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COMMUNITY ASSEMBLY MECHANISMS OF *Pinus massoniana* PLANTATIONS UNDER DIFFERENT CLIMATIC CONDITIONS: A FUNCTIONAL TRAITS AND PHYLOGENETIC STRUCTURE PERSPECTIVE

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ABSTRACT

Community assembly elucidates mechanisms of species coexistence and diversity maintenance in plant communities, providing a basis for sustainable forest management. However, studies on understory community assembly mechanisms in plantation forests across climatic zones are scarce. This study selected nine leaf functional traits, using methods based on functional traits and phylogenetic structure to investigate the community structure and assembly mechanisms of woody plant communities in *Pinus massoniana* plantations under varying climatic conditions in Guangxi, China. Key findings include: 1) Among the plant functional traits, LT, LTD, SLA, LDMC, LNC_{mass}, and LKC_{mass} are phylogenetically conserved. 2) Community structure based on functional traits was consistent with community phylogenetic structure in the woody plant communities of young *P. massoniana* plantation in southern and central subtropical Guangxi, middle-aged *P. massoniana* plantation in northern tropics and central subtropics, and overripe *P. massoniana* plantation in northern tropics, where the main driving force affecting community construction was habitat filtering. In contrast, in the middle-aged and overripe woody plant communities of *P. massoniana* plantations in southern subtropical Guangxi, functional traits tended to aggregate while phylogeny shifted from aggregation to dispersion, revealing a mismatch between them. Habitat filtering and similarity limitation were common driving forces in community assembly. 3) Community structure based on functional traits showed increased clustering with latitude in young and overripe forests, but decreased in middle-aged forests, reflecting climate-driven assembly shifts. Phylogenetic patterns across latitudes further indicate combined effects of habitat filtering and competition. Overall, understory woody community structure responds dynamically to climate, with functional and phylogenetic structures largely consistent. Community assembly is primarily shaped by habitat filtering, alongside a moderate influence of limiting similarity.

Keywords: Functional traits; Community assembly; *Pinus massoniana* plantations

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MECANISMOS DE MONTAGEM DE COMUNIDADES EM PLANTAÇÕES DE *Pinus massoniana* SOB DIFERENTES CONDIÇÕES CLIMÁTICAS: UMA PERSPECTIVA DE TRAÇOS FUNCIONAIS E ESTRUTURA FILOGENÉTICA

RESUMO A montagem de comunidades elucida mecanismos de coexistência de espécies e manutenção da diversidade em comunidades vegetais, baseando o manejo florestal sustentável. Contudo, estudos sobre mecanismos de montagem do sub-bosque em florestas plantadas ao longo de zonas climáticas são escassos. Este estudo selecionou nove traços funcionais foliares, utilizando métodos baseados em traços e estrutura filogenética para investigar a estrutura comunitária e mecanismos de montagem de comunidades lenhosas em plantações de *Pinus massoniana* sob diferentes climas em Guangxi, China. Principais resultados: 1) Traços LT, LTD, SLA, LDMC, LNC_{mass} e LKC_{mass} são filogeneticamente conservados. 2) Estrutura baseada em traços foi consistente com a filogenética em comunidades jovens (sul/centro subtropical), de meia-idade (norte tropical/centro subtropical) e maduras (norte tropical), com filtragem ambiental como força dominante. Em comunidades de meia-idade e maduras no sul subtropical, traços tenderam à agregação enquanto a filogenia variou de agregação para dispersão, revelando discordância. Filtragem ambiental e limitação de similaridade foram forças comuns. 3) A estrutura baseada em traços mostrou maior agregação com aumento da latitude em plantações jovens e maduras, mas redução em plantações de meia-idade, refletindo mudanças climáticas na montagem. Padrões filogenéticos latitudinais indicam efeitos combinados de filtragem ambiental e competição interespecífica. Globalmente, a estrutura das comunidades lenhosas responde dinamicamente às variações climáticas, com consistência entre estruturas funcionais e filogenéticas. A montagem é moldada principalmente pela filtragem ambiental, atuando conjuntamente com limitação de similaridade.

Palavras-Chave: Traços funcionais; Montagem de comunidades; Plantações de *Pinus massoniana*

1. INTRODUCTION

The study of community assembly is a crucial approach for uncovering the mechanisms of species coexistence and the processes underlying the formation and maintenance of biodiversity. Community assembly, a concept initially proposed by Diamond (1975), has since evolved with the advancement of community ecology research. Concepts and theories such as species pool, dispersal limitation, environmental filtering, and niche theory have gradually emerged (Götzenberger et al., 2012; Vellend, 2010), aiming to explain the processes and rules governing community assembly. Community assembly can be understood as the process by which species interact through various ecological processes under specific environmental conditions, ultimately shaping community structure (Chesson, 2000; Tilman, 1982). In recent years, the integration of phylogenetic and functional trait approaches has provided new perspectives for understanding community assembly. Phylogenetic structure focuses on the evolutionary history of coexisting species, and studying the phylogenetic structure of communities also aids in elucidating the temporal and spatial dynamics of biodiversity (Jarzyna & Jetz, 2016). Functional trait structure, on the other hand, emphasizes the variation in functional traits among species within a community. By combining analyses of phylogenetic structure and functional trait structure, researchers can gain a more comprehensive understanding of the ecological processes influencing community assembly.

In the composition of global forest resources, plantation forests are not only efficient in ensuring the supply of timber and derived products for human needs, but also in further improving the ecological environment (Y. Chen et al., 2024). In

China's forestry industry, Guangxi is one of the more important plantation production areas (Z. Chen et al., 2024), and *P. massoniana* plantations are one of the three major timber forests in Guangxi, especially because it is highly productive due to its resistance to drought and infertile conditions and its high adaptability (Jiangming et al., 2002).

However, in the process of management and nurturing and long-term management, *P. massoniana* plantation forests have been operated in the form of pure forests for a long time, and the ecosystem functions have not been given full play (Li et al., 2020; Rongchang et al., 2018). Woody plant communities in planted forests play a key role in regulating the structure of forest communities, maintaining biodiversity and stand production (Chen et al., 2013; Yiling & Maoyi, 2002). For a long time, research on planted forests of *P. massoniana* has focused on the classical areas of species composition and community structure (Gao et al., 2018; Wu et al., 2020; Zhangping et al., 2018), diversity patterns at multiple scales (Chen et al., 2019; Zhang et al., 2020) and community succession (Cheat et al., 2010). In order to further improve the quality and efficiency of ecosystem services in plantation forests of *P. massoniana*, research on the species grouping and community assembly of woody plants in plantation forests has become an important part of the transformation of pure plantation forests.

