

Successional changes in woody floristic composition and diversity in karst mountain tropical seasonal rainforests in southwestern China

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Keywords: karst mountains, seasonal rainforest, succession, floristic composition, species diversity

Abstract

The seasonal tropical rainforests in karst regions of southwestern China are well known for their high biodiversity and rich array of endemic species. However, changes in the woody floristic composition and diversity during forest succession remain unclear. In this study, we used the space-for-time substitution method to analyse the floristic composition and diversity of woody plants across three successional stages (young secondary forests, old secondary forests and primary forests). Our results indicated significant differences in species composition among the various successional stages, with species richness peaking in the old secondary forests. Additionally, as succession progresses, the proportion of the relative importance values of dominant species in the community gradually decreases compared to the total importance values. In the β -diversity, the species richness, Simpson index and Shannon–Wiener index all reached an apex in the old secondary forest, whereas the Pielou evenness index gradually increased over time, reaching its maximum in the PF. The β -diversity analysis suggested that species turnover occurred during succession, with no significant similarity between communities at different stages. This study demonstrated that the floristic composition and diversity of woody plants underwent continuous changes as succession progressed in karst forests. Anthropogenic disturbances and competitive exclusion may co-regulate the floristic composition and diversity at different forest stages in mountainous karst areas.

Profile

Protected area

Nonggang National

Nature Reserve

Country

China

Introduction

Vegetation succession is a critical ecological issue (Chang & Turner 2019). According to Clements' theory of climax communities (Yang et al. 2015; Yıldız et al. 2022), under relatively stable environmental conditions, plant communities transition from pioneer to stable climax stages. Throughout this process, changes in species composition and diversity occur dynamically (Collins 1990). Currently, two main hypotheses exist regarding the changes in species richness during vegetation succession. The classic hypothesis suggests that species diversity increases as succession progresses and peaks in climax communities (Margalef 1963). In contrast, Odum (1969) proposed that species diversity increases during the early and middle stages of succession as forest ecosystems develop, but declines in later stages. Understanding the patterns and mechanisms of vegetation succession can contribute to the optimization and management of forest ecosystems (Geng et al. 2022).

Karst landscapes are geological formations that have developed primarily on limestone and dolomite (He et al. 2008). Globally, karst areas cover 22 million km², approximately 15% of the Earth's land surface (Xu et al. 2021; Zhang et al. 2023). China has one of the largest karst distributions worldwide, with an area of 3.44 million km², accounting for approximately 36% of the total land area (Ni et al. 2015). Owing to

their unique geochemical background of high calcium and alkaline conditions and diverse habitat conditions, karst regions have extremely diverse vegetation types and are rich in endemic and rare species (Zhang et al. 2012; Liu et al. 2020). Tropical karst seasonal rainforests, which are typical of the karst mountains of southwestern China, are characterized by complex community structures, rich species compositions and prominent endemic elements. This particular region of China is recognized as having one of the world's most distinct tropical karst forests (Guo et al. 2015), a forest type that provides essential ecosystem services such as biodiversity conservation, surface karst zone regulation, and carbon storage (Lang & Song 2018; Gao et al. 2021). The forests of the area serve as a valuable ecological research site for karst forest vegetation more generally, and an important reference model for biodiversity conservation and restoration of degraded vegetation in karst mountains (Guo et al. 2017).

The Nonggang National Nature Reserve (NNNR) protects the largest and most representative karst seasonal rainforest in China. The NNNR serves as a unique and vast genetic reservoir of biodiversity and has been recognized as one of the world's 36 key biodiversity hotspots (Wang et al. 2014). Located at the northern edge of the tropics, the flora of the reserve exhibit a tropical marginal nature with transitional characteristics towards the subtropical zone, establishing

