Postprint: Temporal Dynamics of Species Diversity in Deutzianthus tonkinensis Community in Karst Seasonal Rainforest of Southwestern Guangxi

Authors: Yang Xufei, Wang Bin, Li Dongxing, Lu Fang, Li Jianxing, Tao Wanglan, Tang Nianwu, Guo Yili, Xiang Wusheng, Li Xiankun

Date: 2024-12-02T00:00:00+00:00

Abstract

Deutzianthus tonkinensis is a national second-class key protected wild plant, and communities with it as the constructive species represent one of the primary rare vegetation types in northern tropical karst seasonal rainforests, harboring rich biodiversity and numerous endemic species with significant ecological and economic value. However, the dynamic characteristics and driving mechanisms of community species diversity remain unclear. To elucidate the temporal dynamics and driving factors of D. tonkinensis communities, this study analyzed the temporal dynamics of community species diversity from 2012 to 2022 based on data from three periodic censuses of a 1 hm^2 long-term permanent monitoring plot of a D. tonkinensis community in Nonggang, Guangxi, and examined the effects of topographic factors on community species diversity dynamics. The results indicate that over the 10-year period: (1) The importance value of dominant species remained stable, basal area at breast height increased, while species abundance declined. (2) A total of 18 rare and occasional species were lost from the community; species richness decreased by 14%, and the Shannon-Wiener diversity index declined significantly ($P < 0.05$). (3) The number of quadrats contributing significantly to beta diversity decreased by 2%, with the temporal beta diversity index declining in 80% of quadrats, indicating that species loss substantially exceeded species gain in the plot. (4) Elevation exerted a significant influence on species loss within the plot ($P < 0.05$). These findings demonstrate that although the community structure of D. tonkinensis remained generally stable over the decade, both alpha and beta diversity exhibited marked changes, driven by the loss of rare and occasional species, with elevation among topographic factors significantly affecting species diversity dynamics. This study provides important insights for advancing understanding

of biodiversity dynamics and their driving mechanisms in karst seasonal rainforests.

Full Text

Preamble

DOI: 10.11931/guihaia/gxzw202405053

Title: Temporal Dynamics of Species Diversity in Deutzianthus tonkinensis Communities of the Karst Seasonal Rainforest in Southwest Guangxi

Authors: YANG Xufei[1],[2],[3], WANG Bin[2],[3], LI Dongxing[2],[3], LU Fang[2],[3], LI Jianxing[2],[3], TAO Wanglan[2],[3], TANG Nianwu[2],[3], GUO Yili[2],[3], XIANG Wusheng[2],[3]*, LI Xiankun[2],[3]

[1]College of Tourism and Landscape Architecture, Guilin University of Technology, Guilin 541006, Guangxi, China
[2]Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, Guangxi, China
[3]Nonggang Karst Ecosystem Observation and Research Station of Guangxi, Chongzuo 532499, Guangxi, China

*Corresponding author: XIANG Wusheng, Researcher, specializing in plant ecology (E-mail: xwusheng@qq.com)

Funding: National Natural Science Foundation of China (32360281, 32271599, 32260276); Scientific Capacity Building Project of Nonggang Karst Ecosystem Guangxi Field Scientific Observation and Research Station (Task No.: Guike 23-026-273); Guangxi Natural Science Foundation (2022GXNSFBA035552)

First Author: YANG Xufei (1999—), Master's student, research focuses on landscape architecture and forest ecology (E-mail: 371743316@qq.com)

Abstract

Deutzianthus tonkinensis is a national second-class key protected wild plant in China. Communities dominated by this species constitute one of the main rare vegetation types in northern tropical karst seasonal rainforests, containing rich biodiversity and numerous endemic species with important ecological and economic value. However, the temporal dynamic characteristics and driving mechanisms of species diversity in these communities remain unclear. To clarify the temporal dynamics and driving factors of D. tonkinensis communities, this study analyzed three periodic re-survey datasets from a 1-hectare permanent monitoring plot in Nonggang, Guangxi, examining the temporal dynamics of community species diversity between 2012 and 2022 and exploring the effects of topographic factors on these dynamics. The results indicate that over the ten-year period: (1) The importance values of dominant species remained stable, basal area at breast height increased, while species abundance decreased. (2) A total of 18 rare and occasional species were lost from the community; species richness decreased by 14%, and the Shannon-Wiener diversity index declined significantly ($P < 0.05$). (3) The number of quadrats making significant contributions to β-diversity decreased by 2%, with the temporal β-diversity index declining in 80% of quadrats, indicating that species loss clearly exceeded species gain. (4) Elevation had a significant effect on species loss within the plot ($P < 0.05$). These findings demonstrate that while the overall community structure of D. tonkinensis remained stable over the decade, both α- and β-diversity changed markedly, driven by the loss of rare and occasional species, with elevation among topographic factors exerting a significant influence on species diversity changes. These results provide important insights for understanding biodiversity dynamics and their driving mechanisms in karst seasonal rainforests.

Keywords: Deutzianthus tonkinensis, β-diversity, spatiotemporal dynamics, B-C plot, Nonggang National Nature Reserve

Introduction

The ongoing loss of biodiversity has become a global challenge (Luo et al., 2023). To achieve the goal of halting and reversing biodiversity loss as proposed in the Kunming-Montreal Global Biodiversity Framework, monitoring and identifying the primary drivers of biodiversity change across different ecosystems is critical (Ma, 2023; Zhang et al., 2023).

Forests serve as the most important terrestrial gene banks, with tropical forests harboring over 50% of all discovered terrestrial species (Wright et al., 2021). Understanding the dynamic changes in their biodiversity and underlying drivers is therefore essential. However, current research has yet to reach consistent conclusions regarding the dynamic characteristics of biodiversity and their driving factors across different forest types.

