

Dynamic Changes in the Phylogenetic Structure of Taiwan Beech Communities Across Temporal and Spatial Scales: Postprint

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Abstract

Community phylogenetic structure constitutes a fundamental research topic for understanding community assembly processes. However, the majority of existing research has concentrated on spatiotemporal variation in community composition and structure, with relatively limited investigation into dynamic changes in phylogenetic structure. This study examined the dynamic changes in phylogenetic structure over a 10-year period in a *Fagus hayatae* forest—a nationally second-class protected plant—located in Qingliangfeng National Nature Reserve, Zhejiang Province. Utilizing three community dynamics survey datasets from 2006, 2011, and 2016, we investigated the phylogenetic structure dynamics at three spatial scales (10, 20, and 50 m), analyzed the influence of spatiotemporal scales on the phylogenetic structure of the *Fagus hayatae* community, explored the primary factors regulating community dynamic changes, and provided a theoretical foundation for future conservation of *Fagus hayatae* forests. The findings revealed that: (1) Throughout the 10-year forest dynamic process, the community's MPD index decreased while the MNTD index increased. The NRI and NTI indices exhibited significant temporal increases at large spatial scales, but no significant changes at small scales. (2) The dynamic trends of these indices were all amplified with increasing spatial scale. These results demonstrate that between 2006 and 2016, the overall phylogenetic structure of the *Fagus hayatae* community displayed a progressive clustering trend, whereas phylogenetic relationships among close relatives became increasingly distant; furthermore, the clustering trend of community phylogenetic structure intensified with increasing spatial scale. Environmental filtering operating at large scales, combined with stochastic processes and interspecific competition at small scales, may represent the principal ecological processes driving the dynamic changes in phylogenetic structure of *Fagus hayatae* communities in this region.

Full Text

Dynamics of Phylogenetic Structure in *Fagus hayatae* Communities Across Temporal and Spatial Scales

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Abstract

Community phylogenetic structure is a fundamental component in our ability to understand community assembly processes and species coexistence. However, although numerous studies have examined spatial and temporal variation in community composition, few have applied these observations to the dynamics of phylogenetic structure itself. Here, we performed such an analysis to investigate temporal and spatial variations in the phylogenetic structure of *Fagus hayatae* communities, a Class II protected plant species in China, using dynamic survey data from secondary communities in Qingliangfeng National Nature Reserve, Zhejiang Province. We examined phylogenetic structure dynamics across three census periods (2006, 2011, and 2016) at three spatial scales (10 m, 20 m, and 50 m). Using global seed plant phylogenetic data, we constructed a phylogenetic tree for the community and selected the mean phylogenetic distance (MPD), mean nearest taxon distance (MNTD), net relatedness index (NRI), and nearest taxon index (NTI) to characterize community phylogenetic structure. Additionally, we randomly resampled 999 plots at 10 m, 20 m, and 50 m scales using a moving split-window technique to create plots at different spatial extents.

Analysis across spatial and temporal scales produced the following results: (1) On decadal time scales, both species richness and abundance in the communities decreased. MPD decreased while MNTD increased. NRI and NTI both showed significant positive increases at large spatial scales, but did not change at small scales. (2) As the spatial extent of analyses increased, so did the strength of the observed trends. Thus, the phylogenetic structure of communities showed a clustering pattern that was spatial scale-dependent, with the largest variation in phylogenetic structure across time found at the 50 m scale. We concluded that from 2006 to 2016, the phylogenetic structure of *Fagus hayatae* communities was increasingly clustered, whereas phylogenetic relationships between nearest taxa became more distant. Moreover, environmental filtering dominated the phylogenetic structure dynamics at large scales, in contrast to the effects of

stochastic processes and interspecific competition, which dominated at small scales. Against a background of global climate change and forest degradation, further studies on scale dependence are needed to gain a better understanding of community assembly mechanisms and to protect these endangered species.