The leaf is an important nutrient organ that is directly related to the plant's atmospheric environment and represents the plant's access to and use of resources under habitat conditions, so easily measurable and actionable leaf functional traits have become more important indicators of plant functional traits (X. Zhang et al., 2024). Leaf functional traits often exhibit consistent trait relationships across different plant groups, making them valuable in ecological studies. These traits not only help reveal species' adaptation strategies to environmental changes but also contribute to understanding key ecological processes, such as community assembly mechanisms (Cornelissen et al., 2003). Thus, leaf functional traits play a crucial role in predicting community and ecosystem functions, as well as in understanding patterns of functional diversity and the mechanisms underlying species coexistence along environmental gradients (Zhou et al., 2023).

In order to further explain the maintenance mechanism of community species coexistence and predict the future development of the community, this study examines the structural characteristics of understory woody plant communities in *Pinus massoniana* plantations under varying climatic conditions from both functional trait and phylogenetic perspectives. Specifically, we address the following questions: 1) Do functional and phylogenetic community structures exhibit congruence in the understory woody plant communities of *P. massoniana* plantations in Guangxi? 2) Do community structures of the woody plant communities of *P. massoniana* plantations shift with climate?

To this end, we first constructed the phylogenetic tree and tested the phylogenetic signals of the leaf traits to evaluate their phylogenetic conservatism. This step provides the foundation for the first question: strong phylogenetic signals suggest a higher likelihood of structural congruence between traits and phylogeny, while weak signals may indicate divergence. Second, we examined whether the functional and phylogenetic structures of communities at different stand ages under each climatic condition exhibit consistent patterns of clustering or dispersion, in order to determine the degree of congruence between the two structural dimensions, thus further addressing the first question. Third, we compared the functional and phylogenetic structures of communities with the same stand age across different climatic conditions to assess whether community structures vary with climate, thereby addressing the second question. Finally, we synthesized the results to infer the key ecological drivers shaping community assembly in *P. massoniana* plantations.

2. MATERIAL AND METHODS

2.1 Study area and sampling design

Guangxi, China, has 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 (Figure 1).

Huashan forest farm is located in the central part of 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, and has a mid-subtropical monsoon climate with an average annual temperature of 19. 8 °C and an average annual precipitation of 1402.1 mm. Zhenlong forest farm is located in the north of Hengxian County in south-central Guangxi, with geographical coordinates of 109°08′-109°19′ E, 23°02′-23°08′ N. It is a low mountainous terrain with an altitude of 400-700 m above sea level and a southern subtropical monsoon climate, with an average annual temperature of 21. 5 °C and an average annual precipitation of 1477. 8 mm. 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, is a low mountainous terrain with an altitude of 200-800 m. It has a northern tropical monsoon climate, with an average annual temperature of 21. 8 °C and an average annual precipitation of 1475 mm.

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 with similar stand conditions and different geographical conditions for the study. The details of the sample plots are shown in Table 1. For each type, three standard sample plots of 20 m×20 m were set up, and four small sample plots of 10 m×10 m in each sample plot, all of which were established by the Guangxi Forestry Research Institute of China for long-term fixed monitoring (Fan & Yang,

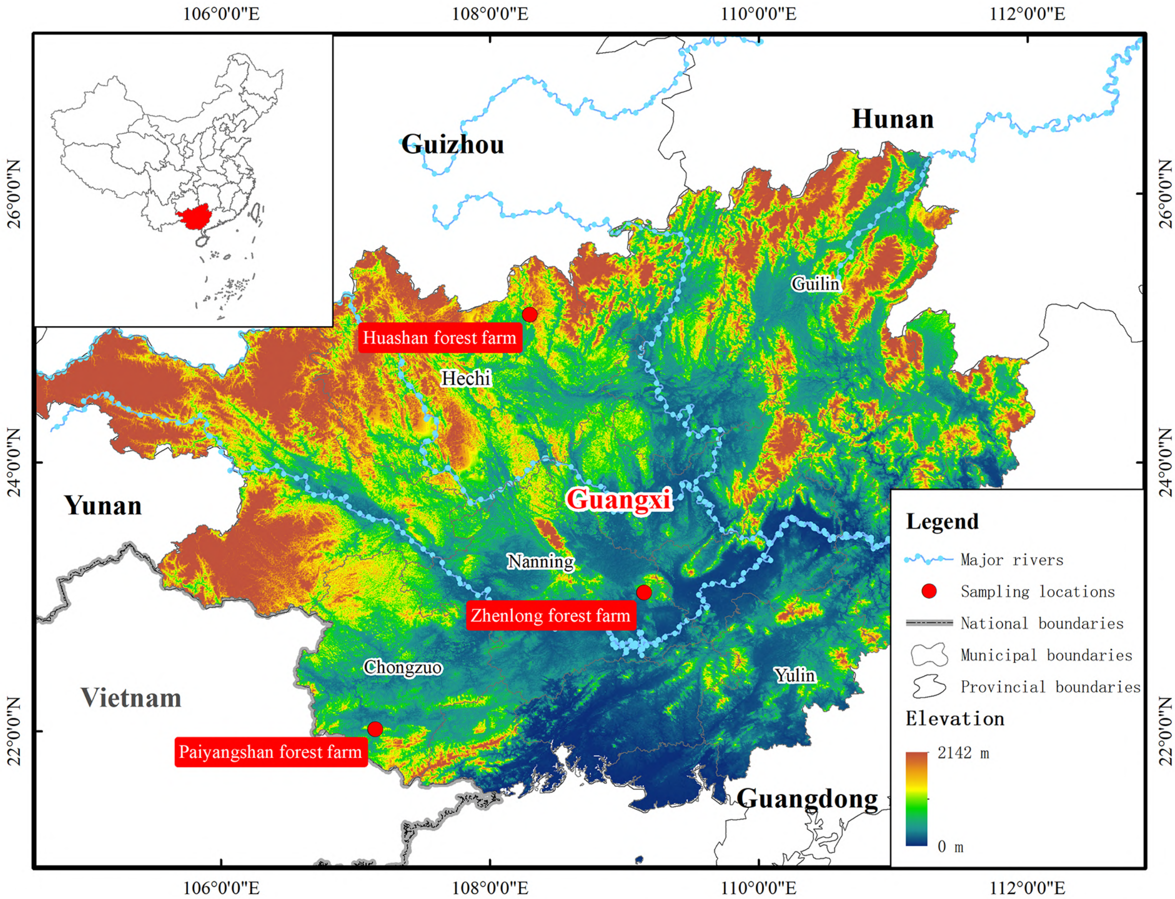

Figure 1. Map of the study area showing the location of the three forest farms in Guangxi
Figura 1. Mapa da área de estudo mostrando a localização das três fazendas florestais em Guangxi

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 and number were recorded. The study site was planted in the early stages of the plantation of *P. massoniana* for three consecutive years. Field community science surveys and sampling are carried out in July and August each year. Unidentified plant specimens are collected in the field and some species are identified by the Guangxi Institute of Botany. Species nomenclature was adopted from the Flora of China (https://www.iplant.cn/foc) and the Flora of China database (https://www.iplant.cn/foc).