The temporal dynamics of community α-diversity have long been a central focus in biodiversity research (Chen et al., 2024). Earlier studies suggested that α-diversity generally increases with succession (i.e., over time) (Li et al., 2021). However, recent research indicates that the temporal dynamics of forest α-diversity are stage-dependent. During early succession, α-diversity typically increases gradually due to population dispersal and establishment (Li et al., 2022), whereas in later successional stages, intensifying interspecific competition may eliminate less competitive species (Shen et al., 2013), leading to declines in α-diversity. Consequently, the temporal dynamics of forest α-diversity may exhibit divergent trends depending on forest type and environmental conditions, though this remains insufficiently explored, particularly in highly heterogeneous and biodiverse karst forests. Furthermore, most previous studies have employed space-for-time substitution approaches, with relatively few based on long-term monitoring of permanent plots (Zhou et al., 2021; Wei et al., 2024), which limits their ability to capture the true temporal dynamics of forest α-diversity.

β-diversity is recognized as spatial variation in community composition within a given region (Legendre et al., 2005), reflecting the mechanisms underlying community change and maintenance processes (Whittaker, 1972). Forest β-diversity has been extensively studied across animals, plants, and microorganisms (Pavel et al., 2022). While spatial β-diversity research has yielded substantial insights, the importance of temporal differences in community composition has become increasingly apparent (Gadelha et al., 2023). Legendre and colleagues proposed the concept and measurement of temporal β-diversity (TBI), decomposing it into components of species (or abundance) loss and gain over a given period (Legendre, 2019; Nakadai, 2020). The TBI framework has been applied to analyze spatiotemporal dynamics in some tropical and subtropical forest communities and to examine the effects of environmental and climatic factors on community TBI (Nakadai, 2020). However, studies exploring TBI changes from a spatiotemporal interaction perspective remain scarce, and further research is needed on TBI dynamics and their drivers across different climate zones and environmental contexts.

Extensive karst forests are distributed across southwestern China, with the northern tropical karst seasonal rainforest representing a typical example (Wang et al., 2014). These forests provide invaluable seed sources and an indispensable reference system for ecological restoration of rocky desertification areas in southwestern China (Li et al., 2003), performing critical ecological functions such as preventing desertification and serving as carbon sinks, thereby forming an important ecological security barrier in the region (Huang et al., 2016). Nonggang in Guangxi harbors a unique limestone mountain seasonal rainforest located south of the Tropic of Cancer, characterized by relatively large conserved areas and relatively intact plant ecosystems—rare both in China and globally (Li et al., 2003). This region contains extremely rich assemblages of rare, endangered, and karst-endemic plants. Previous research on karst seasonal rainforest diversity has primarily focused on the distribution of animal and plant diversity and its relationship with habitats (Deng et al., 2022; Ma et al., 2023), with few studies addressing the temporal dynamics of species diversity. This study focuses on the typical rare vegetation type of karst seasonal rainforests—the D. tonkinensis community—using ten years of continuous monitoring data from a 1-hectare plot. Through multivariate statistical analysis and linear modeling, we analyzed the temporal dynamics of species composition and diversity in the D. tonkinensis community by comparing species composition and diversity metrics across different time points. We aimed to address the following scientific questions: (1) Has the species composition of D. tonkinensis communities changed significantly over the past decade? (2) What are the temporal change characteristics of α-diversity? (3) What are the spatiotemporal change characteristics of β-diversity and their main topographic driving factors? Addressing these questions will enhance understanding of biodiversity dynamics and topographic driving mechanisms in karst seasonal rainforests, providing a scientific basis for the conservation and utilization of numerous rare, endangered, and endemic species.

1 Study Area Overview

Nonggang National Nature Reserve is located at the border of Longzhou and Ningming counties in Guangxi, on the edge of China's tropical zone (106°42 28 —107°04 54 E, 22°13 56 —22°39 09 N), representing a typical example of tropical marginal karst forest ecosystems in China (Huang et al., 2016). The region has an average annual rainfall of 1,150–1,550 mm and an average annual temperature of 22°C. The average temperature of the coldest month exceeds 13°C, while the hottest month averages above 28°C, with extreme maximum temperatures reaching 40.5°C. The climate features abundant heat and plentiful rainfall, exhibiting distinct tropical rainforest characteristics. The reserve has complex topography, typical of karst peak-cluster landforms. The main soil types include primitive limestone soil, black limestone soil, brown limestone soil, hydromorphic brown limestone soil, and leached red limestone soil. The area features a karst "peak-cluster-depression" landform, with absolute elevations from depression to summit ranging only 200–300 m, yet water and heat conditions vary dramatically, resulting in pronounced vertical vegetation changes (Huang et al., 2016).

Deutzianthus tonkinensis is a nationally second-class protected plant and a typical calcicole species. Communities dominated by D. tonkinensis represent typical seasonal rainforests in northern tropical karst mountains (Li et al., 2003). Within Nonggang Nature Reserve, D. tonkinensis communities are mainly distributed in the Longhu and Nonggang sections, representing one of the more stable karst forest types in the reserve. Previous surveys have shown that D. tonkinensis communities have relatively complex structures, dominated by shade-tolerant species. The upper canopy layer consists of D. tonkinensis with extremely high canopy closure, while the understory is rich in species, with abundant shrubs, lianas, and epiphytes, exhibiting typical tropical rainforest characteristics (He, 2012). Common companion tree species in D. tonkinensis forests include *Cephalomappa sinensis*, *Sterculia monosperma*, *Dracontomelon duperreanum*, and *Streblus tonkinensis*.