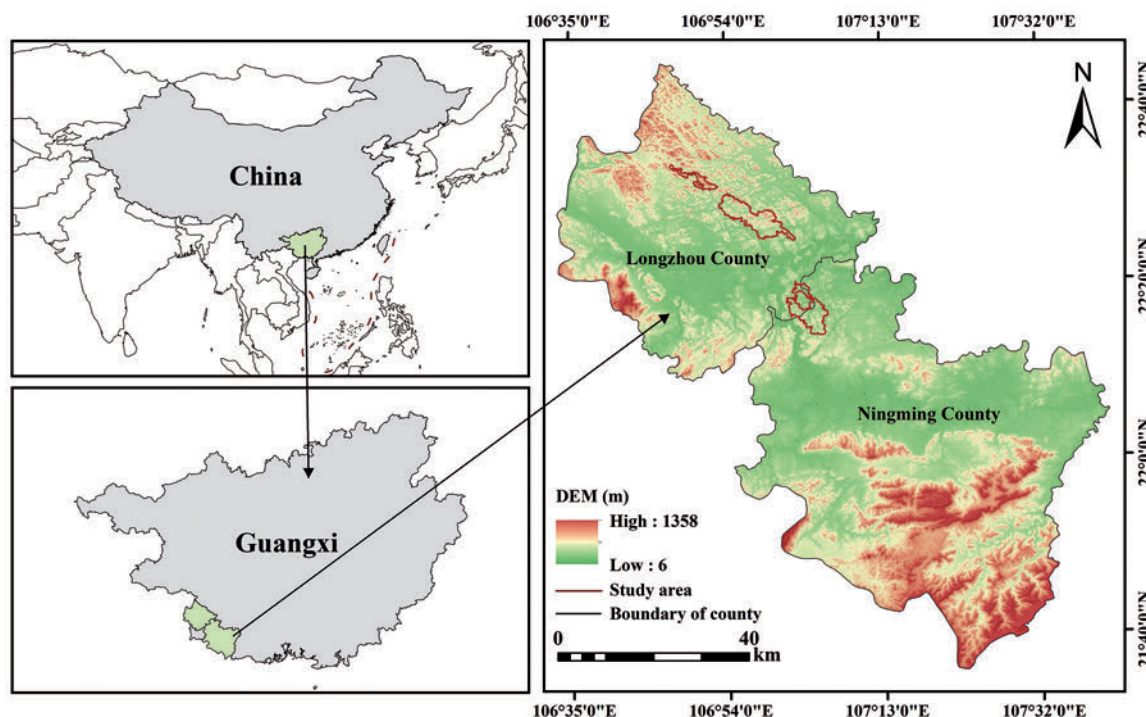


Figure 1 – Geographical location and spatial extent of Nonggang National Nature Reserve, China. Data source: geospatial data provider <https://www.gscloud.cn/>, maintained by the Chinese Academy of Sciences.

this as an ecological transition zone between tropical and subtropical regions (Wang et al. 2014; Zhu & Tan 2023). From the 1940s to the 1980s, rapid population growth significantly exacerbated the human–land conflict. In response to the need for resources, activities such as logging, land reclamation and grazing became widespread, leading to long-term disturbances and the degradation of fragile karst ecosystems in the NNNR (Huang et al. 2018). Extreme weather events driven by climate change, including typhoons and seasonal karst droughts, further stress the forest ecosystem and hinder vegetation growth and recovery (Geekiyana et al. 2019). However, after years of conservation and restoration efforts, vegetation and ecosystems within the reserve have gradually recovered. Both primary and secondary forest coverage have increased, and vegetation diversity has been partially restored (Zhang et al. 2024).

To understand this forest, research has been conducted on plant species composition, community structure, and plant–environment relationships. Based on a large monitoring plot of 15 ha in NNNR, Wang et al. (2014) identified 223 species from 56 families and 157 genera of woody plants with a diameter at breast height (DBH) ≥ 1 cm, totalling 68,010 individual plants. These species exhibit significantly different spatial distributions. Fu et al. (2023) discovered that with succession, the community species and phylogenetic diversity initially increased and then decreased, with the phylogenetic structure shifting from clustering to dispersal. They also observed functional diversity peaks in shrublands and young forests. However,

understanding of how the floristic composition and diversity of woody plants change in karst seasonal rainforests during succession remains relatively limited.

Floristic composition is one of the most critical ecological attributes of forest ecosystems (Rufino et al. 2023). Species diversity reflects community productivity and is a vital indicator of long-term community stability and development (Cheng 2020). Woody plants are essential components of forest ecosystems that significantly influence the overall composition of forest communities (Naidu & Kumar 2016). Therefore, understanding the changes in floristic composition and woody plant diversity in seasonal karst rainforests during succession is crucial for enhancing forest management, improving ecosystem services, and addressing future climate change.

In this study, we used the space-for-time substitution method to investigate three major natural successional communities in the tropical karst seasonal rainforests of the NNNR. Based on extensive plot surveys, we focused on the following questions: (1) How does the floristic composition of woody plants change across successional stages in seasonal karst rainforests? (2) How does community species diversity change during succession? The results of this study enhance our understanding of the successional processes in karst seasonal rainforests and provide a theoretical basis for restoring ecological functions and vegetation reconstruction in karst ecosystems.