2.2 Trait selection and measurements

We cleaned each species collected of debris, separated the leaves from the branches taken by removing the petioles, washed the separated leaves gently under running water to remove soil and impurities from the leaves, washed the leaves and dried them. The leaf area (LA, cm^2) of the woody plant leaves was measured using a leaf area meter; after avoiding the main leaf veins, the leaf thickness (LT, mm) was measured using digital calipers, three measurement points were evenly selected and the mean value was calculated to obtain the individual leaf thickness. The wiped 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 from the leaf surface with clean filter paper, flattened and weighed on an electronic balance (accuracy: 0.0001 g) to obtain the saturated fresh weight (FW, g) of the leaves. All leaf samples were then carefully flattened into serially numbered paper bags, placed in an oven at a constant temperature of 75 °C and dried for at least 48 h until a constant weight was reached, then removed and quickly weighed to obtain the dry leaf weight (DW, g). Specific leaf area (SLA), leaf dry matter content (LDMC, g/g) and leaf tissue density (LTD, kg/m^3) were calculated using the following equations.

$$LDMC(g/g) = DW(g) / FW(g) \quad \text{(Eq. 1)}$$

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

$$LTD(kg/m^3) = 1 / (SLA(cm^2/g) \times LT(mm) \times 104 \quad \text{(Eq. 3)}$$

In each species, three additional healthy, mature plants were selected, the complete leaves were collected in different orientations, the petioles were removed, dried to a constant weight, crushed and sieved through 80 mesh. The samples obtained were crushed, sieved and used mainly to determine the nutrient content of the leaves of woody plants. The carbon content (LCC_{mass}, $mg·g^{-1}$) and nitrogen content (LNC_{mass}, $mg·g^{-1}$) per unit mass of leaf were determined using an elemental analyser. Plant samples were digested with H_2SO_4-H_2O_2 and the phosphorus content per unit mass of leaf (LPC_{mass}, $mg·g^{-1}$) was measured by the

Table 1. Basic information on sample plots of *Pinus massoniana* plantations
Tabela 1. Informações básicas sobre as parcelas amostrais de plantações de *Pinus massoniana*

Climate zones	Plots	Ages	Planting age	Aspect	Slope position	Altitude(m)	Longitude	Latitude
Northern tropical	Paiyangshan forest farm	middle-aged forests	2005	SW	Mid	426	107°09′E	22°01′N
Northern tropical	Paiyangshan forest farm	overripe forests	1958	NE	Mid to Upper	425	107°12′E	22°01′N
Southern subtropical	Zhenlong forest farm	young forests	2012	NW	Mid	313	109°16′E	23°01′N
Southern subtropical	Zhenlong forest farm	middle-aged forests	1999	SE	Mid to Upper	378	109°10′E	23°03′N
Southern subtropical	Zhenlong forest farm	overripe forests	1960	SE	Upper	326	109°09′E	23°02′N
Central subtropical	Huashan forest farm	young forests	2009	N	Mid to Upper	314	108°18′E	25°07′N
Central subtropical	Huashan forest farm	Middle-aged forests	2000	SE	Mid	315	108°18′E	25°06′N

molybdenum antimony colorimetric method. Potassium content per unit mass of leaf (LKC_{mass}, $mg \cdot g^{-1}$) was measured by atomic absorption spectrometry, and finally C/N and N/P were calculated.

2.3 Construction of phylogenetic tree

First, species were checked against the Flora of China, their Latin scientific names were queried and recorded, while the Latin names of woody plants in *P. massoniana* plantations were then checked and corrected. In the corrected plant list, in comma-separated (csv) format, the data boxes include three columns: species (e.g. *Acacia berlandieri*), genus (e.g. *Acacia*) and family (e.g. Fabaceae). The phylogenetic relationships of the woody plants in the *P. massoniana* plantations are based on the global plant phylogenetic tree established by Yi Jin and Hong Qian (Jin & Qian, 2019). Finally, correlation operations were performed based on the obtained phylogenetic tree (Figure 2).

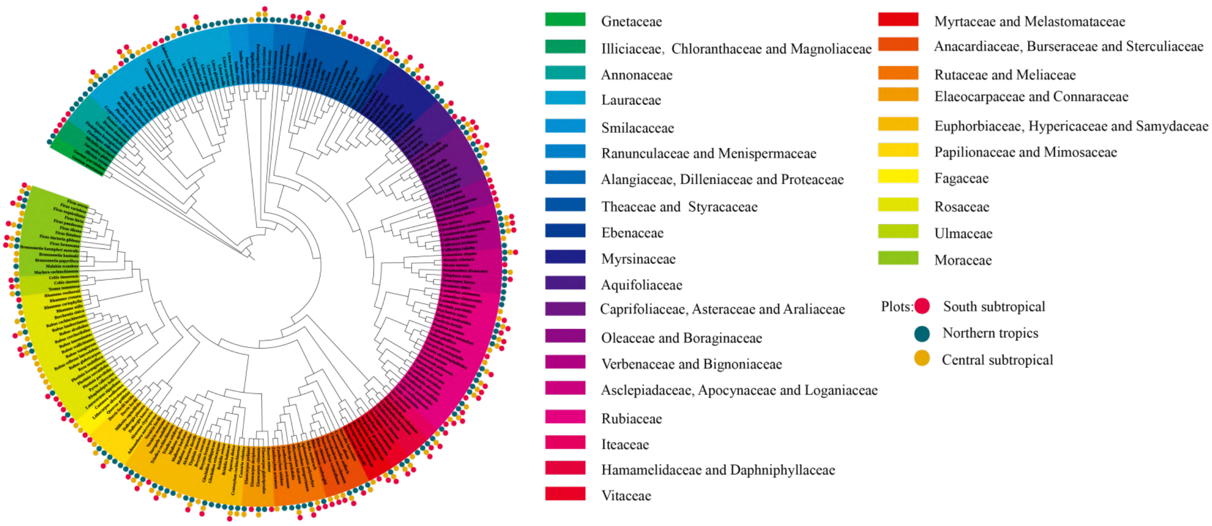

Figure 2. Phylogenetic tree of understory woody plants in *P. massoniana* plantations
Figura 2. Árvore filogenética de plantas lenhosas do sub-bosque em plantações de *P. massoniana*

