuring LA, LT, LTD, SLA, LDMC, LNC_{mass}, LKC_{mass}, LCC_{mass}, and LPC_{mass} from leaves collected from woody plants in *P. massoniana* plantations. Functional traits can be associated with phylogenetic signals to determine the extent to which a community evolved functional traits together as a response to a common environmental stressor, which can in turn be used to indicate the particular causes of community-building (Weiher et al., 2011).

We used *Blomberg's K* to measure phylogenetic signal of these woody plant communities in different climates in Guangxi, and found that the phylogenetic signals of LT, LTD, SLA, LDMC, LNC_{mass}, and LKC_{mass} were significant ($P < 0.05$), indicating that these functional traits are closely linked to the communities' phylogenetic histories and are significantly influenced by genetic differences. As species evolve, their functional traits are usually conserved. In other words, if species within a community are closer in their evolutionary history, they will likely have more similar functional traits. Thus, if species within these woody plant communities in *P. massoniana* plantations are more closely related to each other, they are likely to have similar LT, LTD, SLA, LDMC, LNC_{mass}, LKC_{mass}, etc. are in the. Although all of these traits had significant phylogenetic signals, their *K* values were all small, ranging from 0.054 to 0.196, implying that the phylogenetic conservation of these traits was not strong. This could be due to a combination of phylogenetic relationships and environmental factors that influenced the traits. Previous studies have corroborated that functional traits do not always have significant phylogenetic signals (Blomberg et al., 2003). In regards to our findings, this could mean that not all leaf functional traits are significantly associated with phylogenetic history, which is consistent with our findings.

Effects of climate on community structure based on functional traits

In this study, functional trait structures of woody plant communities were characterized using an affinity index to investigate community-building mechanisms based on data collected about leaf traits. We found that in *P. massoniana* plantations, these woody plant communities' functional traits varied based on their climates. Using functional trait pattern, the community structures in young plantations in the southern and central subtropics tended to be aggregated, and the degree of aggregation increased as the spatial scale increased. This is likely because woody plant communities tend to be influenced by habitat filtering in the ecological niche theory (Hong, 2018). In middle-aged forest in these plantations, there was an overall decrease in the degree of aggregation with changes in climatic conditions, reflecting that this community is equally affected by habitat filtering, but that this effect tends to diminish with community age.

In general, these communities tended to aggregate regardless of climate, except for significant aggregation (trait SES(MPD) and trait SES(MNTD) > 1.96) in southern subtropical old-growth *P. massoniana* plantations. This effect intensified with latitude, suggesting an increased competitive effect between individuals. Thus, changing climate likely plays a key role in the construction of plant communities. When plant communities are being constructed where environmental constraints exist, environmental filtering tends to dominate. In this study, as latitude increased and temperature decreased, only species that could adapt to these changes could survive. As this environmental filtering takes place, the surviving species must carry forward traits that allow them to adapt to the habitat. These species co-existing within one community, and thus tend to have similar functional traits. Functional traits exhibit a certain degree of conservatism in phylogenetic structure, it is likely

that the functional trait structure of species as a whole in the woody plant communities of the *P. massoniana* plantations under different climatic conditions tends to cluster.

Effect of climate on community phylogenetic structure

There are two community phylogenetic indices included in Phylocom, the Net Relative Index (NRI) and the Nearest Relative Index (NTI). The NRI is community-level and characterizes the phylogenetic pattern of the entire developmental tree; whereas the NTI is based on nearest relatives, and characterizes the most recent phylogenetic relationships at the end of the phylogenetic evolutionary tree. In analyzing how joint functional traits and phylogenetic structure relate to community construction, Campbell and Webb (2022) suggested that in a phylogenetically conserved state, habitat filtering leads to aggregation of phylogenetic structure, while similarity limitation produces random or divergent phylogenetic structure. From a phylogenetic point of view, the structure of the community is aggregated in young *P. massoniana* plantations in southern and central subtropical Guangxi, indicating that the species in these communities are closely related. This could be because woody plants in young forest communities playing a pioneering role: young forest communities are mainly composed of species with similar adaptive abilities and close affinities, and are forced by habitat filtering to form ecological niche aggregations.