2.1 Plot Establishment and Community Survey

In the concentrated distribution area of D. tonkinensis in Nonggang Reserve, we established a long-term monitoring plot with a projected area of 1 hectare [Figure 1: see original paper] following the protocols of the Smithsonian Tropical Research Institute's Center for Tropical Forest Science (CTFS) (Condit, 1998).

The plot measures 100 m × 100 m and was divided into 100 quadrats of 10 m × 10 m using a total station.

In 2012, all tree individuals with diameter at breast height (DBH) $\geq$ 1 cm in each quadrat were tagged, with their species, coordinates, DBH, height, and survival status recorded. The plot was resurveyed in 2017 and 2022, with survey content consistent with 2012, and newly recruited individuals with DBH $\geq$ 1 cm and dead individuals were documented in detail.

[Figure 1: see original paper] Fig. 1 3D DEM map of the *Deutzianthus tonkinensis* forest plot

---

2.2 Data Processing

Statistical analyses were performed using R software, with preliminary data processing conducted in Microsoft Excel 2010. All data were processed and calculated in R software (version 4.0.0), and figures were generated using the ggplot2 package in R.

2.2.1 Temporal Changes in Species Composition Characteristics

Species importance values (IV) were calculated using the formula from Curtis and McIntosh (1951). Basic changes in species composition were assessed through changes in importance values and basal area at breast height, with trends analyzed using Wilcoxon signed-rank tests. The change rate for each species between 2012 and 2022 was calculated using the following formula (Li et al., 2020):

$$R = \frac{\text{Value}_{2022} - \text{Value}_{2012}}{\text{Value}_{2012} \times T} \times 100\%$$

where R represents the change rate, T represents the time interval between the two surveys, and Value_{2022} and Value_{2012} represent the importance value or basal area at breast height of a species in the two surveys.

Species abundance is an important aspect of species composition. This study used the difference in species abundance between 2012 and 2022 to reflect changes in abundance, with significance tested using pairwise t-tests with 999 permutations (Legendre et al., 2019). Additionally, population mortality and recruitment rates were used to further analyze detailed changes in species abundance. Mortality (M) and recruitment (R) rates were calculated as follows (Zhang et al., 2019):

$$M = \frac{\ln(N_0) - \ln(N_t)}{T} \times 100\%$$

$$R = \frac{\ln(N_t) - \ln(N_0)}{T} \times 100\%$$

where N$_0$ represents the number of individuals of a species in the first survey, N represents the number of individuals after time T, and T is the time interval between the 2012 and 2022 surveys.

Linear models were also used to analyze relationships between species abundance, average DBH, and mortality rates, with scatter plots as visualization tools. To more clearly reveal potential relationships between species abundance and mortality, we log-transformed the species abundance data.

Non-metric multidimensional scaling (NMDS) was used to analyze overall changes in species composition. We conducted the analysis using the Bray-Curtis method based on abundance data (Anderson et al., 2011), applying the metaMDS function in the vegan package in R to ordinate species individual counts in different quadrats from 2012, 2017, and 2022, with the first two axes used to generate ordination plots.

2.2.2 Temporal Changes in Species α-Diversity

This study selected four common species diversity indices to measure community α-diversity: richness index (S), Shannon-Wiener index (H), Simpson diversity index (D), and Pielou evenness index (E). The richness index (S) reflects species richness in a community, emphasizing the role of rare species. The Simpson diversity index (D) reflects species dominance, emphasizing the role of dominant species. The Shannon-Wiener index (H) considers both species number and relative abundance changes, comprehensively reflecting species richness and evenness. The Pielou evenness index (E) reflects the uniformity of species distribution in a community; higher E values indicate more uniform species distribution, with few or no species holding absolute dominance and stronger community resistance to disturbance (Ma et al., 1994). Calculation methods for the four diversity indices are described in Ma et al. (1994).

Following Hubbell and Foster (1986), rare species were defined as those with $\leq$ 1 individual per hectare, and occasional species as those with 2–10 individuals per hectare.

2.2.3 Changes in Spatial β-Diversity Components

We used the method proposed by Legendre et al. (2013) to partition total β-diversity into local contributions to beta diversity (LCBD) for individual quadrats and species contributions to beta diversity (SCBD). LCBD was used to reflect changes in spatial β-diversity components. LCBD reflects the uniqueness of a quadrat relative to others in the region; larger LCBD values indicate more significant uniqueness distinguishing a quadrat from others in the region. LCBD was calculated as follows (Legendre et al., 2013):

Total β-diversity:

$$BD_{total} = \frac{\sum(y_{ij} - y_j)^2}{n \times p}$$

Local contribution:

$$LCBD_i = \frac{\sum(y_{ij} - y_j)^2}{p \times BD_{total}}$$

where the community composition matrix Y consists of n quadrats (rows) and p species (columns), with each value y representing the abundance of species j in quadrat i, and y representing the mean abundance of species j across all quadrats. The significance of LCBD was tested using 999 permutations (Legendre et al., 2013).

2.2.4 Spatial Variation in Temporal β-Diversity and Analysis of Influencing Factors

Statistical results from different time periods for quadrats within a region are termed temporal beta diversity indices (TBI). TBI extends total regional β-diversity to the temporal scale, projecting total β-diversity onto temporal dynamics through quadrat data from time 1 (T1) and time 2 (T2) (Legendre, 2019). TBI consists of two components: B = species (or abundance) loss and C = species (or abundance) gain. The B-C plot generated from these components intuitively illustrates community changes over time (Legendre et al., 2019). C and B statistics for all locations in the study plot can be tested for significance using paired t-tests. Analysis was conducted using the TBI function in the adespatial package in R.