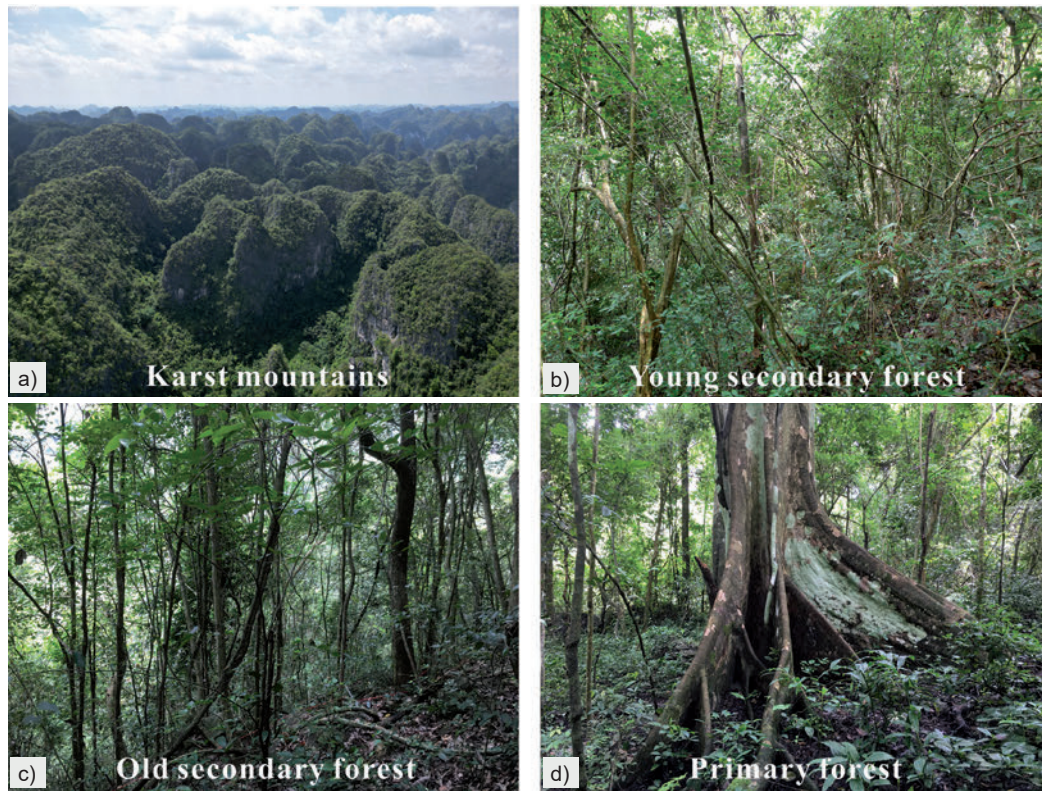


Figure 2 – Karst landscape (a) and three successional stages (b–d) of the tropical seasonal rainforests in southwestern China. © Gang Hu

Methods

Study area

The NNNR (106°42'28" to 107°04'54" E, 22°13'56" to 22°39'09" N) is situated in Longzhou and Ningming counties of Chongzuo City, Guangxi, China (Figure 1). This region has a tropical monsoon climate, with an average annual temperature of 22°C. The frost-free period typically lasts for more than 330 days per year, and the average annual rainfall is between 1,150 and 1,550 mm. The region typically encounters two to three typhoons each year, which can vary in severity, during the summer and autumn months. The geomorphology is predominantly karst peak cluster depressions from 300 to 600 m asl (Figure 2). The relative height from the bottom of the depressions to the top of the peaks typically ranges from 200 to 300 m. The soil is predominantly composed of black and brown limestone. In depressions, the bedrock exposure is low, with a thick soil layer. On slopes, bedrock exposure is high and the soil layer is shallow. Established in 1980, the NNNR is dedicated to safeguarding rainforest ecosystems and the rare flora and fauna they harbour. To achieve this, the reserve has introduced a variety of management strategies such as enhancing patrols and monitoring, promoting community co-management, conducting ecological restoration projects, and facilitating scientific research and education. As a result of these efforts, the reserve has seen a notable recovery in vegetation and ecosystems,

alongside enhanced protection of habitats for rare and endangered species. Currently, the reserve contains 1,725 species of vascular plants belonging to 184 families and 810 genera. These include 33 nationally rare and endangered species, 101 species endemic to Guangxi, and 278 karst species. It is one of 14 key terrestrial biodiversity areas of international importance in China.

Plot establishment and data collection

During the peak growing seasons from 2019 to 2021, we used the space-for-time substitution method to select forest plots in the NNNR. Three typical successional stages representing the transition from secondary to primary forests were selected: young secondary forests (YSF), old secondary forests (OSF), and primary forests (PF) (Figure 2). Specifically, based on the disturbance history of the plots, we classified plots with forest ages between 15 and 30 years as YSF, those between 30 and 100 years as OSF, and plots with forest ages exceeding 100 years as PF (Sattichanh et al. 2019; Teixeira et al. 2020). Three experienced forest rangers assisted in determining the forest age. Using a total station (Topcon GTS-336, Topcon Positioning Systems, Tokyo, Japan), we established 35 plots of 20 m × 20 m at each successional stage, totalling 105 plots. In each plot, all the woody plants with a DBH of ≥1 cm were tagged and identified. The data recorded included plant ID, species name, DBH, height and relative coordinates. Environmental parameters, such

Table 1 – Information on forest plots at three successional stages. The data are expressed as average $\pm$ standard deviation.

Forest type	Altitude (m)	Slope (°)	Canopy coverage (%)	Rock exposure rate (%)
Young secondary forest	305.28 $\pm$ 13.04	22.50 $\pm$ 6.95	67.50 $\pm$ 4.18	44.20 $\pm$ 13.63
Old secondary forest	215.71 $\pm$ 22.42	13.20 $\pm$ 13.74	72.00 $\pm$ 2.74	39.40 $\pm$ 18.35
Primary forest	219.07 $\pm$ 11.74	16.40 $\pm$ 13.28	66.00 $\pm$ 4.18	41.00 $\pm$ 13.21

as elevation, slope, canopy cover and rock exposure, were also documented. Elevation was measured using a handheld global positioning system (GPS) receiver (Garmin GPSmap 62s). Canopy cover was determined using the Canopeo application on a smartphone with a fisheye lens (Kase FISHEYE LENS II, Guangdong, China). Three experienced observers estimated the slope and rock exposure. The information on forest plots at the three successional stages is presented in Table 1.

Data analysis

The importance value index (IVI) of a species is determined by adding its relative abundance, frequency and dominance (Curtis & McIntosh 1951). The family importance value (FIV) is calculated by summing the relative diversity, density and dominance of the family (Mori et al. 1983).

α - and β -diversities are used to describe changes in species diversity during succession. The α -diversity is assessed using species richness (S), the Simpson index (D), the Shannon–Wiener index (H'), and the Pielou evenness index (E) to reflect variations in species richness and evenness within a community (Spellerberg & Fedor 2003). β -diversity measures the similarity in species composition between communities using the Jaccard index (C_j) and Sørensen index (C_s) (Small et al. 2004). The calculation methods for α - and β -diversity are as follows:

Species Richness (S): number of species in a community. (1)

Simpson Index (D): $D = 1 / \sum_{i=1}^S (P_i)^2$ (2)

Shannon–Wiener Index (H'): $H' = 1 / \sum_{i=1}^S (P_i \ln P_i)$ (3)

Pielou Evenness Index (E): $E = H' / \ln S$ (4)

S – total number of species,

P_i – proportion of the abundance of a specific species to the total abundance of all species ($P_i = N_i / N$),

N_i – number of individuals of the specific species,

N – total number of individuals of all species.