In southern middle-aged and old-growth *P. massoniana* plantations in Guangxi, the NRI index indicated that community phylogenetic structure tended to aggregate, whereas the NTI index showed aggregation and divergence. This may be because habitat filtering is the primary force for species coexistence in northern tropical and central subtropical middle-aged forest communities, while similarity limitation is a secondary force. The phylogenetic aggregation of young and middle-aged communities tends to decrease with increasing latitude, and the phylogenetic aggregation of the communities tends to decrease with increasing latitude. In this case, it is possible that there are differences in habitat heterogeneity, and the habitat filtering effect diminishes with latitude. The phylogenetic structure of woody plant communities in middle-aged and old-growth *P. massoniana* plantations in northern Guangxi tended to aggregate. Communities in middle-aged forests had little change in the degree of community phylogenetic aggregation with increasing latitude, while old-growth forests tended to increase phylogenetic aggregation with increasing latitude. This phenomena could be due to a combination of greater heterogeneity in old-growth forests and stable environmental filtering in the region, resulting in phylogenetic aggregation.

Habitats influence growing conditions for plant species in a variety of ways, which can reduce interspecific competition, and allow more plant species to co-exist in the habitat. Habitat filtering leads to a greater convergence of functional traits in species than would be expected by chance. In this study, the mean NRI values of middle-aged and old-growth stands of *P. massoniana* in South Asia tended to cluster and the mean NTI values tended to diverge, with the two indices yielding opposite results. This seeming inconsistency could indicate that the species composition in the middle-aged and old-growth stands evolved convergently due to environmental pressures. Although species with similar traits aggregate due to habitat filtering, they are not closely related to each other, causing the phylogenetic structure to show a dispersed state. Meanwhile, competitive exclusion leaves some species “behind,” granting them different traits even though they are grouped together. Without a certain regularity of kinship, the phylogenetic structure of the community left behind might become phylogenetically random or diffuse. In this way, our results suggested recent community

differentiation (Kress et al., 2009), where the community was influenced by a combination of habitat filtering and competitive exclusion. The inconsistency between NTI and NRI may have also been influenced by the scope and sensitivity of the two parameters themselves, as NRI measures phylogenetic differences between all species on the basis of a whole community, but NTI measures phylogenetic differences between species on the basis of closest affinity. In this case, the inconsistency between NTI and NRI reflects that these indices are not synergistic.

In many ecosystems, habitat filtering is a key processes that affects resource gradients (Cornwell and Ackerly, 2009). Weiher and Keddy (2001) proposed a theory of community construction and the principle of phylogenetic conservatism of ecological niches. They suggested that under habitat filtering, species more easily develop habitat preferences, enabling plants in the community to survive in their optimum habitat. Swenson et al. (2006) noted a phylogeny is more likely to exhibit aggregation as the species pool exist in larger spatial scales (Sweson et al., 2006). Typically, environmental factors are characterized by varying gradients at larger spatial scales. Thus, climate, as a typical large-scale factor, greatly influences plant screening mechanisms. In summary, most communities demonstrated that ecological niche processes were more important for woody plant community composition and maintenance in *P. massoniana* plantations in different climates in Guangxi.

Determining consistency of functional trait structures and phylogenetic structures of communities

Combining functional trait structure with phylogenetic structure is an effective method to evaluate community building mechanisms. In the woody plant communities of *P. massoniana* plantations in Guangxi, all woody plant leaf functional traits showed weak but significant phylogenetic signals, meaning that at the sample-scale, phylogenetic relationships could be roughly used as a proxy for trait similarity. Community construction of woody plants in *P. massoniana* plantations is a complex and specific process, and the intensity of different ecological processes in woody plant communities varies in different climates. Varying latitudes create differences in water and heat conditions, to which the communities must adapt to survive. The structure of woody plant communities based on functional traits was consistent with the phylogenetic structure of the community, and the main driving force influencing community construction was habitat filtering. Alternatively, in middle-aged and old-growth woody plant communities, community structure based on functional traits was inconsistent with community phylogeny. In this instance, functional trait-based community structure showed a tendency towards aggregation, whereas phylogeny showed a shift from aggregation to dispersion. Regardless, habitat filtering and similarity limitation were likely the driving forces for community construction. Both functional trait-based community structure and community phylogenetic structure are somewhat scale-dependent. The functional and genealogical structure of communities at the same spatial scale are likely to be inconsistent and, in most cases, to show different patterns (Cavender-Bares et al., 2006). In addition, although the signal was weak, the significant ($P < 0.05$) phylogenetic signal for most of the plant functional traits in this study may be why the structure of functional traits in most communities were corroborated by their phylogenetic structure. The role of environmental factors in plant communities can lead to a convergence of phylogenetic relationships between certain communities (Goldsmith et al., 2013). Pipenbaher et al. (2013) studied northern Adriatic meadows and found that the limiting effect of similarity was the main driving force for community-building mechanisms, while environmental filtering played a more important role in forage community-building. By studying the phylogenetic structure and functional trait structure of forests in the