The effects of topography on TBI changes were analyzed using generalized linear models (GLM). The glm() function in R was used to construct GLM models with binomial distribution for logistic regression analysis. In model construction, species gain or loss in each 10 m × 10 m quadrat between 2012 and 2022 served as the dependent variable, while four topographic factors for each quadrat—mean elevation, convexity, slope, and aspect—served as independent variables. Topographic factors were calculated following standard methods for CTFS plots, with aspect converted from 0°–360° compass measurements to values between 0 and 1 using the formula (Roberts and Cooper, 1989), making the northeast direction -1 and the southwest direction 1:

$$\text{Aspect index} = 1 - \frac{\cos(\text{Aspect angle} - 30°)}{2}$$

where Aspect_{index} represents the aspect index and Aspect_{angle} represents the aspect direction angle. After conversion, values range from 0 to 1, with 0 representing northeast and 1 representing southwest.

3 Results and Analysis

3.1 Temporal Changes in Basic Characteristics of Species Composition

Between 2012 and 2022, the ranking of the top 20 tree species by importance value in the D. tonkinensis forest plot showed little overall change, with Wilcoxon signed-rank test results indicating no significant difference (P = 0.698). *Deutzianthus tonkinensis* and *Ardisia thyrsiflora* maintained high importance values across all years. The importance value rankings of *Orophea polycarpa*, *Amesiodendron chinense*, *Streblus tonkinensis*, *Alphonsea monogyna*, and *Chassalia curviflora* increased, while those of *Antidesma japonicum*, *Celtis timorensis*, *Archidendron robinsonii*, *Catunaregam spinosa*, and *Bischofia javanica* decreased. Total community basal area increased overall, though Wilcoxon signed-rank test results indicated no significant change in overall ranking (P = 0.639). Species with large absolute increases in basal area included D. tonkinensis, A. chinense, and *Dracontomelon duperreanum*, while those with large relative changes included A. chinense, C. timorensis, O. polycarpa, S. tonkinensis, and *Chionanthus ramiflorus*, with C. ramiflorus showing the largest decrease .

Over the ten-year period from 2012 to 2022, total species abundance in the 1-hectare D. tonkinensis community plot decreased from 5,808 to 4,647 individuals, with 800 new individuals recruited. Pairwise t-tests with 999 permutations revealed that 29 species showed significant abundance decreases, only 1 species increased significantly, and 100 species showed no significant change. Among the top 20 species by importance value, 13 showed significant abundance changes, all decreases, while 7 showed no significant change. Most species had mortality rates exceeding recruitment rates, with *Chionanthus ramiflorus* showing particularly high mortality, decreasing by 125 individuals over the ten-year period . As shown in [Figure 2: see original paper], no significant relationship existed between species abundance and mortality. The regression coefficient between average DBH and mortality was negative, indicating that larger DBH was associated with relatively lower mortality, but the coefficient was extremely small with low R^2 values and was not statistically significant.

[Figure 2: see original paper] Fig. 2 Relationship between species abundance, average diameter at breast height (DBH), and mortality rate within the 1 hm^2 *Deutzianthus tonkinensis* community from 2012 to 2022

Note: slope and R^2 refer to the slope and coefficient of determination of the linear model, respectively.

The NMDS ordination plot shows that sample points from 2017 and 2022 almost completely overlap, indicating high similarity in community species composition between these two years. Samples from 2012 were slightly separated from the later years, showing differences in species composition. Overall, while the number of plant individuals in the D. tonkinensis forest community changed somewhat between 2012 and 2022, this change stabilized after 2017 [Figure 3: see original paper].

[Figure 3: see original paper] Fig. 3 NMDS analysis of species composition within the 1 hm^2 *Deutzianthus tonkinensis* community

3.2 Dynamics of α-Diversity

In terms of species richness, 130 species belonging to 106 genera and 45 families were recorded in 2012, compared to 112 species from 94 genera and 41 families in 2022. Compared to 2012, the community lost 4 families, 12 genera, and 18 species by 2022. Among the 18 species lost, 12 were rare species, mostly small-diameter shrubs or tree individuals, while only *Diospyros* sp. (DBH $>$ 10 cm) and *Saguerus westerhoutii* (DBH $>$ 30 cm) had larger DBH values. The remaining 6 species were occasional species, with only *Oreocnide rubescens* having a relatively large DBH ($>$ 10 cm). Species richness declined more substantially between 2012 and 2017, with the decreasing trend becoming more gradual between 2017 and 2022.

Between 2012 and 2022, Shannon-Wiener, Simpson, and Pielou diversity indices all showed decreasing trends at the 10 m × 10 m scale. The Shannon-Wiener diversity index decreased significantly ($P < 0.05$), while changes in the Simpson index and Pielou evenness were not significant [Figure 4: see original paper]. The trends of the three diversity indices were consistent with that of species richness, indicating an overall decline in α-diversity within the plot.

[Figure 4: see original paper] Fig. 4 Changes in α-diversity index within the 1 hm^2 plot of *Deutzianthus tonkinensis* community from 2012 to 2022

Note: NS represents P > 0.05, represents $P < 0.05$.*

3.3 Temporal Changes in β-Diversity and Its Components

Comparison of LCBD distributions between 2012 and 2022 shows that 20 quadrats made significant contributions to β-diversity in 2012, decreasing to 18 quadrats in 2022, a reduction of 2 quadrats [Figure 5: see original paper]. In both years, quadrats making significant contributions to β-diversity were clustered in the northeast corner of the plot at higher elevations and steeper slopes.