Keywords: Zhejiang Qingliangfeng National Nature Reserve; *Fagus hayatae*; phylogenetic structure; scale; environmental filtering

Introduction

Community composition represents the combined result of evolutionary and ecological processes. Community phylogenetic structure incorporates species' evolutionary history to reflect compositional characteristics, playing an important role in understanding long-term community assembly, interspecific relationships, and aggregation processes [1-2]. In 2000, Webb et al. first applied phylogenetic trees to analyze forest community assembly mechanisms [3], and in 2002 further systematically elaborated on specific methods for studying community phylogenetic structure, such as using the net relatedness index (NRI) and nearest taxon index (NTI) to describe community phylogenetic patterns [4]. The clustering or overdispersion of community phylogenetic structure is closely related to ecological processes such as environmental filtering or competitive exclusion [4-6], allowing researchers to explore the ecological processes and mechanisms regulating community assembly. For example, studies on plant community phylogenetic structure in Dinghushan forest found that environmental filtering is the dominant community assembly mechanism in that region [7], while Whitfield et al. discovered that tropical forest succession follows an environmental filtering process [8].

Since many important functional traits of plants show strong phylogenetic conservatism, phylogenetic structure also reflects community functional structure to some extent [9-10]. Meanwhile, local community phylogenetic structure is influenced by both biotic and abiotic processes, reflecting habitat selection on species' evolutionary history [4]. Existing research indicates that community phylogenetic structure is affected by many factors, including spatial scale, habitat factors, and others [11-14]. Swenson et al. found that plant community phylogenetic structure tends to be overdispersed at small scales but clustered at large scales [15], while Baldeck et al. found that phylogenetic diversity is related to soil and topographic differences [16]. Therefore, studying the factors influencing community phylogenetic structure can provide deeper understanding of how environmental change and scale dependence affect plant communities.

Rare and endangered plants are sensitive to habitat conditions and climate change, making them highly valuable for research and conservation. However, previous studies on rare plants have focused primarily on population aspects [17-18], with less attention to entire communities. *Fagus hayatae* (Fagaceae) is a deciduous tree species under second-class national protection [19]. Zhejiang

Qingliangfeng National Nature Reserve contains well-developed *F. hayatae* communities of considerable conservation and research value [20]. However, frequent extreme weather events in recent years have significantly impacted vegetation in the region. Analyzing the phylogenetic structure of *F. hayatae* communities can reveal their development trends and endangerment mechanisms. Therefore, this study uses the Qingliangfeng monitoring plot as a research object to analyze the dynamic phylogenetic structure of *F. hayatae* communities across temporal and spatial scales, which is important for future conservation efforts.

1. Study Area

The study area is located in Qingliangfeng National Nature Reserve in western Lin'an City, Zhejiang Province (118°52'-119°11' E, 30°5'-30°17' N), bordering Jixi in Anhui Province and forming part of the northern Baiji Mountains. Longtangshan lies on the northern edge of the mid-subtropical zone with distinct subtropical montane climate characteristics. Annual precipitation ranges from 1500-1900 mm, unevenly distributed across seasons with greater rainfall in spring and autumn, varying with altitude. Relative humidity ranges from 78%-82%, with average temperature varying between 7.8-15.3°C across different elevations and seasons. The accumulated temperature range is 2200-4800°C [20-22].

2. Plot Establishment and Survey

In 2006, we established a 1 hm² (100 m × 100 m) forest dynamic plot dominated by *Fagus hayatae* at Longtangshan Protection Station in Qingliangfeng Reserve (118°07.270' E, 29°15.098' N). Detailed plot description is available in [23-24]. All free-standing woody stems with diameter at breast height (DBH) ≥ 1 cm were tagged, mapped, identified to species, and measured for DBH and height. In 2011 and 2016, we recensused the plot, recording survival status and DBH for previously tagged stems and documenting new stems with DBH ≥ 1 cm. Species nomenclature was standardized using the *Flora of China* online database (www.efloras.cn) and *Identification Manual of Seed Plants in Zhejiang* [25].

