Beta Diversity of Herbaceous Layer Plant Communities and Its Driving Factors in Natural Forests of Henan Province (Postprint)

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Abstract

Studying β-diversity and its components, which reflect spatiotemporal differences or changes in species composition among different communities, helps improve understanding and knowledge of community structure and its maintenance mechanisms. The forest herbaceous layer is an important component of forest communities and forest ecosystems. Although there have been some relevant studies on β-diversity of understory herbaceous plant communities, there is still a lack of unified understanding regarding the relative proportions of β-diversity components (such as species turnover and nestedness components), influencing factors, and their degree of influence. This study, based on survey data of herbaceous layer plant communities from 168 natural forest plots in Henan Province, analyzes the β-diversity patterns of natural forest herbaceous layer plant communities in Henan Province through methods such as Jaccard dissimilarity index and variance partitioning, and quantifies the relative contributions of influencing factors such as spatial distance, environmental factors, and species richness to their β-diversity. The results show that: (1) The Jaccard dissimilarity index of total β-diversity for natural forest herbaceous layer plant communities in Henan Province is 0.94, which mainly originates from the species turnover component (accounting for 96.8% of total β-diversity). (2) The total β-diversity and species turnover component of natural forest herbaceous layer plant communities show a significant increasing trend with increasing spatial distance, while the nestedness component shows a significant decreasing trend with increasing spatial distance. (3) Mantel test shows that spatial distance, environmental factors, and species richness all have significant effects on the total β-diversity of natural forest herbaceous layer plant communities, with environmental factors having the greatest influence, followed by spatial distance, and species richness having the smallest influence; variance partitioning results further show that spatial distance, environmental factors, and species richness together explain 27.14% and 20.35% of the variation in total β-diversity and its turnover component, respectively, with environmental factors alone explaining the most variation (accounting for 10.62% of total β-diversity and 9.35% of the turnover component, respectively). This study helps enhance understanding of the patterns of plant composition changes and their influencing factors in natural forest herbaceous layers, thereby providing a solid scientific basis for forest vegetation conservation management and ecological restoration.

Full Text

Preamble

β-Diversity of Herbaceous Layer Plant Communities in Natural Forests and Its Influencing Factors in Henan Province

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Abstract: Research on β-diversity and its components, which reflect spatial or temporal variations in species composition among communities, enhances our understanding of community structure and its maintenance mechanisms. The herbaceous layer constitutes an important component of forest communities and ecosystems. Although some studies have examined β-diversity in understory herbaceous plant communities, consensus remains lacking regarding the relative proportions of β-diversity components (such as species turnover and nestedness), their influencing factors, and the magnitude of their effects. Based on survey data from 168 natural forest plots in Henan Province, this study analyzed β-diversity patterns of herbaceous layer plant communities using the Jaccard dissimilarity index and variance partitioning methods, while quantifying the relative contributions of spatial distance, environmental factors, and species richness. The results showed: (1) The total β-diversity of herbaceous layer plant communities in Henan Province, measured by the Jaccard dissimilarity index, was 0.94, derived primarily from the species turnover component (accounting for 96.8% of total β-diversity). (2) Both total β-diversity and its turnover component increased significantly with spatial distance, while the nestedness component decreased significantly with spatial distance. (3) Mantel tests revealed that spatial distance, environmental factors, and species richness all significantly influenced total β-diversity, with environmental factors having the greatest effect, followed by spatial distance, and species richness the least. Variance partitioning further showed that these three factors jointly explained 27.14% and 20.35%

of the variation in total β-diversity and its turnover component, respectively, with environmental factors alone explaining the most variation (10.62% of total β-diversity and 9.35% of turnover component). This study enhances understanding of plant composition variation patterns and their drivers in natural forest herbaceous layers, providing a scientific foundation for forest vegetation conservation management and ecological restoration.

Keywords: β-diversity, species turnover, species nestedness, spatial distance, natural forest herbaceous layer, Henan Province

Introduction

β-diversity reflects spatial or temporal differences in species composition among communities (Chen et al., 2010; Jiang et al., 2021; Qu et al., 2022; Qian & Qian, 2023), linking local-scale α-diversity with regional-scale γ-diversity (Whittaker, 1972; Li et al., 2023). β-diversity can be decomposed into two components: species turnover and species nestedness. Species turnover describes the phenomenon of species replacement along spatial or environmental gradients, while nestedness describes the presence or absence of species in specific environments (Baselga, 2010). Investigating these components and their influencing factors improves our understanding of community structure and functioning (Si et al., 2017; Soininen et al., 2018; Jiang et al., 2020; Jiang et al., 2022).