2.4 Examination of phylogenetic signals

We used Blomberg's K to examine the phylogenetic signal for functional traits (Blomberg et al., 2003). Blomberg's K is a continuous value that takes values from 0 to infinity. If K = 1, species' functional traits evolve randomly following a Brownian motion model, indicating a moderate phylogenetic signal. If K > 1, closely related species exhibit greater trait similarity than expected under a Brownian motion model, K value suggesting a stronger phylogenetic signal. Conversely, if K < 1, closely related species are less similar than expected, indicating a weaker phylogenetic signal. By comparing the observed s with the K values generated by randomly rearranging species at the end of the phylogenetic tree 999 times, if the actual value was greater than the random zero model value more than 950 times (P <0.05), there was a significant phylogenetic signal for functional traits, otherwise there was no significant phylogenetic signal (Swenson, 2014).

2.5 Phylogeny-based quantification of community structure

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

$$\mathrm{NRI} = -1 \times \left[\frac{\mathrm{MPD_{obs}} - \mathrm{mean(MPD_{rand})}}{\mathrm{sd(MPD_{rand})}}\right] \quad \text{(Eq. 4)}$$

$$\mathrm{NTI} = -1 \times \left[\frac{\mathrm{MNTD_{obs}} - \mathrm{mean(MNTD_{rand})}}{\mathrm{sd(MNTD_{rand})}}\right] \quad \text{(Eq. 5)}$$

In Eqs. (4) and (5): MPD_{rand} and $MNTD_{rand}$ represent the expected MPD and MNTD of a random community (n=999), respectively, MPD_{ob}s and $MNTD_{obs}$ are the calculated values of the actual community, mean(MPD_{rand}) and mean($MNTD_{rand}$) are the means, and sd(MPD_{rand}) and sd($MNTD_{rand}$) are the standard deviations. In contrast to NRI, NTI is calculated using the same formula, except that MPD is replaced by MNTD.

2.6 Trait-based quantification of community structure

Functional trait structure was calculated using mean pairwise trait distance (trait(MPD)) and nearest trait distance (trait(MNTD)). After comparing trait(MPD) and trait(MNTD) to the pattern generated by the null model, respectively, they are finally expressed in terms of standardised community mean pairwise trait distances (trait SES(MPD)) and nearest trait distances (trait SES(MNTD)). The index is calculated similarly to the community phylogenetic structure with the following equation.

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

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

In Eqs. (6) and (7): MPD_{rand} and $MNTD_{rand}$ represent the expected MPD and MNTD of a random community (n=999), respectively, MPD_{obs} and $MNTD_{obs}$ are the calculated values of the actual community, mean(MPD_{rand}) and mean($MNTD_{rand}$) are the means, and sd(MPD_{rand}) and sd($MNTD_{rand}$) are standard deviations. Compared to trait SES(MPD), trait SES(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, the phylogenetic or functional trait structure of the species is aggregated; if both are negative, the phylogenetic or functional trait structure of the species is divergent; if both are zero, the phylogenetic or functional trait structure of the species is in a random state (Tang 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, significant aggregation or significant divergence is indicated (Zhao et al., 2020).

2.7 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 initially collated using Excel 2022 software and statistical analyses and plots were completed via R(4.1.2) software and Origin 2019.

3. RESULTS

3.1 Phylogenetic signalling of functional traits

To investigate the conservativeness of leaf functional traits, we did the Blomberg's K test for phylogenetic signal on the mean values of leaf functional traits of 96 woody plants in planted forests of *P. massoniana* under different climatic conditions (Table 2). The K values of all traits were greater than 0, ranging from 0.054 to 0.196, indicating an overall low level of phylogenetic signal. Among the nine leaf functional traits, LT, LTD, SLA, LDMC, LNC_{mass}, and LKC_{mass} showed significant phylogenetic signals ($P < 0.05$) compared to the null model, suggesting that these are conserved traits. However, their K values were close to 0, indicating that their phylogenetic signals were weaker relative to the expectations of a Brownian motion evolutionary model. This suggests that the evolutionary processes of these traits are more stochastic, with relatively weak conservatism. In contrast, the K values of LA, LCC_{mass}, and LPC_{mass} were less than 1, even lower than the expected values under the Brownian motion model. Additionally, their P values were all greater than 0.05, indicating non-significant phylogenetic signals. These traits can therefore be considered non-conservative, suggesting that LA, LCC_{mass}, and LPC_{mass} are weakly associated with the evolutionary history of species.

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Table 2. Phylogenetic signatures of functional leaf traits in woody plants of *P. massoniana* plantations under different climatic conditions
Tabela 2. Assinaturas filogenéticas de traços foliares funcionais em plantas lenhosas de plantações de *P. massoniana* sob diferentes condições climáticas

Traits	Blomberg's *K*	P
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 >0.05, indicating a non-significant difference; 0.01 <P <0.05, indicating a significant difference; P <0.01, indicating a highly significant difference.
Nota: P >0,05, indicando uma diferença não significativa; 0,01 <P <0,05, indicando uma diferença significativa; P <0,01, indicando uma diferença altamente significativa.

3.2 Community structure based on functional traits

3.2.1 *The young forests of P. massoniana plantations in south subtropical and central subtropical of Guangxi*

In the community structure of woody plants based on functional traits in young forests of *P. massoniana* in south and central subtropical Guangxi (Fig. 3-a), the mean values of trait SES (MPD) and trait SES (MNTD) were 0.80 and 0.39 for young forests of *P. massoniana* plantations in the southern subtropics, and 0.86 and 0.80 for trait SES (MPD) and trait SES (MNTD) in the central subtropics. The mean trait SES (MPD) and trait SES (MNTD) values for young forests of *P. massoniana* plantations in Guangxi were greater than 0. The community structure based on functional traits showed a tendency to aggregate. In general, the community structure based on functional traits in young forests of *P. massoniana* plantations in different climatic conditions in Guangxi increased with latitude.