French Neotropics, Baraloto et al. (2012) found that environmental filtering drove the formation of Neotropical forest communities. Luo et al. (2019) found that the phylogeny and functional structure of trees showed aggregation in both low- and high-elevation communities, suggesting that environmental filtering may play a dominant role when there is drought at low elevation and low temperatures at high elevation. The relationship between phylogeny and functional traits is generally reflected at larger taxonomic scales of study (Luo et al., 2019). However, as our study shows, functional traits and phylogenetic patterns do not always coincide. Hao et al. (2018) performed a study at a scale similar to ours, and similarly found that the phylogenetic structure and functional trait structure of secondary mixed coniferous forests in the Jiaohe region and the middle- and lower-elevations of the northern slopes of the Qinling Mountains were inconsistent.

Conclusion

In studying the community structure of woody plants in *P. massoniana* plantations in different climates in Guangxi, we found that the species from young (southern and central subtropic), middle-aged (northern tropic and central subtropic), and old-growth (northern tropic) *P. massoniana* plantations had community structures consistent with their phylogenetic structure. Filtering. The community structure based on functional traits was inconsistent with the phylogenetic structure of the community, because the community structure had a tendency to aggregate, while the phylogenetic structure had a tendency to shift from aggregation to dispersion. This study provides a theoretical basis for exploring the community building mechanisms of woody plants in the *P. massoniana* plantations, as well as a theoretical basis for revegetation in the region.

Abbreviations

LT, leaf thickness; LTD, leaf tissue density; LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LCC_{mass} , leaf carbon content content per unit mass; LNC_{mass} , leaf nitrogen content per unit mass; LPC_{mass} , leaf phosphorus content per unit mass; LKC_{mass} , leaf potassium content per unit mass; NRI, Net relatedness index; NTI, nearest taxon index; (trait SES(MPD)), the mean pairwise nodal distance (MPD); (trait SES(MNTD)), the mean nearest taxa nodal distance (MNTD)

Declarations

Acknowledgements

We are supported in part by the Open Research Fund of Guangxi Key Laboratory of Superior Timber Trees Resource Cultivation (2019-B-04-01), Guangxi Key Research and Development Program (AB21220057), the Science and Technology Major Project of Guangxi (AA17204087-7).

We would like to thank the HighEdit company for its assistance editing the English version of this manuscript.