The distribution patterns of plant community β-diversity are influenced by multiple factors (Chen et al., 2010; Weng et al., 2019; Shi et al., 2021), generally including biotic factors, abiotic environmental factors, and spatial distance. Abiotic environmental factors such as climate (Wang et al., 2021; Li et al., 2022; Qu et al., 2022; Yang et al., 2023), elevation gradients (Lu et al., 2010; Han et al., 2023; He et al., 2023), slope position (Tan et al., 2013; Hu et al., 2024), slope gradient (Tan et al., 2013; He et al., 2023), convexity (Yang et al., 2014; He et al., 2022), and soil (Wang et al., 2013; Xu et al., 2022; Jiang et al., 2022) affect plant β-diversity. Spatial distance relates to dispersal processes, with studies reporting that β-diversity increases with spatial distance (Soininen et al., 2007; Chapman & McEwan, 2013; Li et al., 2016; Fang et al., 2023). Canopy composition (Singh et al., 2023) and canopy size (Sha et al., 2023) also influence plant community β-diversity. Additionally, human disturbance affects β-diversity patterns (Schulz et al., 2019; Gao et al., 2022).

Current research on the formation and maintenance mechanisms of plant community β-diversity primarily focuses on niche theory and neutral theory. Niche theory posits that species composition is influenced by both environmental factors and species interactions, changing along environmental gradients (Chase & Leibold, 2009; Fang et al., 2023). Generally, as environmental differences between communities increase, so do differences in species composition, leading to higher β-diversity (Tuomisto et al., 2003; Tan et al., 2013; Jiang et al., 2021). Neutral theory considers dispersal limitation as a primary factor affecting β-

diversity patterns (Hubbell, 2001; Soininen et al., 2007; Niu et al., 2009), with β-diversity typically increasing with spatial distance due to dispersal constraints (Cacciatori et al., 2020; Jiang et al., 2021; Yang et al., 2021; Li et al., 2023). Some studies have found that habitat filtering and dispersal limitation jointly determine β-diversity patterns, with their relative importance varying across communities and scales (McClain & Rex, 2015; Mi et al., 2022; Mugnai et al., 2022; Peguero et al., 2022; Zhao et al., 2023). Integrating niche and neutral theories and considering multiple dimensions from species to function to phylogeny has gained increasing attention in β-diversity research.

Previous research on forest community β-diversity has focused more on tall trees or woody plants (Weng et al., 2019; Shi et al., 2021; Yang et al., 2023). As understanding of the crucial role of understory herbaceous layers in forest ecosystems has grown—such as promoting biodiversity, accelerating litter decomposition, and driving nutrient cycling (Gilliam, 2007)—the herbaceous layer has received increasing attention (Nilsson & Wardle, 2005). Studies on understory plant β-diversity have emerged, including research on understory vegetation in major forest types of Saihanba (Yang & Tian, 2012), herbaceous layers of old-growth forests in southeastern Kentucky, USA (Chapman & McEwan, 2013), temperate forest understories in eastern North America (Buskey et al., 2020), understory plants of *Castanopsis hystrix* forests in Pingxiang, Guangxi (You et al., 2016), herbaceous layers of planted forests in the central Loess Plateau (Shi et al., 2019), understory plants of *Pinus tabulaeformis* and *Quercus wutaishanica* forests on the Loess Plateau (Wang et al., 2021), understory herbs in the alpine valley area of the lower Yarlung Zangbo River (Du et al., 2022), and understory plants of natural *Betula platyphylla* forests in the Greater Khingan Mountains (Zhang, 2023). Understory herbaceous layer β-diversity is typically influenced by multiple factors. For example, Deng et al. (2023) identified temperature as an important factor affecting understory plant community diversity in *Platycladus orientalis* and *Pinus elliottii* communities. Shi et al. (2019) found that geographic distance explained the highest proportion of variation in species composition among plots, followed by annual precipitation. Zhang (2023) discovered that latitudinal differences influenced understory herbaceous species composition in *Betula platyphylla* forests. Other studies have found that elevation gradients affect understory plant community composition (Wang et al., 2021; Du et al., 2022; Han et al., 2023). Jiang et al. (2021) found that increasing stand age reduced heterogeneity of understory vegetation communities in *Haloxylon persicum* plantations, while Mao et al. (2021) found no significant effect of stand age on understory species diversity in *Castanopsis hystrix* plantations. Despite existing research on understory herbaceous layer β-diversity, consensus remains lacking regarding the proportions of its components (turnover vs. nestedness), influencing factors, and their relative effects.