[Figure 5: see original paper] Fig. 5 The distribution of LCBD within the 1 hm^2 *Deutzianthus tonkinensis* community from 2012 to 2022

Note: Red-edged squares represent quadrats that significantly contribute to beta diversity within the plot, while green density lines represent contour lines.

At the 10 m × 10 m quadrat scale, 15 quadrats showed species gains, 80 showed species losses, and 5 showed balanced species loss and gain. Additionally, the red line in the figure lies below the green line, indicating that over the decade, species loss substantially exceeded species gain in the plot, with β-diversity in the D. tonkinensis community showing a decreasing trend [Figure 6: see original paper].

Note: The green line represents the balance between species loss and gain from 2012 to 2022. When the red line is below the green line, it indicates that species loss dominated the decade, and vice versa.

[Figure 6: see original paper] Fig. 6 Species loss (B) - species gain (C) plot of the 1 hm^2 *Deutzianthus tonkinensis* community

3.4 Spatial Variation in Temporal β-Diversity

[Figure 7: see original paper] shows that TBI indices in the D. tonkinensis community mostly exhibited decreasing trends in spatial distribution. TBI indices increased in 15 quadrats, which were randomly distributed in space, while 5 quadrats showed stable TBI indices.

Note: + represents an increase in TBI index, - represents a decrease, 0 represents no change, and yellow density lines represent contour lines.

[Figure 7: see original paper] Fig. 7 Spatial variation of temporal beta diversity indices (TBI) within the 1 hm^2 *Deutzianthus tonkinensis* community

Among topographic factors, mean elevation, convexity, slope, and aspect had no significant effects on TBI index changes ($P > 0.05$) . Further analysis of topographic effects on species loss (B) and species gain (C) revealed that mean elevation had a significant effect on species loss (B) ($P < 0.05$) but not on species gain (C) ($P > 0.05$). Convexity, aspect, and slope had no significant effects on either species loss (B) or species gain (C) ($P > 0.05$) [TABLE:2, TABLE:3].

Table 1 Model coefficients for the effects of topography on changes in temporal beta diversity indices

Table 2 Model coefficients for changes in topography on species loss (B)

Table 3 Model coefficients for changes in topography on species gain (C)

Note: represents $P < 0.05$.*

---

4 Discussion

4.1 Temporal Changes in Community Species Composition

Analysis of species composition revealed that the D. tonkinensis community remained relatively stable in the short to medium term. However, analysis of species abundance changes showed significant declines in most species, indicating that while overall community composition remained stable, obvious fluctuations occurred within the community. Climax succession theory posits that late-successional communities remain relatively stable, but this is not a static state. Competition among species for limited resources such as light, water, and nutrients leads to the disappearance of some species, resulting in continued species turnover and change within the community (Odum, 1969; Poorter et al., 2024). The D. tonkinensis community represents a mid-to-late successional type of karst seasonal rainforest, and our findings on the temporal dynamics of community species composition and abundance align with predictions from climax succession theory.

Tree mortality represents one of the most important factors affecting forest species composition dynamics (Lewis et al., 2004). This study demonstrates that overall mortality in the D. tonkinensis community was relatively high, particularly for small-diameter individuals, with mortality rates exceeding recruitment rates for most species. These results are consistent with findings from studies on evergreen broad-leaved forests in Tianmushan (Zhang and Tang, 2021), deciduous forests in Changbai Mountain (Zhang et al., 2013), and monsoon evergreen broad-leaved forests (Wei et al., 2024). However, no significant relationship existed between species abundance and mortality, suggesting that changes in species numbers in the D. tonkinensis community may be driven by other factors. Due to special geological background conditions, karst regions are prone to geological drought (Wu et al., 2023), which can cause massive tree mortality in forests. Meteorological observation data indicate that severe droughts occurred in the study area in 2013, 2014, 2020, and 2021, which may have caused substantial mortality of trees, especially small-diameter individuals, in the D. tonkinensis community. Additionally, disturbance represents a primary cause of species number changes in natural forests, with previous research showing that karst seasonal rainforests in Nonggang experience extensive gap disturbances that alter understory microclimatic conditions, leading to mortality of non-pioneer trees (Xiang et al., 2019). In summary, geological drought and natural disturbances such as canopy gaps may be the main factors driving fluctuations in species composition of D. tonkinensis communities.

4.2 Temporal Changes in Community α-Diversity

α-diversity analysis revealed that α-diversity in the D. tonkinensis community decreased markedly with succession. This result aligns with previous space-for-time studies in this region showing that diversity in late-successional karst seasonal rainforests is lower than in early-successional stages (Ou et al., 2003). Li et al. (2022) also found that α-diversity in Changbai Mountain coniferous-broadleaved mixed forests decreased significantly with succession. However, Wei et al. (2024) showed that α-diversity changed little over time in monsoon evergreen broad-leaved forests, while Zhou et al. (2021) found that α-diversity increased over a 5-year study period in evergreen broad-leaved forests in Badagongshan. The subjects of these studies were all well-protected forests in reserves, representing mid-to-late successional types. These comparative results indicate that even for well-protected, mid-to-late successional forests, temporal dynamics of α-diversity differ among forest types. Whether changes in α-diversity in D. tonkinensis communities are driven by climatic disturbances such as extreme drought or by internal natural disturbances requires further long-term monitoring research to clarify.