Jaccard Index (C_j): $C_j = j / (a + b - j)$ (5)

Sørensen Index (C_s): $C_s = 2j / (a + b)$ (6)

j – number of species common to both communities,

a and b – number of species in each community.

The Jaccard index (C_j) ranges from 0 to 1. Specifically, $0 < C_j < 0.25$ indicates extremely dissimilar; $0.25 < C_j < 0.50$ indicates moderately dissimilar; $0.50 < C_j < 0.75$ indicates moderately similar, and $0.75 < C_j < 1$ indicates very similar (Geng et al. 2022).

The Kruskal–Wallis test was used to analyse the α -diversity indices of communities at different succes-

sional stages, with significance determined at $P < 0.05$. A rank-abundance curve was generated by plotting the log of the relative abundance of a species against the species rank. Here, species rank refers to the relative ranking of a species based on its abundance within a community. All statistical analyses were performed using SPSS 25.0 and R 4.0.3.

Results

Floristic composition

A total of 16,825 woody plants with a DBH ≥ 1 cm, belonging to 68 families 194 genera and 281 species, were recorded across 105 plots. In the YSF, 6,197 individuals were recorded, representing 49 families 111 genera and 151 species. In the OSF, 6,233 individuals representing 58 families 148 genera and 192 species were recorded. In the PF, 4,395 individuals were recorded, representing 52 families 129 genera and 170 species (Table 2).

Based on the number of species within each family (Table 3), the three most species-rich families at different successional stages were as follows. In the YSF, these were Moraceae (12 species), Fabaceae (11 species), and Phyllanthaceae (11 species); in the OSF, Euphorbiaceae (15 species), Phyllanthaceae (12 species), and Moraceae (11 species); and in the PF, Euphorbiaceae (12 species), Rubiaceae (12 species), and Phyllanthaceae (12 species). *Ficus* exhibited the highest species richness at each successional stage. *Litsea* also had a high species richness, ranking as the second most species-rich genus in both the YSF and OSF (Table 4). Based on stem counts in each plot (Table 5), *Ficus hispida*, *Ardisia thyrsoiflora* and *Streblus tonkinensis* were the most common species in the YSF and OSF, while *Litsea variabilis* var. *oblonga*, *Leea indica* and *Cryptocarya lyoniifolia* were the most common species in the PF. As succession progressed, the species composition within the community changed continuously, with the highest family, genus and species richness recorded in the OSF.

Table 2 – Tree species richness in three tropical seasonal rain-forest successional stages. YSF – Young secondary forest; OSF – Old secondary forest; PF – Primary forest.

Forest type	Number of			Sum of individuals
	families	genera	species	
YSF	49	111	151	6,197
OSF	58	148	192	6,233
PF	52	129	170	4,395
Total	68	194	281	16,825

Table 3 – The ten most important families of woody plants in decreasing order of family importance value (FIV) at three succession stages. NG – number of genera; NS, number of species; NI – number of individuals in a family; FIV – family importance value.

Family	NG	NS	NI	FIV
Young secondary forest				
Moraceae	4	12	2,184	19.91
Malvaceae	6	8	444	9.03
Primulaceae	3	5	1,165	7.99
Euphorbiaceae	5	7	182	7.47
Lamiaceae	4	4	212	6.52
Phyllanthaceae	6	11	323	5.73
Rubiaceae	7	9	300	5.69
Fabaceae	9	11	60	4.44
Annonaceae	4	6	257	3.00
Lauraceae	3	7	205	2.90
Old secondary forest				
Moraceae	6	11	1,760	21.49
Euphorbiaceae	10	15	361	8.42
Phyllanthaceae	6	12	567	7.18
Malvaceae	7	8	401	6.73
Rubiaceae	7	8	507	4.66
Lauraceae	3	7	511	4.44
Araliaceae	7	8	137	4.20
Lamiaceae	5	6	195	4.10
Primulaceae	2	4	523	3.89
Arecaceae	1	1	34	2.97
Primary forest				
Lauraceae	3	6	1,056	13.62
Euphorbiaceae	11	12	464	10.05
Phyllanthaceae	6	12	414	8.76
Anacardiaceae	2	2	52	7.09
Malvaceae	7	8	250	6.31
Moraceae	5	11	272	5.57
Fabaceae	6	8	202	4.76
Rubiaceae	11	12	199	4.56
Vitaceae	2	2	432	3.81
Rutaceae	3	7	144	3.33

Dominant families, genera and species

The 10 most important families accounted for approximately 70% of the total FIV at each successional stage (Table 3). In the YSF and OSF, Moraceae was the most important family because of its high species richness and abundance. However, Lauraceae emerged as the most important family in the PF. In the OSF and PF, Euphorbiaceae and Phyllanthaceae had high numbers of individuals, making them the second and third most important families respectively.

At the genus level (Table 4), the top 10 genera accounted for 54.97%, 52.74% and 43.71% of the total importance values of their respective communities. *Ficus* was the most abundant genus in the YSF and OSF. It was also the most important genus, with the highest species richness and number of individuals. Although *Ficus* was the most species-rich genus in the PF, *Litsea* was the most important.

In the YSF, OSF and PF, the 10 most important species accounted for 51.79%, 45.27% and 39.22% of

Table 4 – The ten most important genera of woody plants in decreasing order of importance value index (IVI) at three succession stages. NS – number of species; NI – number of individuals in a genus.