Henan Province, located in central China and being a major agricultural and populous province, urgently requires strengthened scientific research on natural vegetation conservation and restoration, including studies on β-diversity. This research focuses on herbaceous layer plant communities in 168 natural forest plots in Henan Province, analyzing patterns and influencing factors of total β-diversity and its components to address three scientific questions: (1) What are the patterns of total β-diversity and its turnover and nestedness components in natural forest herbaceous layers? (2) How does β-diversity change with increasing spatial distance? (3) What are the relative effects of environmental factors, spatial distance, and biotic factors on β-diversity and its components? The findings will provide a scientific basis for forest vegetation conservation and ecological restoration.

1.1 Study Area

Henan Province is located in central-eastern China, with geographic coordinates of 110°21 –116°39 E, 31°23 –36°22 N. The province spans approximately 580 km east-west and 550 km north-south. Most of the region lies in the warm temperate zone, with the southern part crossing into the subtropical zone, characterized by a continental monsoon climate transitioning from north subtropical to warm temperate. Over the past decade, the average annual temperature in Henan has been 15.1–15.9 °C, average annual precipitation 512.6–1,129.1 mm, average annual sunshine hours 1,774.5–2,024.1 h, and frost-free period 207.9–271.7 d (https://www.henan.gov.cn/2023/06-13/2760285.html). The climate exhibits transitional characteristics from plains to hilly mountains, with distinct seasons, concurrent rainfall and heat, and high complexity. Major vegetation types include forests, shrublands, grasslands, and croplands, with forests being the dominant natural vegetation type. Natural forest resources are mainly distributed in the Dabie, Funiu, and Taihang Mountains, accounting for 90.09% of the province's total natural forest area (Zhang et al., 2009). Understory herbaceous plants play crucial roles in regulating forest community structure stability and ecosystem functioning, representing an indispensable component of forest ecosystems.

[Figure 1: see original paper] Distribution map of the studied sites in Henan Province

1.2 Plot Establishment and Species Richness Data Collection

We surveyed 168 herbaceous layer plant community plots in natural forest environments across Henan Province, recording species names, heights, and abundance for all herbaceous plants. For each plot, we conducted complete tree surveys for individuals with diameter at breast height (DBH) $\geq$ 5 cm, recording density, average height, and basal area. Each natural forest herbaceous layer plot measured 50 m × 20 m. Within each plot, we established three 10 m × 10 m shrub subplots, and within each shrub subplot, one 2 m × 2 m herbaceous layer quadrat, totaling 504 herbaceous quadrats. We used GPS to determine the latitude and longitude coordinates of all 168 plots. Minimum and maximum distances between plots were 0.12 km and 485.40 km north-south, and 0.39 km and 555.16 km east-west, respectively. Elevation ranged from 52 to 1,720 m.

1.3 Environmental Factor Acquisition and Analysis

We used elevation data recorded during field surveys as the topographic factor. Nineteen climate variables were obtained from the WorldClim database (http://www.worldclim.org/) and extracted using ArcGIS based on plot coordinates: annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), max temperature of warmest month (BIO5), min temperature of coldest month (BIO6), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), mean temperature of warmest quarter (BIO10), mean temperature of coldest quarter (BIO11), annual precipitation (BIO12), precipitation of wettest month (BIO13), precipitation of driest month (BIO14), precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18), and precipitation of coldest quarter (BIO19).

To avoid multicollinearity, we standardized elevation and the 19 climate variables using the "scale" function in R to eliminate dimensional differences, then performed cluster analysis using the "varclus" function in the "Hmisc" package (Harrell, 2023). We assessed collinearity by calculating Spearman correlation coefficients and removed variables with Spearman $^2 > 0.7$, retaining seven climate variables: elevation, temperature seasonality, min temperature of coldest month, max temperature of warmest month, mean temperature of warmest quarter, temperature annual range, mean diurnal range, and precipitation of wettest month. Stand structure characteristics such as tree density, average tree height, and total basal area can affect understory plant growth by influencing light penetration. We included 11 variables as environmental factors: tree density, average tree height, basal area, elevation, and the seven climate variables. We calculated environmental distances (Euclidean distance) using the "vegan" package (Oksanen et al., 2019) and spatial distances based on plot coordinates using the "geosphere" package (Hijmans et al., 2022).