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Figures

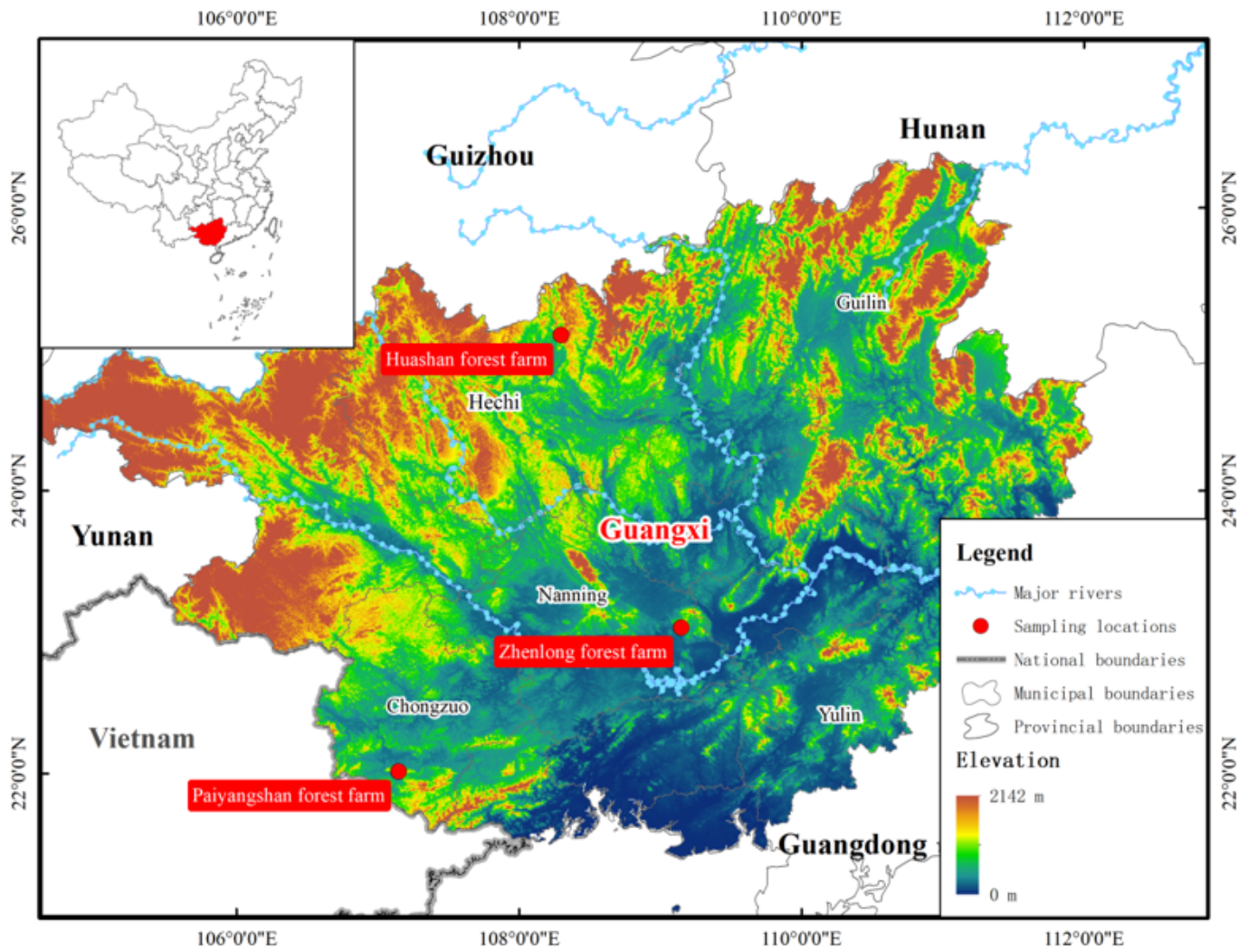


Figure 1

Location of the study area

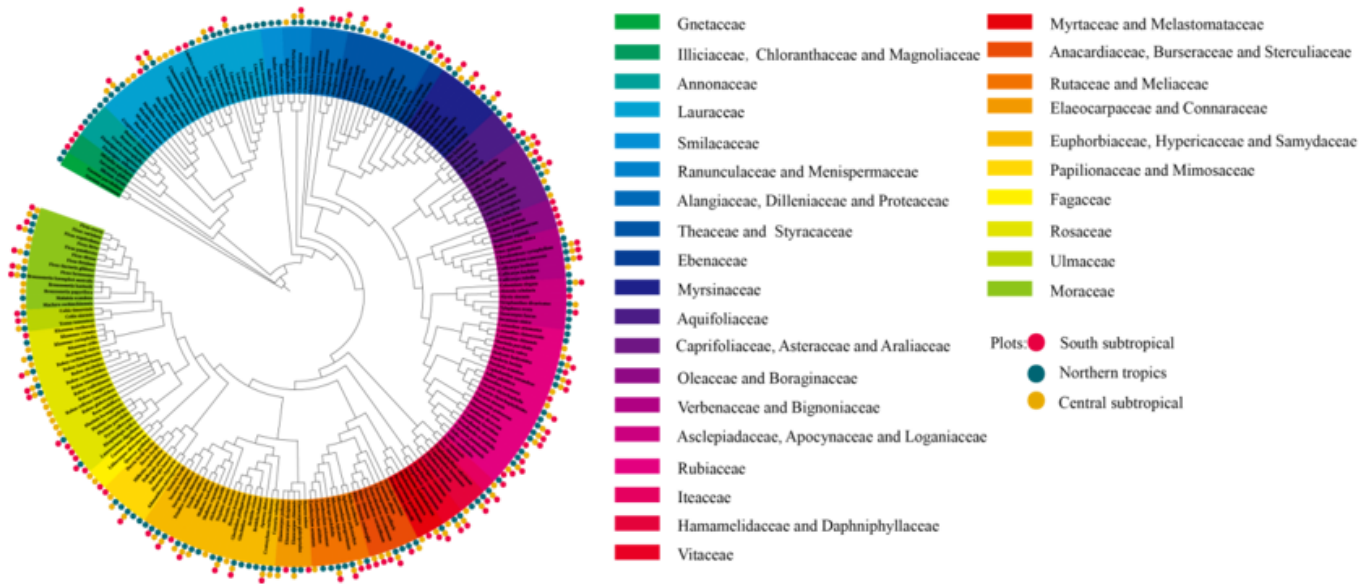


Figure 2