Our results on α-diversity dynamics in D. tonkinensis communities demonstrate that the loss of rare and occasional species clearly drove α-diversity changes, with rare species comprising a larger proportion of species lost from the community, highlighting their important role in maintaining community biodiversity. Previous studies have found that dominant species, due to their larger populations, have stronger resistance to environmental fluctuations and disturbances and typically remain more stable, while rare and occasional species, due to their small numbers, are more prone to local extinction (Ceballos et al., 2021). Our results show that dominant species in the community (mostly mature trees) had increasing DBH values over time , giving them clear competitive advantages for key resources such as light and soil nutrients. In contrast, shrub and small tree seedlings, being relatively less competitive, struggled to persist under resource-limited conditions and were therefore more likely to be excluded (Guo et al., 2015), ultimately leading to local extinction. Most species lost from the D. tonkinensis community had relatively small DBH values, indicating they were small-diameter individuals or had not reached maturity, such as *Grewia henryi* and *Glochidion lanceolarium*, which are typically more sensitive to environmental changes and less competitive, making them more vulnerable to disappearance due to disturbance and environmental change. This aligns with Guo et al. (2021) regarding drivers of tree mortality in Nonggang Reserve. Additionally, many lost species were pioneer species, such as *Alangium chinense*, *Mallotus barbatus*, and *Triadica cochinchinensis*, which typically adapt to high-light environments in open canopies or forest edges. As succession progresses and canopy closure increases, environmental resource conditions such as light no longer match the requirements of these species, placing them under greater survival pressure (Xiao et al., 2015) and ultimately leading to their disappearance from local habitats. These results suggest that conserving diversity in D. tonkinensis communities requires attention to the protection of rare and occasional species, particularly small-diameter understory rare species. In addition to D. tonkinensis communities, tropical karst seasonal rainforests preserve many other rare community types, such as *Excentrodendron tonkinense* communities, *Hainaniodendron* communities, *Litsea dilleniifolia* communities, *Horsfieldia kingii* communities, and *Parashorea chinensis* communities (Su et al., 2014). Future comparative studies could clarify the diversity dynamics and maintenance mechanisms of these rare community types like D. tonkinensis to better protect the unique and precious species diversity of karst seasonal rainforests.

4.3 Spatiotemporal Changes in β-Diversity

Analysis of the spatial component of β-diversity (LCBD) in D. tonkinensis communities revealed that different locations contributed inconsistently to community β-diversity, and these unique contributions changed over time. Legendre et al. (2019) found that different habitats in the Panama BCI plot contributed inconsistently to community β-diversity, with this inconsistency changing over time. Our study further confirms the inconsistency and temporal variability of different habitats' contributions to community β-diversity. These results suggest that different habitat types in forest communities require different conservation strategies in practice, with enhanced protection needed for locations making unique contributions to community β-diversity, and that conservation of different locations or habitats should be adjusted based on monitoring results.

Results on TBI changes in D. tonkinensis communities showed no significant relationship between temporal β-diversity changes and topography, indicating that TBI changes have a certain degree of spatial randomness. Analysis of species loss and gain in quadrats revealed that quadrat species loss was an important driver of TBI changes. Generalized linear model results showed that species loss in quadrats had a significant relationship with mean elevation, with greater species loss at higher elevations. Previous studies have shown that in karst seasonal rainforests, higher mean elevations experience longer direct sunlight exposure, have thinner soil layers and higher rock exposure, and are more prone to geological drought (Huang et al., 2016), leading to greater species loss in these areas. Topographic factors, as indirect factors, may also drive changes in soil physicochemical properties, thereby significantly affecting community structure and diversity (Li et al., 2024). Therefore, factors such as soil moisture and nutrient content may be important influences on species loss in D. tonkinensis communities, though how soil factors drive diversity dynamics requires further research. In addition to abiotic factors, biotic factors such as neighbor competition may also significantly affect species survival and growth (Ke and Miki, 2015). Previous studies on other vegetation types in karst seasonal rainforests found that neighbor density could increase tree species survival (Guo et al., 2021), showing significant neighbor facilitation effects. In high-elevation areas of D. tonkinensis communities, plant individual density is relatively low, resulting in weaker conspecific or heterospecific neighbor facilitation effects and thus lower tree individual survival rates. In summary, specific conservation practices for D. tonkinensis communities should strengthen protection of high-elevation, steep-slope areas within the community.

Between 2012 and 2022, the D. tonkinensis community in the 1-hectare plot in Nonggang National Nature Reserve showed obvious dominant species. Although overall species composition remained stable, obvious fluctuations occurred within the community. Community α-diversity decreased markedly with succession, with local extinction of rare and occasional species serving as an important driver of α-diversity changes, demonstrating the significance of rare and occasional species for maintaining community biodiversity. β-diversity analysis of D. tonkinensis communities revealed differences in how different areas of the forest community contributed to community β-diversity at different times. Temporal β-diversity changes showed no significant relationship with topography, but quadrat species loss was significantly positively correlated with mean elevation. Geological drought and natural disturbances such as canopy gaps may be important drivers of species diversity changes in D. tonkinensis communities.

References

ANDERSON MJ, CRIST TO, CHASE JM, et al., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist[J]. Ecology Letters, 14(1): 19-28.

CEBALLOS SJ, BLUNDO C, MALIZIA A, et al., 2021. Dynamics of tree mortality in subtropical montane forests of Northwestern Argentina[J]. Forest Ecology and Management, 497(5): 119482.

CHEN YQ, GUO JJ, CAI GJ, et al., 2024. Evolution characteristics of submerged plant community diversity in the middle and lower reaches of the Yangtze River in the past seventy years (1954–2021)[J]. Biodiversity Science, 32(3): 1-16.

CONDIT R, 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots[M]. Berlin: Springer: Springer Science & Business Media: 3-7.

CURTIS JT, MCINTOSH RP, 1951. An upland forest continuum in the prairie-forest border region of Wisconsin[J]. Ecology, 32(3): 476-496.