1.4 Data Analysis

We calculated β-diversity indices (Jaccard dissimilarity index) between different plots to represent species composition differences (Jaccard, 1912; Chen et al., 2010; Fang et al., 2023). This method considers only species presence-absence data (1 for presence, 0 for absence) (Si et al., 2017; Fang et al., 2023). We used the "betapart" package in R (Baselga & Orme, 2012; Baselga et al., 2023) to calculate total β-diversity (βtotal) and its turnover (βturnover) and nestedness (βnestedness) components, then analyzed how these processes affect community diversity differences. We used linear and logarithmic equations to model relationships between total β-diversity (and its components) and spatial distance.

Jaccard dissimilarity index:

$$\beta_{total} = \frac{b+c}{a+b+c}$$

Turnover component:

$$\beta_{turnover} = \frac{\min(b,c)}{a+\min(b,c)}$$

Nestedness component:

$$\beta_{nestedness} = \beta_{total} - \beta_{turnover}$$

Simulation equations:

$$y = a_{1x} + b_1 \quad \text{(linear)}$$

$$y = a_2 \log(x) + b_2 \quad \text{(logarithmic)}$$

where a is the number of shared species between two communities, b and c are species unique to each community, x is spatial distance, y is β-diversity, and a_1, a_2, b_1, b_2 are coefficients.

We used Mantel analysis to test correlations between spatial distance, environmental factors, species richness, their pairwise interactions, and their combined effects with plant community total β-diversity and its components as response variables. Partial Mantel tests controlled for geographic, environmental, or species richness effects to examine correlations between pairwise interactions and β-diversity components. We used Pearson correlation with 999 permutations to obtain r values and significance levels. We performed multiple regression on dissimilarity matrices (MRM) analysis (Lichstein, 2007) using the "vegan" package to test effects on community composition. Variance partitioning using the "varpart" function in "vegan" decomposed β-diversity into components explained by spatial distance, environmental factors, and species richness, plus unexplained variation. All analyses and figures were produced using R version 4.2.3.

Results

2.1 β-Diversity and Its Components in Natural Forest Herbaceous Layers

Analysis of β-diversity (measured by Jaccard dissimilarity index) and its components in natural forest herbaceous layers of Henan Province showed that total β-diversity among communities was approximately 0.94. Decomposition using the betapart package revealed that turnover component (0.91) far exceeded nestedness component (0.03), accounting for 96.8% and 3.2% of total β-diversity, respectively (Fig. 2).

[Figure 2: see original paper] Total β-diversity (left), turnover component (middle), and nestedness component (right) in herbaceous layer of natural forests in Henan Province in China

2.2 Spatial Distance Relationships of β-Diversity

Analysis of β-diversity patterns with spatial distance showed that logarithmic regression models provided better fit than linear models (Fig. 3). Both total β-diversity and its turnover component increased significantly with spatial distance ($P < 0.001$), while the nestedness component decreased significantly with spatial distance ($P < 0.001$).

[Figure 3: see original paper] The relationships between total β-diversity (left) and its components of turnover (middle) and nestedness (right) and spatial distance for herbaceous layer of natural forests in Henan Province

2.3 Effects of Spatial Distance, Environmental Factors, and Species Richness

Mantel and partial Mantel tests revealed: (1) For total β-diversity, the ranking of highly significant correlations ($P < 0.001$) was: combined effect of spatial distance × environmental factors × species richness > spatial distance × environmental factors > environmental factors > environmental factors × species richness > spatial distance > spatial distance × species richness > species richness (Table 1). (2) For turnover component, the ranking was: spatial distance × environmental factors > environmental factors > spatial distance > combined effect of all three > environmental factors × species richness > spatial distance ($P < 0.001$); species richness and spatial distance × species richness showed no significant correlation ($P > 0.05$). (3) For nestedness component, only spatial distance × species richness and species richness showed highly significant correlations ($P < 0.001$); spatial distance, environmental factors, and their interactions showed no significant correlations ($P > 0.05$).