Phylogenetic tree of understory woody plants in *P. massoniana* plantations

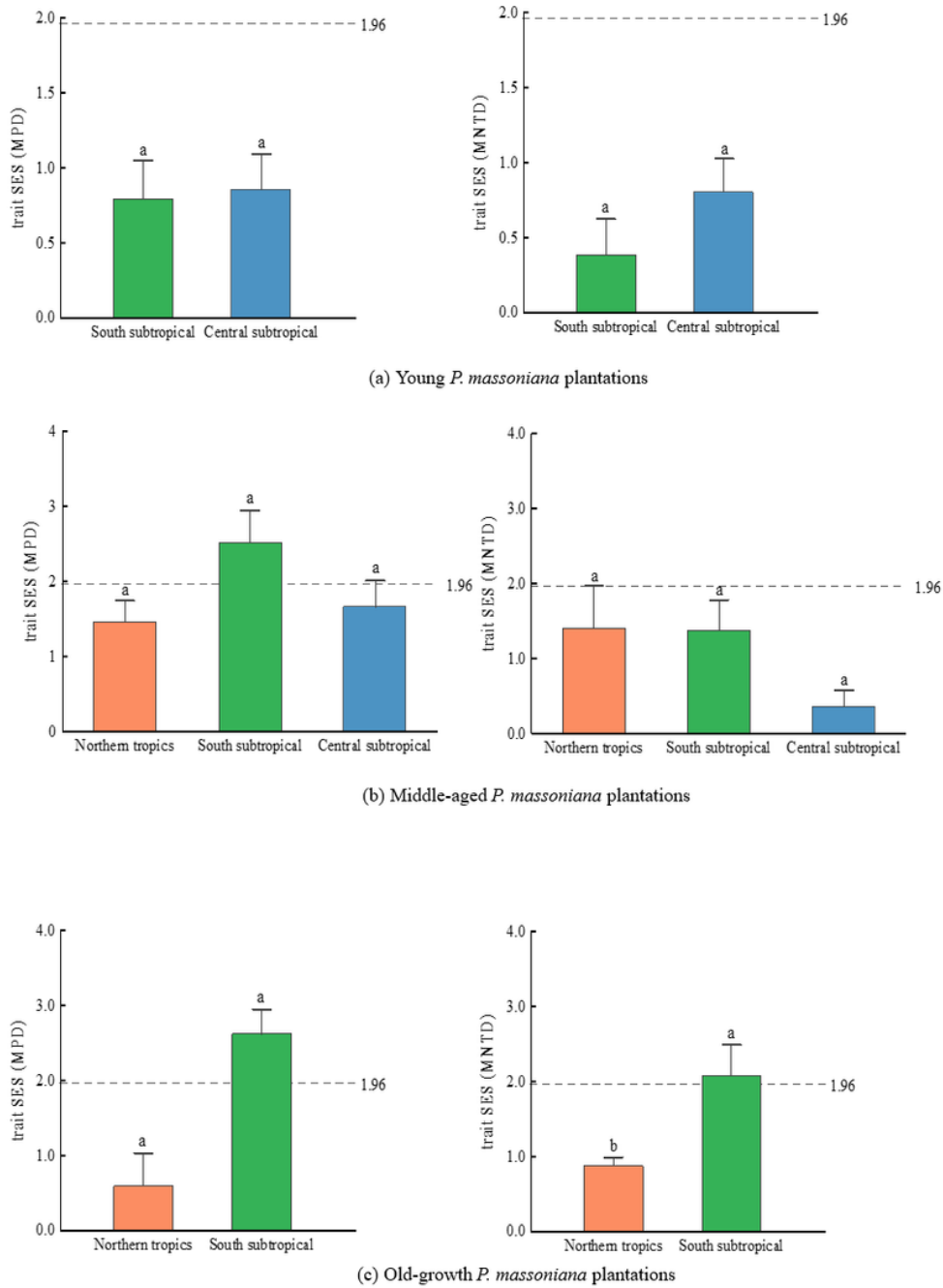


Figure 3

Community structure of woody plants based on functional traits in *P. massoniana* plantations in different climates in Guangxi

