Postprint: Biomass Dynamics of Dominant Species and Community Succession Characteristics in the Evergreen-Deciduous Broad-Leaved Mixed Forest of Tianmu Mountain

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Abstract

Based on a 1 hm^2 permanent plot of typical subtropical evergreen-deciduous broad-leaved mixed forest established in Tianmu Mountain Nature Reserve, comprehensive processing and analysis were conducted on field survey and monitoring data from 1996 and 2012 (a 16-year time span), examining niche breadth, niche overlap, interspecific association, and biomass of dominant species to deeply explore community succession characteristics. The results showed that from 1996 to 2012, the niche breadth index of dominant species decreased for Cyclocarya paliurus and Liquidambar acalycina, while it increased significantly for Cyclobalanopsis myrsinifolia and Lithocarpus harlandii; furthermore, niche overlap among dominant species was higher in 2012 compared to 1996. The total biomass of tree species with diameter at breast height (DBH) 10 cm was 151.03 t and 148.53 t in 1996 and 2012, respectively, while the total biomass of saplings of dominant species with DBH of 5-10 cm reached 10.03 t in 2012, indicating considerable growth potential. Overall, the results align with the succession trend of evergreen-deciduous broad-leaved mixed forests in Tianmu Mountain, thereby providing data support and reference for revealing community succession patterns of subtropical evergreen-deciduous broad-leaved mixed forests in Tianmu Mountain.

Full Text

Biomass Change and Community Succession Characteristics of Dominant Species in Evergreen and Deciduous Broad-leaved Mixed Forests in Tianmu Mountain

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Abstract

Characterizing the spatial distribution of tree species within forest stands is a central focus of global forest ecology research. Tree arrangement provides forest ecologists with significant information on ecological processes such as competition, facilitation, mortality, and dispersal, which tend to follow specific spatial patterns in forest stands. Assessment of inter- and intraspecific interactions that reduce growth and induce mortality, or enhance establishment and growth, has important consequences for both forest dynamics and management. Additionally, the biomass ratio distribution of various dominant tree species is a synthetic reflection of community structure and function in interspecific relationships, niche differentiation, and population dynamics. The objective of this study was to reveal spatial associations of dominant tree species in a subtropical evergreen-deciduous broad-leaved forest in southeast China, and to quantitatively identify their ecological relationships and explain possible causes for their successful coexistence in these forest ecosystems.

To accomplish this objective, niche breadth, niche overlap, and interspecific associations were used to analyze inter- and intraspecific interactions of trees based on field data collected from forest permanent plots (1 hm^2) in the National Nature Reserve of Mount Tianmu, Zhejiang Province. Furthermore, the biomass structure of the stand was studied at the community level. Field surveys of the forest permanent plots were conducted in 1996 and 2012, respectively.

Field measurements showed that the niche breadth index of the dominant species *Liquidambar acalycina*, *Cyclobalanopsis myrsinifolia*, and *Lithocarpus harlandii* decreased; conversely, that of *Cyclocarya paliurus* increased. Moreover, the niche overlap degree of dominant species in 2012 was higher than that in 1996, which showed that the sharing and utilization of resources was higher in 2012. Species with similar biological features, ecological adaptability to the habitat, or a higher degree of niche overlap tended to be positively related, whereas those with different biological features, adaptability to the habitat, or existing interspecies competition tended to be negatively related. The test showed that positive correlations of the majority of the dominant species-pairs in 1996 and 2012, accounting for 48.48% and 71.21%, respectively, were followed by negative correlations of dominant species pairs accounting for 31.82% in both 1996 and 2012. Only some species pairs displayed no correlations in 1996.

The results showed that all the dominant species showed similarity and niche overlap adaptability to the community environment and the ecological characteristics of the subtropical evergreen-deciduous broad-leaved forest were affected by niche breadth, proportional similarity, and overlap in vegetation succession. The biomass of trees with diameter at breast height (DBH) 10 cm decreased from 151.03 Mg in 1996 to 148.53 Mg in 2012. The biomass of dominant species with DBH of 5–10 cm in 2012 was 10.03 Mg, which suggested considerable growth potential. Our results explained the successful coexistence of dominant tree species at the study site and highlighted detailed tree-tree interactions of the species in the subtropical evergreen-deciduous broad-leaved forest.