3.2.2 *The middle-aged forests of P. massoniana plantations in Guangxi under different climatic conditions*

In the community structure of middle-aged *Pinus massoniana* forests based on functional traits under different climatic conditions in Guangxi (Fig. 3-b), the mean values of trait SES(MPD) and trait SES(MNTD) in the northern tropical region were 1.47 and 1.40, respectively. In the southern subtropical region, the mean values of trait SES(MPD) and trait SES(MNTD) were 2.52 and 1.38, respectively. In the central subtropical region, the mean values of trait SES(MPD) and trait SES(MNTD) were 1.66 and 0.36, respectively. Trait SES(MPD) exhibited a pattern of first increasing and then decreasing with rising latitude, while trait SES(MNTD) showed an overall decreasing trend with increasing latitude. In terms of the community structure based on functional traits, all communities exhibited a clustered pattern. Among them, the southern subtropical *P. massoniana* middle-aged forests had a mean trait SES(MPD) greater than 1.96, indicating significant clustering. Overall, the functional trait-based community structure of *P. massoniana* middle-aged forests under different climatic conditions in Guangxi demonstrated a certain degree of variability with increasing latitude.

3.2.3 *The overripe forests of P. massoniana plantations in northern tropical and south subtropical of Guangxi*

In the community structure of woody plants based on functional traits in overripe forests of *P. massoniana* in Northern tropical and South subtropical of Guangxi (Fig. 3-c), the mean values of trait SES (MPD) and trait SES (MNTD) were 0.60 and 0.88 for overripe forests of northern tropical *P. massoniana* plantations, and 2.63 and 2.09 for overripe forests of southern subtropical *P. massoniana* plantations. The mean trait SES

(MPD) and trait SES (MNTD) values were greater than 0 in the overripe forests of *P. massoniana* plantations in Guangxi. Among them, both trait SES (MPD) and trait SES (MNTD) mean values for overripe forests of southern subtropical *P. massoniana* plantations were greater than 1.96, with significant aggregation, while the rest of the community structure based on functional traits showed a tendency to aggregate. In general, community structure based on functional traits in overripe forests of *P. massoniana* plantations in different climatic conditions in Guangxi increased significantly with increasing latitude.

3.3 The phylogenetic structure of woody plant communities

3.3.1 *The young forests of P. massoniana plantations in south subtropical and central subtropical of Guangxi*

In the phylogenetic structure of woody plant communities in young forests of *P. massoniana* plantations in south and central subtropics of Guangxi (Fig. 4-a), the mean values of NRI and NTI in young forests of *P. massoniana* in south subtropics were 0.61 and 1.07, while those in central subtropics were 1.00 and 0.50. The community phylogenetic structure showed a tendency of aggregation. In the phylogenetic structure of woody plant communities in young *P. massoniana* forests in Guangxi under different climatic conditions, NRI increased with increasing latitude and NTI decreased with increasing latitude.

3.3.2 *The middle-aged forests of P. massoniana plantations in Guangxi under different climatic conditions*

In the phylogenetic structure of the woody plant communities in the middle-aged *Pinus massoniana* forests under different climatic conditions in Guangxi (Fig. 4-b), the mean NRI and NTI values for the northern tropical middle-aged *Pinus massoniana* forest were 1.07 and 0.95, respectively; for the South Asian tropical mid-aged *Pinus massoniana* forest, they were 0.26 and -0.31, respectively; and for the Central Asian tropical middle-aged *Pinus massoniana* forest, the values were 1.22 and 0.43, respectively. The NRI values in the northern tropical and Central Asian tropical regions were significantly higher than those in the South Asian tropical region. Overall, the NRI showed a trend of decreasing and then increasing with latitude. The NTI, on the other hand, showed a decreasing trend as latitude increased. In general, except for the South Asian tropical middle-aged *Pinus massoniana* forest, where the NRI exhibited a clustered pattern and the NTI exhibited a divergent pattern, with the phylogenetic structure being random or divergent, the phylogenetic structures of the other communities showed a clustered pattern.

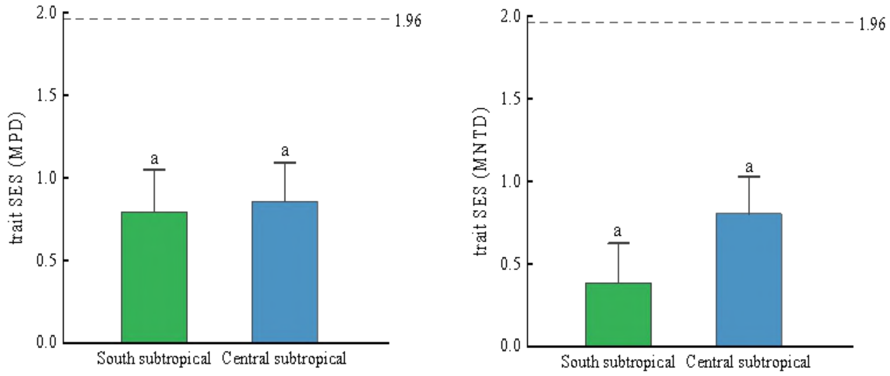
3.3.3 *The overripe forests of P. massoniana plantations in northern tropical and south subtropical of Guangxi*

In the phylogenetic structure of the woody plant communities in the overripe *Pinus massoniana* forests in the northern tropical and South Asian tropical regions of Guangxi (Fig. 4-c), the mean NRI and NTI values for the northern tropical overripe *Pinus massoniana* forest were 0.17 and 1.54, respectively, while for the South Asian tropical overripe *Pinus massoniana* forest, the values were 0.15 and -1.06, respectively. The NRI and NTI values for the northern tropical *Pinus massoniana* overripe forest were both greater than 0, indicating a clustered phylogenetic structure. In contrast, for the South Asian tropical overripe *Pinus massoniana* forest, the NRI value was close to 0, and the NTI value was less than 0, indicating a random or divergent phylogenetic structure.