DENG CJ, YUAN F, BU TD, et al., 2022. Influence of soil fauna on litter decomposition in central Guizhou karst forest[J]. Forest Research, 35(3): 72-81.

GADELHA ES, BÁRBARA D, COLARES LF, et al., 2023. Temporal patterns of alpha and beta diversities of microzooplankton in a eutrophic tidal river in the eastern Amazon[J]. Limnology, 24(3): 193-204.

GUO Y, CHEN HYH, WANG B, et al., 2021. Conspecific and heterospecific crowding facilitate tree survival in a tropical karst seasonal rainforest[J]. Forest Ecology and Management, 481: 118716.

GUO YL, WANG B, XIANG WS, et al., 2015. Density-dependent effects of tree species in a 15 ha seasonal rain forest plot in northern tropical karst in Nonggang, Guangxi, southern China[J]. Chinese Science Bulletin, 60(17): 1602-1611.

HE LJ, 2012. Population distribution patterns and interspecific spatial associations in tropical karst seasonal rainforests at Guangxi Nonggang Nature Reserve[D]. Guilin: Guangxi Normal University: 9.

HUANG FZ, DING T, LI XK, et al., 2016. Species diversity for various associations along an altitudinal gradient in the karst seasonal rainforest in Nonggang[J]. Acta Ecologica Sinica, 36(14): 4509-4517.

HUBBELL SP, FOSTER RB, 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation[M]//SOULÉ ME. Conservation biology: the science of scarcity and diversity. Sunderland: Sinauer Associates: 205-231.

KE PJ, MIKI T, 2015. Incorporating the soil environment and microbial community into plant competition theory[J]. Frontiers in Microbiology, 6: 1066.

LEGENDRE P, 2019. A temporal beta-diversity index to identify sites that have changed in exceptional ways in space-time surveys[J]. Ecology and Evolution, 9(6): 3500-3514.

LEGENDRE P, BORCARD D, PERES-NETO PR, 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data[J]. Ecological Monographs, 75(4): 435-450.

LEGENDRE P, CONDIT R, 2019. Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama[J]. Forest Ecosystems, 6(1): 76-88.

LEGENDRE P, De CÁCERES M, 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning[J]. Ecology Letters, 16(8): 951-963.

LEWIS SL, PHILLIPS OL, SHEIL D, et al., 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary[J]. Journal of Ecology, 92(6): 929-944.

LI J, LI XY, CAO J, et al., 2020. Community structure and dynamics of secondary coniferous and broad-leaved mixed forest in Changbai Mountains[J]. Acta Ecologica Sinica, 40(4): 1195-1206.

LI J, LU F, LI D, et al., 2024. Abundance and species richness of lianas in a karst seasonal rainforest: the influence of abiotic and biotic factors[J]. Forests, 15(6): 1011.

LI J, YANG J, SUN X, et al., 2021. Temporal and spatial succession law of arbor diversity in Xiaoxing'an Mountains[J]. IOP Conference Series: Earth and Environmental Science, 687: 012028.

LI QB, ZHANG CY, ZHAO XH, 2022. Species diversity and influencing factors of coniferous and broad-leaved mixed forest communities in different successional stages of Changbai Mountain[J]. Acta Ecologica Sinica, 42(17): 7147-7155.

LI XK, HE CX, JIANG ZC, 2003. Method and principles of ecological rehabilitation and reconstruction in fragile karst ecosystem[J]. Carsologica Sinica, 22(1): 12-17.

LI XK, SU ZM, LU SH, et al., 2003. The spatial pattern of natural vegetation in the karst regions of Guangxi and the ecological signality for ecosystem rehabilitation and reconstruction[J]. Journal of Mountain Science, 21(2): 129-139.

LUO MF, YANG M, MA KP, 2023. Core targets of Kunming-Montreal Global Framework and recommendations for conservation action in China[J]. Guihaia, 43(8): 1350-1355.

MA KP, 2023. Kunming-Montreal Global Biodiversity Framework: An important global agenda for biodiversity conservation[J]. Biodiversity Science, 31(4): 5-6.

MA KP, HUANG JH, YU SL, et al., 1994. Plant community diversity in Dongling Mountain, Beijing, China: . Species richness, Evenness and Species diversities[J]. Acta Ecologica Sinica, 15(3): 268-277.

MA RX, GUO YL, LI DX, et al., 2023. Spatial distribution pattern and mechanism of sapling regeneration in karst seasonal rainforest in southwestern Guangxi[J]. Biodiversity Science, 31(2): 17-26.

NAKADAI R, 2020. Degrees of compositional shift in tree communities vary along a gradient of temperature change rates over one decade: Application of an individual-based temporal beta-diversity concept[J]. Ecology and Evolution, 10(24): 13613-13623.

ODUM EP, 1969. The strategy of ecosystem development: an understanding of ecological succession provides a basis for resolving man's conflict with nature[J]. Science, 164(3877): 262-270.

OU Z, LI XK, LU SH, et al., 2003. Species diversity in the process of succession of karst vegetation in Southwest Guangxi[J]. Guangxi Sciences, 10(1): 63-67.

PAVEL S, LUKAS C, DAVID H, et al., 2022. Changes in β-diversity of saproxylic beetles along environmental gradients in temperate forests depend on species relative abundances[J]. Journal of Biogeography, 49(3): 551-562.

POORTER L, van Der SANDE MT, AMISSAH L, et al., 2024. A comprehensive framework for vegetation succession[J]. Ecosphere, 15(4): e4794.

ROBERTS DW, COOPER SV, 1989. Concepts and techniques of vegetation mapping[M]//FERGUSON D, MORGAN P, JOHNSON FH. Land classifications based on vegetation: applications for resource management. Ogden: USDA Forest Service: 90-96.