MRM analysis further confirmed that spatial distance, environmental factors, and species richness significantly affected total β-diversity ($P < 0.001$, Table 2), with spatial distance having the largest individual effect, followed by environmental factors and species richness. All factors except species richness significantly affected the turnover component.

Variance partitioning showed that spatial distance, environmental factors, and species richness jointly explained 27.14% of total β-diversity variation (Fig. 4), with environmental factors having the highest individual explanatory power (10.62%), followed by spatial distance (7.89%) and species richness (2.13%). For the turnover component, these factors explained 20.35% of variation, with environmental factors again explaining the most (9.35%), followed by spatial distance (6.01%) and species richness (0.21%). For nestedness, they explained 12.19% of variation, with species richness explaining the most (6.05%), followed by environmental factors (3.43%) and spatial distance (1.57%).

The correlation between β-diversity with spatial distance, environmental factors and species richness for herbaceous layers of natural forest using Mantel and partial Mantel tests

Results of multiple regression analysis on MRM for β-diversity in herbaceous layers of natural forest

[Figure 4: see original paper] Effects of spatial distance, environmental factors and species richness on total β-diversity (A) and its components of turnover (B) and nestedness (C)

Discussion

3.1 β-Diversity and Its Components in Natural Forest Herbaceous Layers

Previous studies decomposing β-diversity have shown that turnover component dominates β-diversity (Li et al., 2022; Qu et al., 2022; Fang et al., 2023). Using the Jaccard dissimilarity index, our results demonstrate that species turnover contributed more to total β-diversity (96.8%) than nestedness (3.2%) in Henan Province's natural forest herbaceous layers. This indicates that β-diversity is primarily driven by species replacement among plots, with relatively low nestedness contribution. The turnover component was mainly influenced by spatial distance, elevation, and temperature seasonality. Since species composition differences primarily arise from turnover, conservation efforts should prioritize establishing protected areas across multiple regions to maximize protection of natural forest herbaceous species.

3.2 Spatial Distance Patterns of β-Diversity

Spatial distance is considered a key metric for dispersal limitation (Blundo et al., 2016). Our results show that both total β-diversity and turnover component increase with spatial distance, consistent with studies on plant community similarity-distance relationships (Qian et al., 2005; Cacciatori et al., 2020; Yang et al., 2021; Qu et al., 2022; Fang et al., 2023). This pattern likely results from combined effects of niche processes, neutral processes, and other mechanisms. The nestedness component decreased with spatial distance, possibly related to differential dispersal abilities, environmental heterogeneity, and biotic interactions. Similar patterns have been reported (Fang et al., 2023), though other studies found different relationships (Qu et al., 2022; Yang et al., 2021).

3.3 Influences of Spatial Distance, Environmental Factors, and Species Richness

Increasing evidence supports that β-diversity is jointly influenced by environmental filtering and dispersal limitation (Wang et al., 2013; Zhao et al., 2017; Peguero et al., 2022; Fang et al., 2023). Our results show significant correlations between all three factors and total β-diversity, indicating that habitat filtering, dispersal limitation, and community structure all shape β-diversity patterns in Henan Province. However, their effects differ: environmental factors have the greatest individual effect on total β-diversity and turnover component, followed by spatial distance and species richness. Environmental factors explaining more variation than spatial distance suggests a stronger environmental than spatial effect, consistent with other studies (Qu et al., 2022; Wang et al., 2022).

Our analysis of individual factor contributions revealed that elevation had the highest influence on total β-diversity and turnover component, along with mean diurnal temperature range, mean temperature of warmest quarter, and max temperature of warmest month. Other studies have also highlighted the importance of elevation and climate factors (Qu et al., 2022; Li et al., 2022). Elevation affects plant communities through its influence on climate and soil, and the maximum elevation difference exceeding 1,600 m among plots likely explains its strong effect. The greater importance of environmental over spatial factors suggests that conservation and restoration should prioritize environmental conditions while also considering spatial factors and their interactions.

The substantial unexplained variation indicates that community species composition is influenced by multiple factors and ecological processes not captured in our study. Soil physicochemical properties and nutrients correlate with plant β-diversity (Wang et al., 2013; Xu et al., 2022; Jiang et al., 2022; Li et al., 2023), and human disturbance also affects β-diversity patterns (Schulz et al., 2019; Gao et al., 2022). Future studies incorporating soil properties could improve explanatory power and enhance understanding of β-diversity patterns and mechanisms.

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