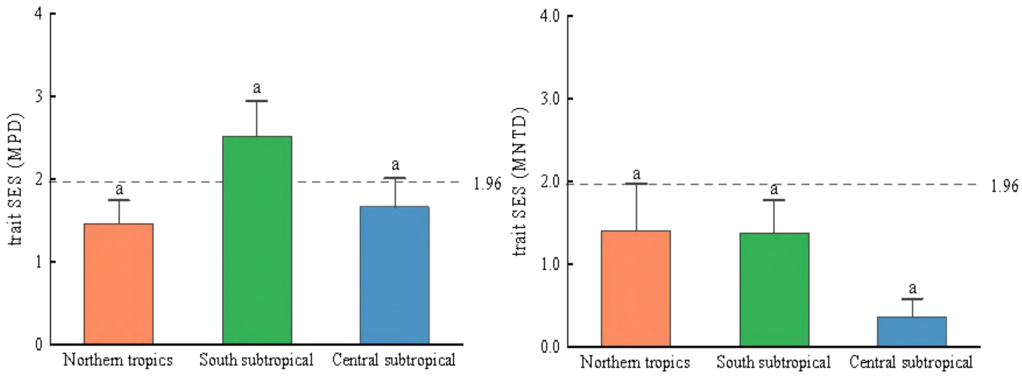
4. DISCUSSION

4.1 Phylogenetic signatures of functional leaf traits

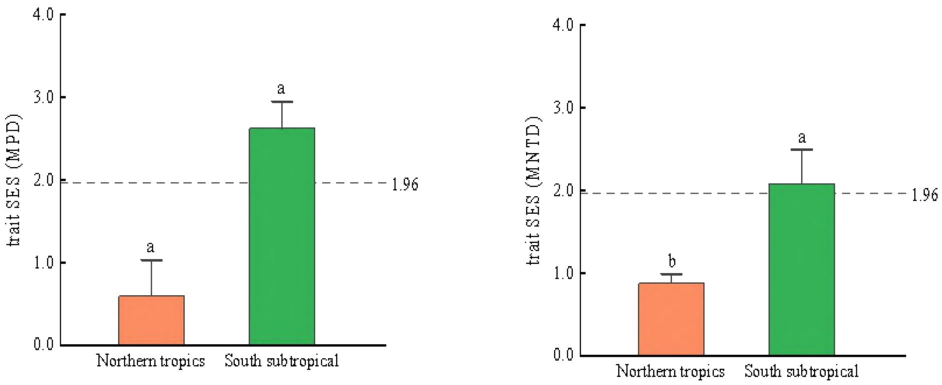
The study of community building mechanisms based on functional traits and phylogeny requires the construction of cross-correlations between the two, which can only be elucidated from a single perspective and the results are one-sided. The use of functional trait phylogenetic signals can effectively measure the extent to which the evolution of functional traits in woody plants of *P. massoniana* plantations can be influenced by interspecific affinities, which can help to reveal the causes of community building in a more comprehensive way (Weiher et al., 2011). Blomberg's K (hereafter



(a) The young forest of *P. massoniana* plantations



(b) The middle-aged forest of *P. massoniana* plantations



(c) The overripe forest of *P. massoniana* plantations

Figure 3. Community structure of woody plants based on functional traits in *P. massoniana* plantations under different climatic conditions in Guangxi. Note: Different lowercase letters indicate significant differences between different climatic zones (P <0.05), as below

Figura 3. Estrutura da comunidade de plantas lenhosas com base em traços funcionais em plantações de *P. massoniana* sob diferentes condições climáticas em Guangxi. Nota: Letras minúsculas diferentes indicam diferenças significativas entre as diferentes zonas climáticas (P <0,05), conforme abaixo

K value) is a widely used metric for detecting phylogenetic signal. Analysis of leaf trait K values in this study revealed significant phylogenetic signals (P < 0.05) for LT, LTD, SLA, LDMC, LNC_{mass}, and LKC_{mass}. This suggests a strong association between these traits and evolutionary history. Generally, species that are more closely related in evolutionary history tend to exhibit more similar traits.