3. Community Phylogenetic Structure

Phylogenetic tree construction was based on the global seed plant phylogeny database published by Zanne et al., which contains phylogenetic data for over 30,000 seed plant species [26]. Combining species information from our plot, we used "Scenario 3" in S.PhyloMaker to match 3143 phylogenetic sites and construct the phylogenetic tree [27]. We selected widely used indices in phylogenetic structure research: mean phylogenetic distance (MPD), mean nearest

taxon distance (MNTD), net relatedness index (NRI), and nearest taxon index (NTI) to represent community phylogenetic structure [4].

MPD represents the average phylogenetic distance between all species pairs in a community, while MNTD represents the average distance between each species and its closest relative [3]. These indices reflect absolute changes in phylogenetic structure [29] and can be used to compare temporal dynamics within the same community. NRI is the standardized MPD, more powerful for testing environmental filtering, while NTI is the standardized MNTD, more powerful for testing competition [1,6,15]. Both can be used to compare phylogenetic structure differences among communities with different sampling intensities.

To explore how different spatial scales affect phylogenetic diversity, we used a moving window approach to randomly select plots within the 1 hm² area based on spatial coordinates of individual trees. We calculated phylogenetic structure indices within subplots at three sampling scales (10 m × 10 m, 20 m × 20 m, and 50 m × 50 m). At each scale, we randomly sampled 999 plots while maintaining species number and individual counts, then randomly resampled species to construct null models and repeated this 999 times. Finally, we standardized observed values using random simulation results. The specific formulas are [4,30]:

$$MPD = \frac{\sum_{i < j} \delta_{ij}}{n(n-1)/2}$$

$$MNTD = \frac{\sum_i \min \delta_{ij}}{n}$$

$$NRI = -\frac{MPD_{obs} - MPD_{rand}}{sd(MPD_{rand})}$$

$$NTI = -\frac{MNTD_{obs} - MNTD_{rand}}{sd(MNTD_{rand})}$$

where δ_{ij} is the phylogenetic distance between species i and j , n is the number of species in the community, MPD_{obs} and $MNTD_{obs}$ are observed values, and MPD_{rand} and $MNTD_{rand}$ are mean values from null models. Positive NRI/NTI values indicate phylogenetic clustering, negative values indicate overdispersion, and values near zero indicate random phylogenetic structure.

All calculations were performed in R 3.2.3, using the Vegan package [31] to calculate species diversity and the Picante package [32] to calculate phylogenetic structure indices. Significance was tested using t-tests.

2. Results

2.1. Dynamic Changes in Community Species Composition Species diversity in the *Fagus hayatae* community decreased over time. During the 2006-2016 forest dynamics, the *F. hayatae* population showed a reverse J-shaped size structure, with decreasing numbers in smaller size classes. The mortality rate was 4.24% in 2011 and 6.95% in 2016, while recruitment was only 1.9% .

Dynamics of species composition of *Fagus hayatae* communities from 2006 to 2016

2.2. Dynamic Changes in Community Phylogenetic Structure The dynamic trends of MPD and MNTD were opposite over time. As time progressed, MPD values showed a decreasing trend while MNTD values increased. NRI and NTI values also increased over time, but their dynamic trends were weaker than those of MNTD. At the 10 m scale, NRI and NTI showed no significant differences over time, but at 20 m and 50 m scales, NRI in 2016 was significantly different from other years, and NTI showed significant differences among 2006, 2011, and 2016 [FIGURE:1, FIGURE:2, FIGURE:3].

[Figure 1: see original paper] Diameter structure of *Fagus hayatae* population

2.3. Relationship Between Spatial Scale and Phylogenetic Structure Dynamics As spatial sampling scale increased, community NRI and NTI values for corresponding years decreased (became more positive), showing significant clustering patterns at all three spatial scales. The clustering pattern became more pronounced with increasing spatial scale, with NRI and NTI values increasing significantly. The dynamic trends of both overall community phylogenetic structure and nearest taxon phylogenetic structure strengthened with increasing spatial scale. At the 50 m scale, 2016 values were significantly different from other years, while at 10 m and 20 m scales, no significant temporal differences were observed. This indicates that spatial scale significantly influences the temporal dynamics of phylogenetic structure, with stronger trends at larger scales.