Genus	Family	NS	NI	IVI
Young secondary forest				
<i>Ficus</i>	Moraceae	8	1,926	17.23
<i>Ardisia</i>	Primulaceae	2	1,141	7.81
<i>Vitex</i>	Lamiaceae	1	152	6.58
<i>Deutzianthus</i>	Euphorbiaceae	1	124	6.34
<i>Sterculia</i>	Malvaceae	2	184	4.01
<i>Litsea</i>	Lauraceae	5	189	2.64
<i>Cleistanthus</i>	Phyllanthaceae	1	239	2.63
<i>Excentrodendron</i>	Malvaceae	1	73	2.59
<i>Catunaregam</i>	Rubiaceae	1	219	2.57
<i>Streblus</i>	Moraceae	1	251	2.57
Old secondary forest				
<i>Ficus</i>	Moraceae	6	1,169	11.99
<i>Streblus</i>	Moraceae	1	582	10.19
<i>Cleistanthus</i>	Phyllanthaceae	2	456	5.11
<i>Ardisia</i>	Primulaceae	2	518	4.24
<i>Litsea</i>	Lauraceae	5	501	4.19
<i>Sterculia</i>	Malvaceae	2	248	3.96
<i>Vitex</i>	Lamiaceae	2	132	3.64
<i>Caryota</i>	Arecaceae	1	34	3.23
<i>Deutzianthus</i>	Euphorbiaceae	1	60	3.16
<i>Metadina</i>	Rubiaceae	1	448	3.03
Primary forest				
<i>Litsea</i>	Lauraceae	2	780	8.22
<i>Dracontomelon</i>	Anacardiaceae	1	47	6.37
<i>Cryptocarya</i>	Lauraceae	2	238	5.13
<i>Leea</i>	Vitaceae	1	430	4.14
<i>Ficus</i>	Moraceae	7	169	3.92
<i>Cleistanthus</i>	Phyllanthaceae	2	247	3.71
<i>Cephalomappa</i>	Euphorbiaceae	1	162	3.39
<i>Excentrodendron</i>	Malvaceae	1	103	3.20
<i>Bischofia</i>	Phyllanthaceae	2	59	2.96
<i>Clausena</i>	Rutaceae	2	108	2.66

the total importance values of their respective communities (Table 5). In the YSF, *Ficus hispida* was the most important species, with the highest number of individuals (1,871). *Ardisia thyrsoiflora*, with 1,128 individuals, was the second most abundant species. In the OSF, *Streblus tonkinensis* had the highest importance because it had the largest basal area (5.25 m²). *Ficus hispida* was the second most important species in the OSF, with the highest number of individuals (962). In the PF, *Litsea variabilis* var. *oblonga* was the most important species, with the highest number of individuals (771). *Dracontomelon duperreanum* was the second most important species because it had the largest basal area (5.70 m²).

α -diversity analysis

Among the three successional stages, OSF had the highest values for species richness, Simpson's index and Shannon–Wiener index. PF had the highest Pielou evenness index (Figure 3). The order of species richness was OSF > YSF > PF. OSF significantly sur-

Table 5 – The ten most important woody species in decreasing order of importance value index (IVI) at three succession stages. NI – number of individuals in a species; BA – basal area (m^2).

Species	Family	NI	BA	IVI
Young secondary forest				
<i>Ficus hispida</i>	Moraceae	1,871	2.36	14.77
<i>Ardisia thyrsiflora</i>	Primulaceae	1,128	0.37	7.68
<i>Vitex kwangsiensis</i>	Verbenaceae	152	2.79	6.58
<i>Deutzianthus tonkinensis</i>	Euphorbiaceae	124	2.92	6.34
<i>Sterculia monosperma</i>	Malvaceae	175	1.02	3.71
<i>Cleistanthus sumatranus</i>	Phyllanthaceae	239	0.61	2.63
<i>Excentrodendron tonkinense</i>	Malvaceae	73	0.89	2.59
<i>Catunaregam spinosa</i>	Rubiaceae	219	0.18	2.57
<i>Streblus tonkinensis</i>	Moraceae	251	0.48	2.57
<i>Wendlandia uvariifolia</i>	Rubiaceae	48	0.98	2.35
Old secondary forest				
<i>Streblus tonkinensis</i>	Moraceae	582	5.25	10.19
<i>Ficus hispida</i>	Moraceae	962	1.72	8.00
<i>Ardisia thyrsiflora</i>	Primulaceae	500	0.27	4.01
<i>Litsea variabilis</i> var. <i>oblonga</i>	Lauraceae	486	0.27	3.61
<i>Sterculia monosperma</i>	Malvaceae	230	1.10	3.55
<i>Vitex kwangsiensis</i>	Verbenaceae	126	1.61	3.37
<i>Caryota obtusa</i>	Palmae	34	2.19	3.23
<i>Deutzianthus tonkinensis</i>	Euphorbiaceae	60	1.89	3.16
<i>Cleistanthus sumatranus</i>	Phyllanthaceae	321	0.33	3.12
<i>Metadina trichotoma</i>	Rubiaceae	448	0.14	3.03
Primary forest				
<i>Litsea variabilis</i> var. <i>oblonga</i>	Lauraceae	771	0.76	7.53
<i>Dracontomelon duperreanum</i>	Anacardiaceae	47	5.70	6.37
<i>Cryptocarya lyoniifolia</i>	Lauraceae	238	2.64	5.13
<i>Leea indica</i>	Vitaceae	430	0.14	4.14
<i>Cephalomappa sinensis</i>	Euphorbiaceae	162	1.98	3.39
<i>Excentrodendron tonkinense</i>	Malvaceae	103	1.95	3.20
<i>Bischofia javanica</i>	Euphorbiaceae	57	1.69	2.76
<i>Catunaregam spinosa</i>	Rubiaceae	152	0.52	2.31
<i>Strophoblachia fimbriolax</i>	Euphorbiaceae	223	0.06	2.24
<i>Cleistanthus petelotii</i>	Phyllanthaceae	123	1.06	2.15