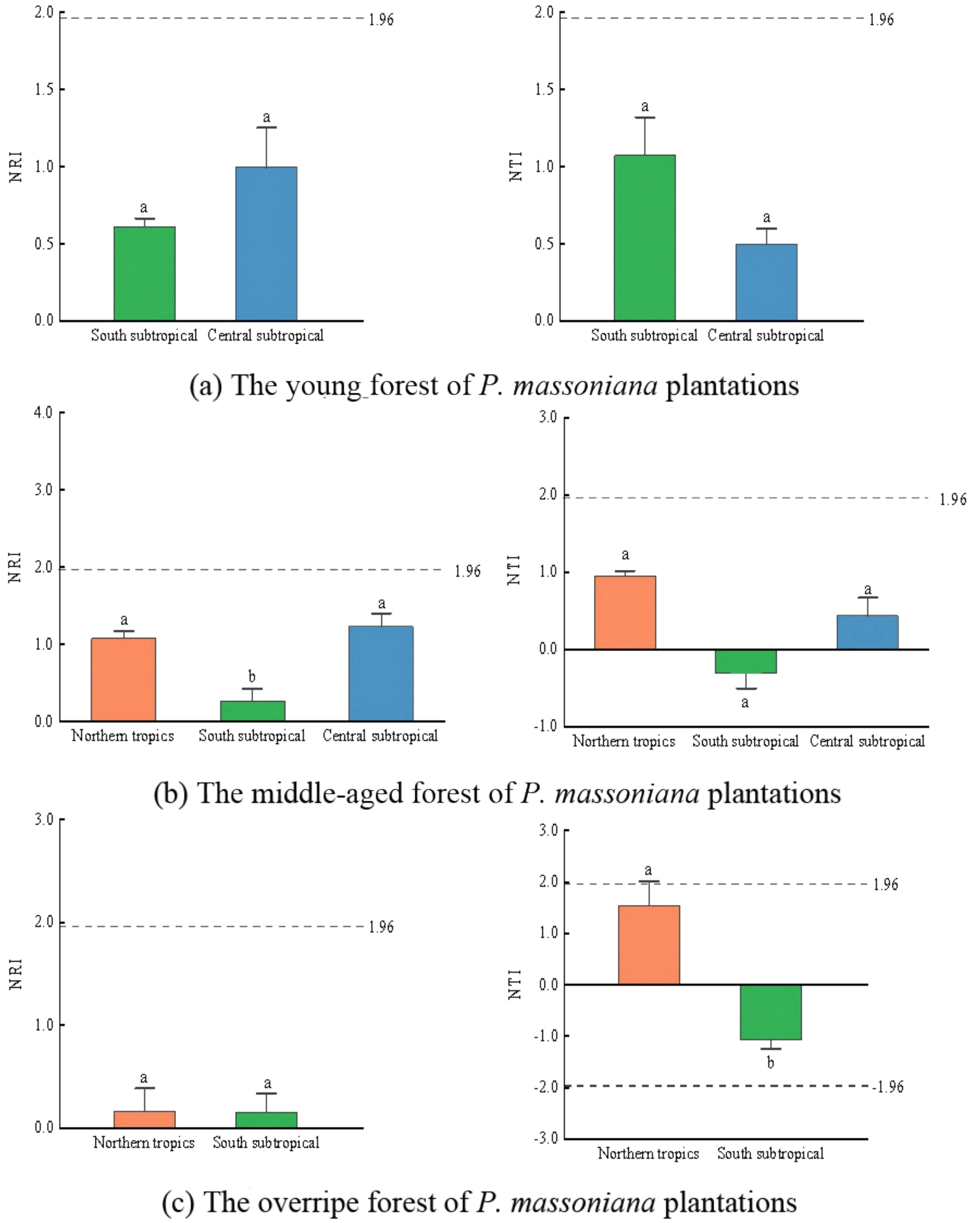


Figure 4. Phylogenetic structure of woody plant communities in *P. massoniana* plantations in Guangxi under different climatic conditions
Figura 4. Estrutura filogenética das comunidades de plantas lenhosas em plantações de *P. massoniana* em Guangxi sob diferentes condições climáticas

Thus, within the woody plant communities of the *Pinus massoniana* plantations, species with closer phylogenetic relationships tend to share more similar values for the above traits. Despite the significant phylogenetic signal for these leaf functional traits, their K values are relatively small, ranging from 0.054 to 0.196. This indicates that the phylogenetic conservatism of these functional traits is not strong, possibly due to the combined influence of both phylogenetic relationships and environmental factors on the traits. Prior studies have similarly shown that not all leaf traits exhibit strong phylogenetic signals, supporting the patterns observed here (Blomberg et al., 2003). In general, the evolutionary history has a considerable influence on the woody plant communities in the study areas of the *Pinus massoniana* plantations under different climatic conditions in Guangxi, and functional traits are largely regulated by genetics, exhibiting phylogenetic conservatism.

4.2 Climate gradient changes in community structure based on functional traits

This study uses the two trait-based indices, trait SES(MPD) and trait SES(MNTD), to characterize the functional trait structure of woody plant communities and finds that there are differences in the functional trait structures of *Pinus massoniana* plantation woody plant communities under different climatic conditions. Recent studies further support the idea that plant functional traits exhibit a significant latitudinal gradient pattern, with climate factors having a notable impact on functional trait patterns (Akram et al., 2023; Li et al., 2024). Under the framework of functional trait patterns, in *Pinus massoniana* plantations in Guangxi, the functional trait-based community structure in both the South Asian subtropical and Central Asian tropical young forests tends to be aggregated, with the degree of aggregation increasing with latitude. The woody plant communities may primarily be influenced by the habitat filtering effect described in niche theory (Qian, 2018). In young forests, despite the increase in environmental heterogeneity with latitude, plant individuals typically aim for rapid establishment, and they have not yet experienced significant competition or environmental stress. Therefore, the habitat filtering effect may be more pronounced. In the middle-aged *Pinus massoniana* forests in Guangxi under different climatic conditions, the degree of aggregation in the functional trait-based community structure generally decreases with increasing latitude, reflecting that the functional trait structure in middle-aged forests is also influenced by habitat filtering. However, this effect is weakening, likely because the community structure in middle-aged forests is gradually stabilizing, and interspecific competition becomes a more important ecological process. The increased environmental heterogeneity with latitude provides more opportunities for species differentiation, which leads to a decrease in the degree of functional trait aggregation. In the overripe *Pinus massoniana* forests under different climatic conditions in Guangxi, the functional trait structures of the woody plant communities all exhibit an aggregated trend. Notably, in the South Asian subtropical overripe forest, there is significant aggregation (trait SES(MPD) and trait SES(MNTD) > 1.96). Overall, the degree of aggregation increases with latitude, suggesting a change in habitat filtering and the environmental pressure gradient. Since the community structure in overripe forests is more stable and interspecific competition is weaker, habitat filtering becomes the primary ecological process. Compared to the relatively more favorable climate conditions in the Northern Tropics, the South Asian subtropical climate is more harsh, resulting in stronger selective pressure on community functional traits and thus higher aggregation of functional traits. Overall, under the functional trait framework, the functional trait-based community structure of woody plants in *Pinus massoniana* plantations under different climatic conditions tends to be aggregated. This suggests that habitat change plays a dominant role in the community assembly process to a large extent, and with increasing latitude, this effect shows a certain regularity. The relative importance of habitat filtering and species competition exhibits different patterns at different growth stages and under different climatic conditions. In this study, with the increase in latitude and the decrease in temperature, only species that can adapt to the environmental conditions at different latitudes in Guangxi are likely to survive.

4.3 Changes in climatic gradients in community phylogenetic structure

This study utilized the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI) to assess the phylogenetic structure of the communities. These two indices are interrelated but not fully coordinated, as they are influenced by their inherent applicability and sensitivity. Specifically, the NRI index is based on the community level and primarily characterizes the phylogenetic pattern of the entire phylogenetic tree, while the NTI index, based on the nearest relatedness, reflects the most recent phylogenetic relationships at the tips of the phylogenetic tree (Webb et al., 2002). According to Webb, under phylogenetic conservatism, habitat filtering leads to clustered phylogenetic structure, while limiting similarity leads to random or overdispersed patterns (Webb et al., 2002). At the spatial scale, in the juvenile forests of the south and central subtropical regions of Guangxi, the clustered phylogenetic structure of the community suggests that species are closely related. This may be due to habitat filtering affecting pioneer woody plants and forming ecological niche clustering, where the community is mainly composed of species with similar adaptive abilities and closer phylogenetic relationships. As latitude increases, NRI and NTI trends reflect different ecological processes: rising NRI may indicate harsher climates selecting species with stronger physiological adaptability and closer phylogenetic ties, thus enhancing overall clustering; while decreasing NTI may suggest increased habitat heterogeneity, leading to stronger niche differentiation or competitive exclusion among closely related species, thereby weakening local clustering. Additionally, in the middle-aged and overripe forests of the *P. massoniana* in Guangxi, the NTI decreases with increasing latitude, indicating that at higher latitudes, the functional trait differences decrease. This may be due to harsher environmental conditions, which may drive species to converge on more efficient resource utilization strategies, leading to functional trait similarity to adapt to more extreme habitats, thereby reducing functional differences among species in the community (S. Zhang et al., 2024).