3. Discussion

3.1. Temporal Scale Effects on Community Phylogenetic Structure Temporal dynamics in community phylogenetic structure reflect community development trends. Over the decade of forest dynamics, overall phylogenetic distances decreased while nearest taxon distances increased, indicating that species with more distant phylogenetic relationships and lower environmental tolerance were lost, creating space for more tolerant, closely related species. Temperature and precipitation are dominant factors affecting species and phylogenetic diversity in subtropical forest communities [13]. *Fagus hayatae* has specific habitat requirements, and we hypothesize that declining habitat quality has prevented

less competitive species from surviving, leading to the observed phylogenetic patterns.

The continuous increase in NRI and NTI from 2006-2016 suggests that habitat filtering is the dominant process regulating community assembly, with this process strengthening over time. Studies in Gutianshan and Dinghushan large forest dynamics plots also indicate that habitat filtering plays an important role in local biodiversity and forest regeneration [7,35]. Without intervention, species and phylogenetic diversity in *F. hayatae* communities may continue to decline, affecting overall community stability and resistance. The increasing NTI over time, though weaker than overall phylogenetic structure changes, indicates that competition among close relatives is intensifying, possibly due to habitat quality decline causing enhanced competition for resources among near relatives.

3.2. Spatial Scale Effects on Community Phylogenetic Structure Spatial scale is an important factor affecting phylogenetic structure [37-38], with studies showing increasing clustering at larger scales [15]. Our results confirm that both overall community phylogenetic structure and nearest taxon structure show clustering patterns as study scale increases, consistent with findings from Gutianshan evergreen broad-leaved forest communities at sampling radii of 5, 25, 50, 75, and 100 m [2]. This phenomenon is primarily regulated by environmental filtering, which becomes stronger at larger spatial scales.

We also found that the strength of temporal dynamic trends in phylogenetic structure and their underlying ecological processes are scale-dependent. At large scales, both overall and nearest taxon phylogenetic structures became more clustered over time, indicating strengthening environmental filtering. At small scales, however, no clear temporal trends were observed, possibly due to stochastic processes, interspecific competition, and Janzen-Connell effects from nearby parent trees [39].

3.3. Implications of Phylogenetic Structure Dynamics for *Fagus hayatae* Conservation Combining the dynamic changes and spatial scale effects in *Fagus hayatae* community phylogenetic structure reveals that environmental filtering is the dominant effect influencing future community development. Recent global climate change has increased regional extreme weather events, altering plant community composition and structure [40-41]. Strong environmental filtering is causing functional and phylogenetic homogenization, with particularly negative effects on habitat-specialist rare and endangered species. Phylogenetic and functional simplification reduces community stability and ecosystem function, and once environmental conditions no longer meet the needs of these species, small population effects may drive them to extinction.

The intensification of phylogenetic clustering has also enhanced interspecific competition at small scales, severely affecting *F. hayatae* population regeneration. Environmental filtering reduces overall community stability, while competition among close relatives at small scales hinders population renewal and

development. Therefore, the future prospects for *Fagus hayatae* communities are not optimistic, and conservation challenges are formidable.

4. Conclusion

Our study revealed that from 2006 to 2016, the overall phylogenetic structure of *Fagus hayatae* communities showed increasing clustering while nearest taxon relationships became more distant. As spatial scale increased, phylogenetic structure became more clustered, and the strength of this clustering trend increased with scale. These findings indicate that the phylogenetic structure of *Fagus hayatae* communities in Qingliangfeng National Nature Reserve is gradually homogenizing under current climate conditions, with concerning prospects for the future.

Based on these results, we propose several conservation recommendations. Since evergreen species have stronger environmental tolerance and may outcompete deciduous *F. hayatae* under global warming and environmental degradation, some human intervention may be necessary to maintain deciduous species in the community. Further research should analyze the direct causes of high mortality in *F. hayatae* seedlings and saplings to develop effective targeted measures to improve community recruitment.

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