SHEN Y, SANTIAGO LS, MA L, et al., 2013. Forest dynamics of a subtropical monsoon forest in Dinghushan, China: recruitment, mortality and the pace of community change[J]. Journal of Tropical Ecology, 29(2): 131-145.

SU ZM, LI XK, DING T, et al., 2014. The vegetation of Guangxi (Vol.1)[M]. Beijing: China Forestry Publishing House: 71.

WANG B, HUANG YS, LI XK, et al., 2014. Species composition and spatial distribution of a 15 ha northern tropical karst seasonal rain forest dynamics study plot in Nonggang, Guangxi, southern China[J]. Biodiversity Science, 22(2): 141.

WEI SG, LI L, BAI KD, et al., 2024. Community structure and species diversity dynamics of a subtropical evergreen broad-leaved forest in China: 2005 to 2020[J]. Plant Diversity, 46(1): 70-78.

WHITTAKER RH, 1972. Evolution and measurement of species diversity[J]. Taxon, 21(2-3): 213-251.

WRIGHT JL, BOMFIM B, WONG CI, et al., 2021. Sixteen hundred years of increasing tree cover prior to modern deforestation in Southern Amazon and Central Brazilian savannas[J]. Global Change Biology, 27(1): 136-150.

WU XP, ZHOU ZF, ZHU M, et al., 2023. Spatiotemporal characteristics of drought in different geomorphic types in typical karst cluster areas[J]. Journal of Soil and Water Conservation, 30(1): 336-347.

XIANG WS, LI DX, WANG B, et al., 2019. Characteristics and spatial distribution of forest gap in a northern tropical karst seasonal rainforest in Nonggang, Guangxi, South China[J]. Guihaia, 39(1): 87-97.

XIAO C, LIU S, HUANG Z, et al., 2015. Effects of biotic and abiotic factors on tree seedling survival in a broad-leaved Korean pine (*Pinus koraiensis*) mixed forest on Changbai Mountain[J]. Acta Ecologica Sinica, 35(19): 9.

ZHANG F, DU H, CENG FP, et al., 2019. Regeneration dynamics of primary forest in the karst peak-cluster depression[J]. Acta Ecologica Sinica, 39(22): 8516-8525.

ZHANG LR, LUO M, ZHU ZX, et al., 2023. Implementation path of biodiversity mainstreaming in China under the guidance of Kunming-Montreal Global Biodiversity Framework[J]. Guihaia, 43(8): 1356-1365.

ZHANG YF, TANG MP, 2021. Analysis on spatial structure dynamic characteristics of evergreen broad-leaved forest in Tianmu Mountain[J]. Acta Ecologica Sinica, 41(5): 1959-1969.

ZHANG ZC, HAO ZQ, YE J, et al., 2013. Short-term death dynamics of trees in natural secondary poplar-birch forest in Changbai Mountains of Northeast China[J]. Chinese Journal of Applied Ecology, 24(2): 303-310.

ZHOU T, ZHANG J, QIN Y, et al., 2021. The effects of biotic and abiotic factors on the community dynamics in a mountain subtropical forest[J]. Forests, 12(4): 427.

Supplementary Tables

Supplementary Table S1 Changes in importance value and basal area at breast height of dominant tree species within the 1 hm^2 *Deutzianthus tonkinensis* community plot

Species	Importance value	Basal area ($m^2 \cdot hm^{-2}$)
	2012	2017
Deutzianthus tonkinensis		

Species	Importance value	Basal area ($\mathrm{m}^2 \cdot \mathrm{hm}^{-2}$)
Ardisia thyrsiflora		
Sterculia monosperma		
Clerodendrum wallichii		
Antidesma japonicum		
Orophea polycarpa		
Celtis timorensis		
Archidendron robinsonii		
Streblus tonkinensis		
Amesiodendron chinense		
Dracontomelon duperreanum		
Litsea variabilis var. *oblonga*		
Vitex kwangsiensis		
Catunaregam spinosa		
Ficus hispida		
Bischofia javanica		
Chionanthus ramiflorus		
Alphonsea monogyna		
Excentrodendron tonkinense		
Chassalia curviflora		

Supplementary Table S2 Changes in species abundance of the top 20 dominant tree species ranked by importance value within the 1 hm^2 *Deutzianthus tonkinensis* community plot

Species	T3-T1	Mortality rate	Recruitment rate
Clerodendrum wallichii	-76 (*)		
Sterculia monosperma	-54 (*)		
Antidesma japonicum	-46 (*)		
Deutzianthus tonkinensis	-29 (*)		
Chionanthus ramiflorus	-125 (*)		
Celtis timorensis	-41 (*)		
Catunaregam spinosa	-56 (*)		
Archidendron robinsonii	-20 (*)		
Vitex kwangsiensis	-19 (*)		
Chassalia curviflora	-17 (*)		
Excentrodendron tonkinense	-23 (*)		
Amesiodendron chinense	-17 (*)		
Bischofia javanica	-19 (*)		
Dracontomelon duperreanum	-1 (/)		
Litsea variabilis var. *oblonga*	-1 (/)		
Alphonsea monogyna	-3 (/)		
Ardisia thyrsiflora	-26 (/)		

Species	T3-T1	Mortality rate	Recruitment rate
Ficus hispida	-28 (/)		
Orophea polycarpa	24 (/)		
Streblus tonkinensis			

Note: In the above table, T1 represents the number of individual species in 2012, T2 stands for the number of individual species in 2017, and T3 represents the number of individual species in 2022. indicates $P < 0.05$, and / indicates $P > 0.05$.*

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv — Machine translation. Verify with original.