passed YSF and PF in terms of species richness ($P < 0.05$), with no significant differences between YSF and PF ($P > 0.05$). The Simpson and Shannon–Wiener indices generally followed the order of OSF > PF > YSF. However, the differences between the OSF and PF groups were not significant ($P > 0.05$). Conversely, the Pielou evenness index followed the order PF > OSF > YSF, indicating an increase in the evenness of species distribution with succession (Figure 3). The rank-abundance curve (Figure 4) further illustrates that OSF had the highest species richness, whereas PF had the most even species distribution.

β -diversity analysis

As shown in Figure 5, the Jaccard and Sørensen indices showed a consistent trend of decreasing similarity. Among these, the similarity between YSF and OSF was the highest. According to the Jaccard simi-

larity principle, the similarity coefficients between the YSF and OSF, YSF and PF, and OSF and PF were all between 0.25 and 0.50. This indicates a moderate degree of difference among the communities.

Discussion

Floristic composition in tropical karst seasonal rainforests

In the present study, 281 woody plant species from 68 families and 194 genera were identified (Table 2). Species richness in the tropical karst seasonal rainforest plots of the NNNR was significantly higher than that in the non-karst subtropical evergreen broad-leaved forest plots on Dinghu Mountain (20 ha, 210 species, DBH ≥ 1 cm) and Gutian Mountain (24 ha, 159 species, DBH ≥ 1 cm) (Ye et al. 2008; Zhu et al. 2008). However, species richness in the NNNR was lower than that in the tropical rainforest in Xishuangbanna (1 ha, approximately 216 species, DBH ≥ 1 cm) (Lan et al. 2012). This may be related to the high proportion of endemic species in the NNNR region. Some drought-resistant and calcium-loving species, such as *Excentrodendron tonkinense*, *Garcinia paucinervis* and *Cephalomappa sinensis*, have robust root systems that can grow in rock crevices but are adapted only to karst habitat conditions (Wang et al. 2014; Chen et al. 2022).

The results showed significant variation in the floristic composition of woody plants across the three successional stages, demonstrating clear species turnover, with OSF having the highest number of species. Contemporary succession theory emphasizes the availability of resources as the primary driver of species turnover (Dent & Estrada-Villegas 2021). However, in karst seasonal rainforests, which are characterized by both wet and hot conditions, the availability of light, water, and soil nutrients tends to decrease as succession progresses. Among these factors, light availability emerges as the most critical driver of species turnover (Guariguata & Ostertag 2001). During the secondary succession stage, pioneer species with high light-use efficiency, such as *Deutzianthus tonkinensis*, *Catunaregam spinosa* and *Diplodiscus trichospermus*, dominated the community. However, in shaded environments created by long-lived pioneer species, many shade-tolerant late-successional species (that is, climax species), such as *Excentrodendron tonkinense*, *Cephalomappa sinensis* and *Cleistanthus sumatranus*, begin to colonize and grow within the community. This stage exhibited the highest species diversity within the community. A strong vertical light gradient, however, limits the regeneration of pioneer species. Over time, shade-tolerant climax species dominate community composition (Wittmann et al. 2008; Matsuo et al. 2021). The evolution of community structure during succession can cause changes in habitat conditions. The spatiotemporal heterogeneity of habitats drives species competition, environmental filtering, niche partitioning and species turnover during succession (Albouy et al. 2012; de Assis et al. 2017).