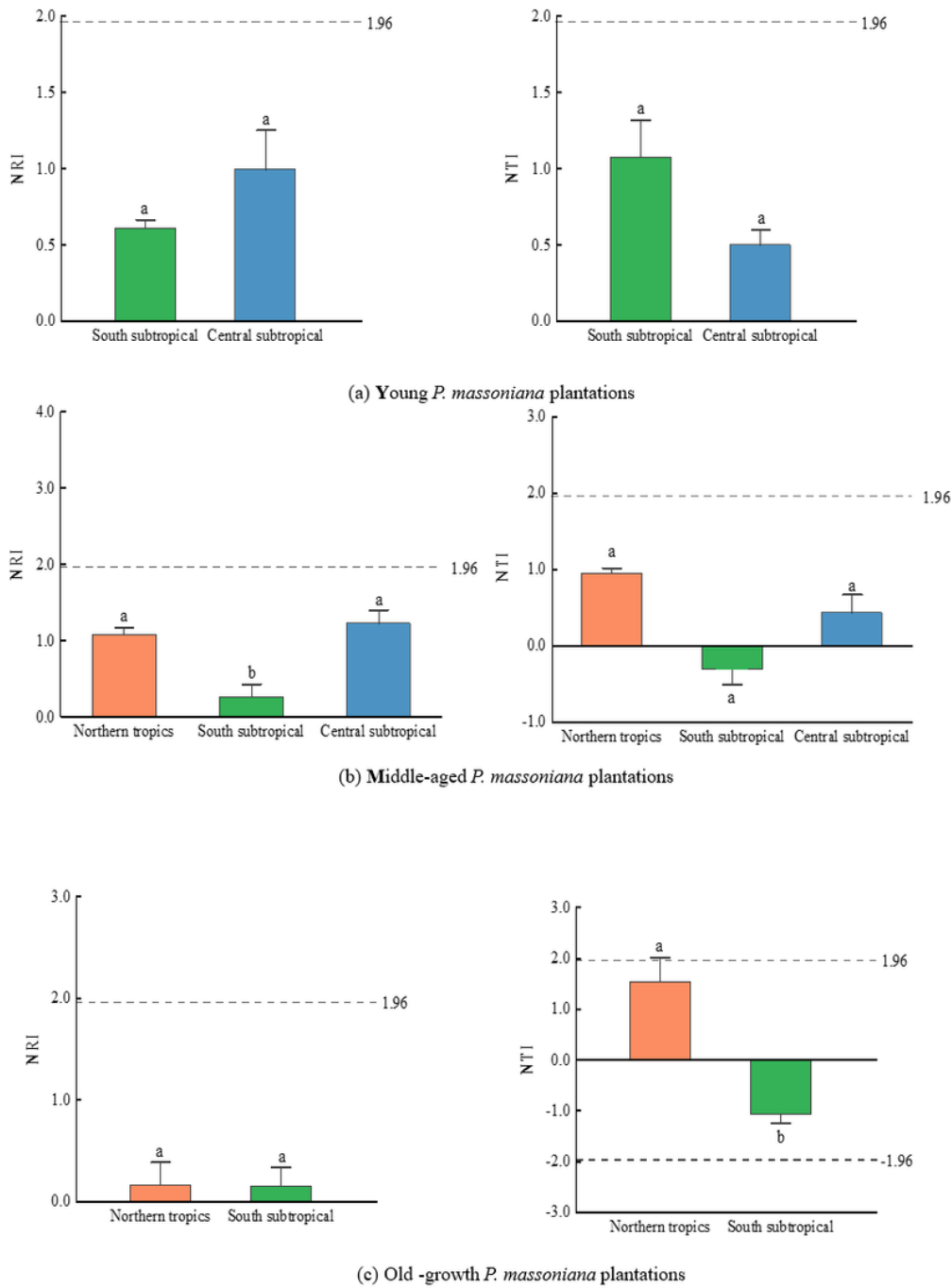


Figure 4

Phylogenetic structure of woody plant communities in *P. massoniana* plantations in Guangxi in different climates