Keywords: evergreen and deciduous broad-leaved mixed forest; dominant species; biomass; community succession; Tianmu Mountain

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1. Study Area Overview

Tianmu Mountain National Nature Reserve is located in Lin' an City, northwestern Zhejiang Province, at the border between Zhejiang and Anhui provinces (119°24 11 –119°28 21 E, 30°18 30 –30°24 55 N). The climate belongs to a transitional type from mid-subtropical to north-subtropical, influenced by warm and humid oceanic airflow. The elevation ranges from 300 to 1556 m, with the main peak, Xianren Ding, at 1506 m. The annual average temperature is 14.8–8.8°C, with four distinct seasons. The annual precipitation reaches 1390–1870 mm, and the frost-free period is 235–209 days. The main vegetation types include evergreen-deciduous broad-leaved mixed forest (typical zonal vegetation), bamboo forest, and coniferous forest. The evergreen-deciduous broad-leaved mixed forest is distributed at 850–1100 m, the deciduous broad-leaved mixed forest at 1100–1380 m, and the coniferous forest at 850 m.

2. Methods

2.1 Plot Establishment A permanent plot of 1 hm² (100 m × 100 m) was established in a typical evergreen-deciduous broad-leaved mixed forest at Shiziwei in Tianmu Mountain National Nature Reserve (30.320°N, 119.230°E, 1065 m elevation). In 1996, all woody plants with DBH 10 cm were measured and mapped, recording species, DBH, height, crown base height, and growth status. The triangular coordinate method using the southwest and southeast corners as base points was used to record positional coordinates of measured plants. In 2012, the plot was re-surveyed under conditions of no human disturbance, using a South Surveying and Mapping NTS-300R total station to restore positions. All woody plants with DBH 1 cm were measured and mapped using the rectangular coordinate system with the southwest corner as the origin, with east-west as the x-axis and north-south as the y-axis.

2.2 Determination of Dominant Species Dominant species are defined as those that have significant influence on other species in the community, with maximum density, coverage, and biomass. The importance value is a key indicator used in forest community research to measure the dominance degree of a tree species. The importance value for the tree layer is calculated as: (relative abundance + relative dominance + relative height). Relative abundance refers to the relative value of a species' individual count to the total count of all species. Relative dominance refers to the relative value of a species' basal area at breast height to the total basal area of all species. Relative height refers to the relative value of a species' height to the total height of all species.

2.3 Niche Breadth Niche breadth represents the environmental limiting factor units occupied by a species. This study adopted the widely cited Levin' s index and Shannon-Wiener information index:

1. **Levin' s Index**: $Bi = 1 / \Sigma(Pij^2)$, where $Pij = nij/Ni$ represents the proportion of individuals of species i in resource state j to the total individuals of species i.
2. **Shannon-Wiener Information Index**: $Bi = -\Sigma(Pij \times \ln Pij)$. This index is based on the Shannon-Wiener information formula. Larger Bi values indicate wider niches. When a species uses each resource state with equal numbers of individuals, Bi is maximized. When all individuals of a species are concentrated in one resource state, Bi is minimized, indicating the narrowest niche.

2.4 Niche Overlap Niche overlap refers to the phenomenon where two species overlap in utilizing resources such as food and space. This study used Levin' s (1968) overlap index: $Oik = \Sigma(Pij \times Pkj)$, where Oik represents the overlap index between species i' s resource utilization curve and species k' s resource utilization curve. Oik and Oki values differ. $Oik = 0$ indicates complete niche separation, while $Oik = 1$ indicates complete niche overlap.

2.5 Interspecific Association Analysis Interspecific association refers to the spatial distribution correlation among different species, typically caused by habitat differences affecting species distribution. It reflects the organic connections formed by species interactions in different habitats and is an important quantitative and structural characteristic of plant communities. This study analyzed interspecific associations among dominant species in 1996 and 2012 using the association coefficient (AC) and percentage co-occurrence (PC).

Association Coefficient (AC) measures the degree of association between species pairs: - When $bc > ad$ and d a: $AC = (ad - bc) / (b + d)$ - When $bc > ad$ and $d < a$: $AC = (ad - bc) / (a + c)$ - When ad bc: $AC = (ad - bc) / (a + b)$

The AC value ranges from [-1, 1]. Values closer to 1 indicate stronger positive association, values closer to -1 indicate stronger negative association, and $AC = 0$ indicates complete independence.

Percentage Co-occurrence (PC) measures the degree of positive association: $PC = a / (a + b + c)$, where a, b, c, d are values from a 2×2 contingency table.

PC values range from [0, 1], with values closer to 1 indicating tighter positive association.

2.6 Biomass Change Estimation Biomass was estimated using species-specific biomass models based on 2012 monitoring data (Table 1). The models use DBH (D), tree height (H), and crown length (L) as variables, measured using steel diameter tapes, Blume-Leiss hypsometers, and tape measures for crown projection length.