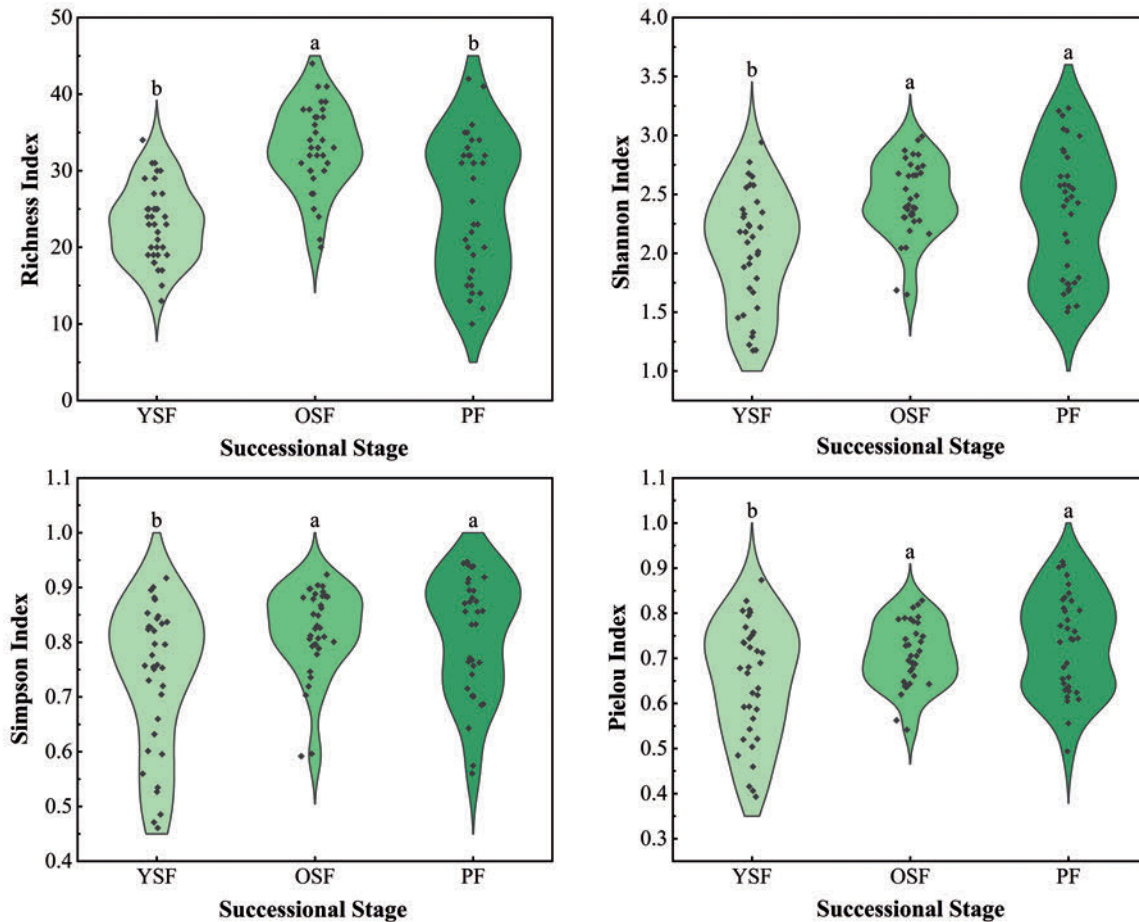


Figure 3 – Species α -diversity indices of communities at three successional stages. YSF, Young secondary forest; OSF, Old secondary forest; PF, Primary forest.

Distribution of dominant families, genera and species in tropical karst seasonal rainforests

The dominant families in the community were Moraceae, Euphorbiaceae and Lauraceae. The dominant genera were *Ficus*, *Litsea* and *Streblus*, with the main dominant species being *Ficus hispida*, *Streblus tonkinensis* and *Litsea variabilis* var. *oblonga*. This result is consistent with the findings of Wang et al. (2014). As succession progressed, the composition of the dominant species within the community changed, and their importance tended to decrease. This phenomenon may be related to environmental heterogeneity, because changes in community habitat conditions during succession affect species selection and adaptation levels (Hilmers et al. 2018; Čepelová & Münzbergová 2012). Owing to their inability to adapt to environmental changes, some dominant species in the early succession stages lose competitiveness in terms of access to and use of resources, leading to a decline in their dominance (Lebrija-Trejos et al. 2011; Geng et al. 2022). *Ficus hispida*, which was a dominant species in the YSF, also appeared in abundance in the OSF but lost its dominance in the PF.

This study identified distinct dominant species during the YSF stage, but no distinct dominant species were observed during the PF stage. In the YSF, the

dominant species, *Ficus hispida*, had an importance value of 14.77. This was significantly higher than that of the second most important species, *Ardisia thyrsiflora*, with an importance value of 7.68. In contrast, in the PF, the dominant species, *Litsea variabilis* var. *oblonga*, had an importance value of 7.53, showing a marginal difference of 1.16 compared to *Dracontomelon duperre-*

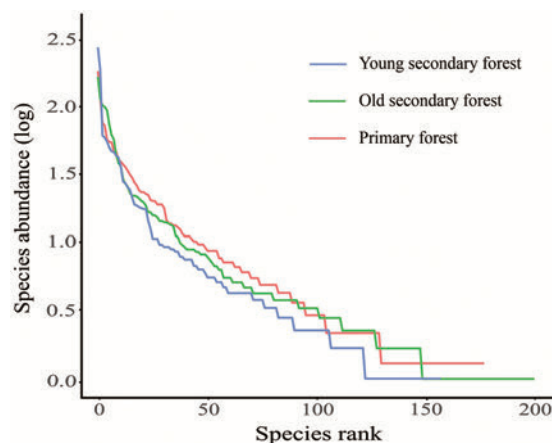


Figure 4 – Rank-abundance curves of woody species at three successional stages.

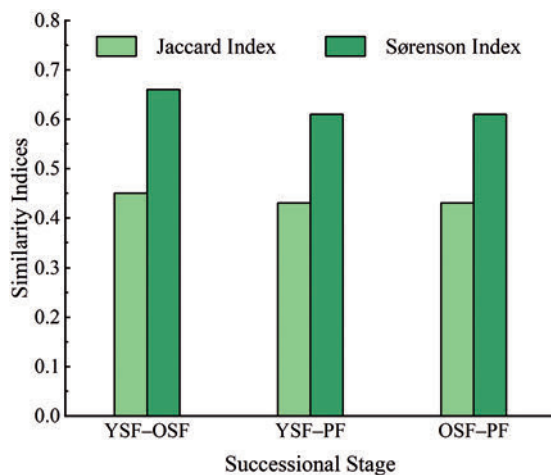


Figure 5 – Similarity indices (Jaccard and Sørensen indices) between communities at different successional stages. YSF, Young secondary forest; OSF, Old secondary forest; PF, Primary forest.

anum, the second most important species. This may stem from the simpler structure of the YSF, which has fewer species in the canopy but a higher density of individuals, thereby enhancing the importance of the dominant species. However, as succession progresses, the effect of similarity limitation among species strengthens owing to ecological niche convergence and the long-term accumulation of herbivorous insects and soil pathogens, potentially limiting the dominance of any single species (Liu et al. 2015; Chen et al. 2019).