Temporally, in middle-aged and overripe forests of the south subtropical region, NRI shows a clustering trend, while NTI exhibits a divergent pattern. This indicates that although phylogenetic similarity persists in later stages, trait diversity increases, likely due to intensified competition and divergent survival strategies. In the north subtropical region, from the middle-aged to overripe forest stages, the NRI decreases and NTI increases, but the community's phylogenetic structure remains clustered. This implies that habitat filtering remains dominant, but phylogenetic differentiation or species turnover may occur. Locally, closely related species still coexist, possibly driven by resource distribution.

In many different types of ecosystems, key processes affecting different resource gradients are primarily influenced by habitat filtering (Cornwell & Ackerly, 2009; Jiang et al., 2024). Weiher and Keddy proposed the theory of community assembly and the principle of phylogenetic conservatism of ecological niches (Weiher & Keddy, 2001). They suggested that under habitat filtering, species' formation of habitat preferences becomes easier, allowing plants in the community to thrive in the most suitable habitats. In this study, the communities are located across three distinct climatic zones with large spatial scales. Swenson et al. pointed out that as the spatial scale of the species pool increases, the likelihood of phylogenetic clustering also increases (Swenson et al., 2006). Typically, environmental factors exhibit gradient changes over larger spatial scales, and climate factors, as typical large-scale factors, are crucial in shaping plant selection mechanisms (Nishizawa et al., 2022). The community assembly of *P. massoniana* artificial forest woody plants is a relatively complex and unique process. Under different climatic conditions, the intensity of various ecological processes in the woody plant community differs due to variations in latitude, water, and thermal conditions. Overall, niche processes—particularly habitat filtering—play a central role in the assembly of *P. massoniana* artificial forest communities in Guangxi, and climate factors, as a typical large-scale environmental variable, significantly influence the ecological processes driving community assembly.

4.4 Determination of the consistency of the functional trait structure and phylogenetic structure of the community

Integrating functional trait structure with phylogenetic structure is an effective approach for evaluating community assembly mechanisms. In the young *Pinus massoniana* plantations of the southern and central subtropical zones, the middle-aged plantations of the northern tropical and central subtropical zones, and the overripe plantations of the northern tropical zone, both structures exhibited consistency, with environmental filtering identified as the primary driver of community assembly. This result is consistent with previous studies. For example, Baraloto et al. found that environmental filtering was a major driver of neotropical forest community formation through analyses of phylogenetic and functional trait structures (Baraloto et al., 2012). Similarly, Luo et al. observed that the phylogenetic and functional structures of tree layers in vertical forest communities at both low and high elevations exhibited clustering, suggesting that environmental filtering played a dominant role under arid conditions at low elevations and cold temperatures at high elevations (Luo et al., 2019). Moreover, the relationship between phylogeny and functional traits is generally more pronounced at broader taxonomic scales. The influence of phylogenetic constraints should not be overlooked. Although phylogenetic signals were relatively weak in this study, most were significant ($P < 0.05$), partly explaining the observed structural congruence.

Both trait-based and phylogeny-based structures may exhibit scale dependence and differ at the same spatial scale (Cavender-Bares et al., 2006). In the middle-aged and overripe *P. massoniana* plantations of the southern subtropical zone, functional trait-based and phylogenetic-based community structures were inconsistent: functional trait structure exhibited a clustering trend, whereas phylogenetic structure transitioned from clustering to overdispersion. This pattern suggests that both environmental filtering and limiting similarity jointly influence community assembly. Additionally, this inconsistency may be attributed to convergent evolution among species in middle-aged and overripe forests under environmental pressure. While species with similar traits may cluster due to environmental filtering, they may not necessarily be closely related phylogenetically. Conversely, species retained through competitive exclusion may exhibit distinct traits, and their phylogenetic relationships may not follow a specific pattern. These findings suggest that recent community differentiation may be occurring, with environmental filtering and limiting similarity jointly shaping community assembly (Kress et al., 2009). However, it is important to note that the time span from middle-aged to overripe forests is only a few decades, which may not be sufficient to form large-scale convergent evolutionary patterns. Mismatches between functional trait structure and phylogenetic structure have also been reported in different ecosystems. For instance, Hao Minhui et al. found significant discrepancies between phylogenetic and functional trait structures at the same spatial scale in secondary coniferous-broadleaf mixed forests in the Jiaohe region and in low to mid-altitude forests forests on the northern slope of the Qinling Mountains (Hao et al., 2018). These findings further support the notion that community assembly mechanisms may exhibit considerable complexity across different spatial scales and environmental gradients.

5. CONCLUSION

This study investigated the structure and assembly mechanisms of understory woody plant communities in *Pinus massoniana* plantations across climatic zones in Guangxi, China, integrating functional traits and phylogenetic dimensions. Most leaf traits exhibited significant phylogenetic signals. Community structure generally showed consistent functional and phylogenetic clustering, indicating habitat filtering as the dominant driver. However, inconsistency in the south subtropical middle-aged forests and overripe forests suggests limiting similarity also played a role. Community structure varied with climate zone even at the same stand age: functional clustering increased with latitude in young and overripe forests but decreased in middle-aged forests, reflecting climate-driven habitat filtering. Phylogenetic structure exhibited variable patterns along the latitudinal gradient, indicating joint effects of habitat filtering and interspecific competition. Overall, functional and phylogenetic community structures were largely congruent. Community assembly is primarily shaped by habitat filtering, alongside a moderate influence of limiting similarity. This enhances understanding of plantation community assembly and informs regional vegetation restoration and management.

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AUTHOR CONTRIBUTIONS

Zhang, H.: Conceptualization, Formal analysis, Writing – Original Draft; Mo, Y.: Formal analysis, Investigation, Validation; Li, Y.: Conceptualization, Visualization, Writing – Review & Editing; Huang, L.: Formal analysis, Investigation; Jian, R.: Formal Analysis, Investigation; Pan, X.: Formal Analysis, Investigation; Ma, J.: Funding acquisition, Supervision, Writing – Review & Editing.

DATA AVAILABILITY

The datasets used in the current study are available from the corresponding author on reasonable request.

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