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3. Results

3.1 Importance Values Based on importance value calculations, species with the highest values were selected as dominant species for each year (Table 2). In 1996, the dominant species ranked by importance value were: *Cyclocarya paliurus*, *Cunninghamia lanceolata*, *Cyclobalanopsis myrsinifolia*, *Liquidambar acalycina*, *Daphniphyllum macropodum*, *Eurya hebeclados*, *Litsea auriculata*, *Cornus kousa* subsp. *chinensis*, *Cryptomeria fortunei*, *Lithocarpus harlandii*, *Catalpa ovata*, and *Lindera erythrocarpa*. In 2012, the dominant species were: *Cyclobalanopsis myrsinifolia*, *Cunninghamia lanceolata*, *Cyclocarya paliurus*, *Daphniphyllum macropodum*, *Lithocarpus harlandii*, *Liquidambar acalycina*, *Cornus kousa* subsp. *chinensis*, *Cryptomeria fortunei*, *Litsea auriculata*, *Eurya hebeclados*, *Cyclobalanopsis stewardiana*, and *Nyssa sinensis*.

Biomass model
Importance values of the dominant species in 1996 and 2012

3.2 Niche Breadth In the 1996 plot, *Cyclocarya paliurus* had the largest niche breadth index (Bi = 1.3165), indicating its dominant position. Other dominant species ranked by Bi values were: *Cunninghamia lanceolata*, *Lithocarpus harlandii*, *Daphniphyllum macropodum*, *Cryptomeria fortunei*, *Eurya hebeclados*, *Litsea auriculata*, *Cornus kousa* subsp. *chinensis*, *Liquidambar acalycina*, *Catalpa ovata*, and *Lindera erythrocarpa*.

In the 2012 plot, *Cyclobalanopsis myrsinifolia* had the largest niche breadth index (Bi = 1.3177), becoming the most dominant species. Other species ranked by Bi values were: *Cunninghamia lanceolata*, *Lithocarpus harlandii*, *Daphniphyllum macropodum*, *Cryptomeria fortunei*, *Cyclocarya paliurus*, *Liquidambar acalycina*, *Cornus kousa* subsp. *chinensis*, *Litsea auriculata*, *Eurya hebeclados*, *Cyclobalanopsis stewardiana*, and *Nyssa sinensis*.

Between 1996 and 2012, *Cyclocarya paliurus* showed the largest decrease in niche breadth index (ΔBi = -0.0890), while *Lithocarpus harlandii* showed the largest increase (ΔBi = 0.4007). Species with decreased Bi values included *Liquidambar acalycina* (ΔBi = -0.0353). Species with minimal Bi value changes included *Cryptomeria fortunei* (ΔBi = 0.0591) and *Eurya hebeclados* (ΔBi = 0.0593).

Niche overlap and the difference value of dominant species in 1996 and 2012

3.3 Niche Overlap The distribution pattern of niche overlap values among dominant species changed significantly between 1996 and 2012 (Table 4). In 1996, 22.73% of species pairs had no niche overlap, and 18.94% had overlap values < 0.1. In 2012, no species pairs showed complete niche separation, and only 3.03% had overlap values < 0.1. The proportion of species pairs with overlap values between 0.1-0.3 decreased from 22.73% to 18.94%, while those between 0.3-0.5 increased from 36.36% to 29.55%. The proportion of high overlap values (0.5-1.0) increased substantially from 31.82% in 1996 to 35.61% in 2012. These results indicate that dominant species in 2012 had higher niche overlap and greater resource sharing and utilization than in 1996.

Distribution pattern of niche overlap of dominant species in 1996 and 2012

3.4 Interspecific Association **Association Coefficient (AC) Analysis**: Among the 66 species pairs in 1996, 48.48% showed positive association (28.79% not significant, 15.15% significant, 4.55% highly significant), 31.82% showed negative association (12.12% not significant, 19.70% significant), and 15.15% showed no association. In 2012, among 66 species pairs, 71.21% showed positive association (57.58% not significant, 9.09% significant, 4.55% highly significant), 28.79% showed negative association (19.70% not significant, 9.09% significant), and no pairs showed complete independence. The ratio of positive to negative associations increased from 1.52 in 1996 to 2.47 in 2012.

[Figure 1: see original paper] AC value of dominant species in 1996
[Figure 2: see original paper] AC value of dominant species in 2012
The contrast of AC value between dominant species in 1996 and 2012

Percentage Co-occurrence (PC) Analysis: In 1996, 48.48% of species pairs showed positive association (31.82% not significant, 15.15% significant, 1.52% highly significant), 31.82% showed negative association, and 15.15% showed no association. In 2012, 71.21% showed positive association (31.82% not significant, 31.82% significant, 7.58% highly significant), with negative and no associations accounting for the remainder. The proportion of highly significant positive associations increased notably.