Plant species diversity in tropical karst seasonal rainforests

Numerous studies indicate that species diversity tends to increase during the early and middle stages of succession, but it decreases during later stages (Gadow et al. 2016; Álvarez-Molina et al. 2012). Our findings support this conclusion. In the present study, species diversity followed a unimodal trend, increasing and then decreasing with succession, reaching a maximum in the OSF. Over the past century, sustained and intensive human activities, including logging, agricultural production and grazing, have caused significant damage and disturbances to the native vegetation of NNNR (Huang et al. 2018). However, since the implementation of a vegetation protection policy in 1979, anthropogenic disturbances have been notably reduced, allowing vegetation to enter a state of natural recovery (Zhang et al. 2024). Consequently, in areas affected by disturbances, numerous fast-growing pioneer species can establish themselves and proliferate during the early stages of vegetation recovery (Fu et al. 2023). As recovery progresses, the accumulation of forest biomass reduces the light conditions in the understorey, allowing climax species to thrive in shaded environments. The coexistence of pioneer and climax species significantly enhances species diversity (Lebri-

ja-Trejos et al. 2010). However, as the forest matures and climax species increasingly dominate the canopy, some pioneer species that are disadvantaged in resource use and competition gradually withdraw from the community because of their inability to adapt to their environments. This results in a reduction in species diversity (Lebrija-Trejos et al. 2011; Jin et al. 2018).

Our study indicated that the Pielou evenness index increased with succession. The rank-abundance curve (Figure 5) showed that the species distribution became more stable and uniform as succession progressed. According to the niche theory, resource availability changes continuously during succession, allowing species with strong resource acquisition abilities to occupy the corresponding niches because of their competitive advantages (Dent & Estrada-Villegas 2021). During this process, competitive exclusion (i.e., species competition) is gradually moderated, community stability increases, and species distribution within the community becomes more uniform (Gadow et al. 2016). Anthropogenic disturbances play a dominant and limiting role in community species diversity during secondary succession. As succession progresses, competitive exclusion gradually replaces the effects of anthropogenic disturbances and becomes a key factor influencing community species diversity (Fu et al. 2023).

In karst seasonal rainforests, it is crucial to note that natural disturbances like typhoons and seasonal droughts significantly affect forest vegetation (Geekiyangage et al. 2019). The strong winds and heavy rainfall from typhoons can lead to tree falls, canopy damage and soil erosion, causing temporary disruptions to the forest structure (Lu et al. 2020). Similarly, seasonal droughts place stress on plants, reducing their growth rates and increasing their vulnerability to wildfires (Wang et al. 2021). Despite these challenges, natural disturbances typically exhibit periodicity and recoverability, aiding in the natural regeneration of plant communities. In contrast, human-induced disturbances are often persistent and irreversible, leading to more prolonged and extensive damage to forest vegetation, including in the karst regions of China (Yue et al. 2024).

In accordance with Jaccard's similarity principle, the similarity between successive stages of succession in this study showed a decreasing trend, with a moderate level of dissimilarity between communities at different stages of succession (Figure 5). This difference may be related to the complex terrain and climatic conditions of the NNNR region. The niche theory suggests that increased environmental heterogeneity leads to reduced community similarity (Chang & Turner 2019; Hu et al. 2024). The high heterogeneity of karst environments might have caused habitat filtering, leading to a decrease in community similarity over time. As illustrated in Figure 5, the similarity between the YSF and OSF was the highest. However, over time, substantial changes in habitat conditions and increased species turnover rates have led to a gradual decrease in

community similarity. Therefore, in highly heterogeneous karst environments, variations in habitat conditions significantly influence the survival and development of species. This phenomenon is reflected in the overall species composition and distribution within the community (Burda et al. 2022).

Conclusion

Our study showed that, in the NNNR, the YSF included 151 woody species from 49 families and 111 genera. The OSF contained 192 woody species from 58 families and 148 genera, while the PF was home to 170 woody species from 52 families and 129 genera. The OSF exhibited the highest richness in terms of family, genus and species composition. The 10 most important species accounted for the highest proportion of the total importance value in the YSF; this proportion was lowest in the PF, indicating that the importance of the dominant species in the community gradually decreased as succession progressed. Species diversity followed a unimodal trend during succession, with the maximum value occurring in the OSF. This pattern could be attributed to anthropogenic disturbances and competitive exclusion. During the secondary succession stage, anthropogenic disturbances probably played a dominant limiting role in plant communities. In the later stages of succession, plant communities may be constrained by competitive exclusion among species owing to more intense competition for resources.

Based on these findings, effective vegetation management in karst mountains should consider key factors, including anthropogenic activities, vegetation distribution, soil properties, and light and moisture conditions. In addition, government agencies, research institutions, conservation organizations and local communities should collaborate closely to ensure the effective protection and management of forest vegetation within the NNNR. Collaboration should focus on several key areas such as strengthening law enforcement, improving management resources, advancing scientific research and promoting public education. Our study is the first to clarify successional changes in woody floristic composition and the diversity of tropical seasonal rainforests in a karst mountainous area of southwestern China. Future studies should include long-term forest monitoring to gather additional data on community dynamics over time. This approach will reveal the precise patterns and mechanisms of karst vegetation succession and development.

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