[Figure 3: see original paper] PC value of dominant species in 1996
[Figure 4: see original paper] PC value of dominant species in 2012
The contrast of PC value between dominant species in 1996 and 2012

3.5 Biomass Change Total biomass of trees with DBH 10 cm in the Tianmu Mountain plot decreased from 151.03 t in 1996 to 148.53 t in 2012, a reduction of 2.50 t/ha. However, biomass of dominant species with DBH 5-10 cm in 2012 reached 10.03 t, indicating substantial growth potential.

Biomass of dominant species with DBH 10 cm was 128.61 t in 1996 and 79.14 t in 2012. Species that lost dominant status by 2012, such as *Lindera erythro-*

carpa and *Catalpa ovata*, had biomasses of 0.59 t and 5.05 t respectively in 1996. Species not present as dominant species in 1996, such as *Cyclobalanopsis stewardiana* and *Nyssa sinensis*, became dominant by 2012 with biomasses of 4.25 t and 8.37 t respectively.

Species that remained dominant in both years showed biomass increases: *Lithocarpus harlandii* increased by 3.99 t (129.90%), *Cyclobalanopsis myrsinifolia* by 8.42 t (174.46%), *Cryptomeria fortunei* by 16.64 t (164.81%), and *Daphniphyllum macropodum* by 11.74 t (146.09%). The biomass of saplings (DBH 1-10 cm) was 25.15 t in 2012, with 16.03 t in the 5-10 cm class, representing 63.74% of total sapling biomass and indicating high growth potential.

Large tree mortality contributed to biomass loss. In 1996, trees with DBH > 60 cm (mostly *Cryptomeria fortunei*) had a total biomass of 10.33 t, accounting for 6.84% of the total biomass of trees with DBH 10 cm. Death of these large trees significantly reduced total biomass.

[Figure 5: see original paper] Diameter distribution of the trees in 1996 and 2012
Biomass of dominant species in 1996 and 2012
Biomass of dominant species trees (DBH > 60 cm) in 1996

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4. Discussion

Analysis of the 1996 and 2012 plot monitoring data reveals changes in dominant species characteristics and community composition and structure trends in the Tianmu Mountain evergreen-deciduous broad-leaved mixed forest. The 2012 dominant species showed higher niche overlap and greater resource sharing than in 1996. Interspecific association analysis using AC and PC values showed that the proportion of negative and no associations decreased while positive associations increased, particularly highly significant positive associations.

From a forest community succession perspective, the climax community of subtropical evergreen-deciduous broad-leaved mixed forest is shade-tolerant evergreen broad-leaved forest. The changes in dominant species between 1996 and 2012 indicate the forest is in mid-succession. Several key trends are evident:

Cyclocarya paliurus showed the largest decrease in niche breadth index (Bi) and was the only dominant species with reduced biomass, decreasing from 14.84 t to 10.34 t. Its individual count also declined sharply. Combined with its interspecific association results, this indicates *Cyclocarya paliurus* is at a disadvantage and being gradually eliminated during succession.

Cyclobalanopsis myrsinifolia became the most dominant species in 2012 with the highest importance value and niche breadth index. Although its biomass increase didn' t reach the maximum, a large proportion was distributed in the

5-10 cm DBH class, indicating substantial growth potential. Its positive growth trend and interspecific associations show it holds a clear advantage in succession.

Lithocarpus harlandii also showed significant increases in importance value, niche breadth index, and biomass, with the largest growth amplitude among dominant species. Its biomass increased markedly from 1996 to 2012, indicating a strong competitive position in succession.

Other species showing increased dominance include *Daphniphyllum macropodum*, *Cornus kousa* subsp. *chinensis*, and *Litsea auriculata*. *Cyclobalanopsis stewardiana* and *Nyssa sinensis* became dominant species by 2012, demonstrating their competitive advantage in this successional process.

The community is transitioning from coniferous-broadleaf mixed forest to broadleaf forest, with broadleaf species gradually replacing coniferous species like *Cryptomeria fortunei* as the main dominant species.

5. Conclusion

This study demonstrates that *Cyclobalanopsis myrsinifolia* and *Lithocarpus harlandii* have clear competitive advantages in the Tianmu Mountain evergreen-deciduous broad-leaved mixed forest, aligning with the community' s successional trend toward evergreen broad-leaved forest. *Cyclocarya paliurus* is at a disadvantage and being gradually eliminated. The community is transitioning from coniferous-broadleaf mixed forest to broadleaf forest, where broadleaf species will replace coniferous species as the main dominant species. Species such as *Daphniphyllum macropodum*, *Cornus kousa* subsp. *chinensis*, and *Litsea auriculata* also show competitive advantages, while *Eurya hebeclados* and *Liquidambar acalycina* do not.

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