环境过滤还是生物竞争对亚热带常绿阔叶次生林群落的影响更显著？

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摘 要：【目的】种内变异不仅是群落功能性状多样性的主要来源，具有与种间变异相似的生态效应，可以深刻地理解群落构建和生态系统功能的内在机制。【方法】本研究选取了浙江省亚热带常绿阔叶次生林 30 块固定监测样地中 79 个物种，3546 个 DBH≥10cm 个体的 9 种性状（比叶面积、叶干物质含量、木材密度、叶面积、叶绿素含量、叶片氮含量、叶片磷含量、叶片钾含量和氮磷比）数据和群落数据。利用性状梯度法将物种功能性状分解成 alpha(群落内)和 beta(群落间)组分，来量化环境梯度和共存物种对性状变异的作用大小。【结果】研究发现，1)常绿阔叶次生林群落中 9 种功能性状均存在一定程度的分异。各性状的 alpha 值变化范围均大于 beta 值。2)常绿阔叶次生林群落各功能性状分异间关联性存在显著差异性。各性状 alpha 与其他组分间的相关性显著性较高；beta 与其他组分间呈现弱显著相关性；各性状的物种性状平均值(Ti)与 Rs 间不存在显著相关性。3)浙江午潮山常绿阔叶次生林影响种内性状变异的因素相对复杂。Alpha 组分对种内性状变异的影响相比于 beta 组分更为显著和强烈。非生物因素(如土壤养分含量、氮磷含量等)对 beta 组分具有直接影响，生物因素(如树木树高变异等)对 alpha 组分具有直接且更为强烈的影响。【结论】我们的研究结果表明了 alpha 和 beta 组分作为共存物种间的独立的分化轴，在不同空间尺度的生态策略的维度上的偏移，不同性状对生境差异等存在不同的灵敏性。性状梯度分析法将物种性状分解成 alpha 和 beta 组分更加能够清楚地展现了物种性状在群落中的变化规律，将有助于理解性状关系的尺度效应和潜在机制。

关键词：功能性状；种内变异；环境过滤；扩散限制；群落构建

Abstract: Intra-specific variation is the main source of functional trait diversity and has similar ecological effects as inter-specific variation. We studied 79 species and 3546 individuals from 30 fixed monitoring plots in subtropical evergreen broad-leaved secondary forests in Zhejiang Province, China. Using trait gradient analysis, we examined nine traits (specific leaf area, leaf dry matter content, wood density, leaf area, chlorophyll content, leaf nitrogen content, leaf phosphorus content, leaf potassium content, and nitrogen-phosphorus ratio) by decomposing species functional traits into alpha (within-community) and beta (among-communities) components to quantify the effects of environmental gradients and coexisting species on trait variation. All nine functional traits showed some degree of differentiation in the forest communities, with a greater range of variation in alpha values than in beta values. Correlations were significantly different between the trait differentiations in the communities. The alpha values of each trait showed a higher correlation with other components than the beta values. The factors affecting intra-specific trait variation were relatively complex. The alpha component had a more significant and stronger effect on intra-specific trait variation compared to the beta component. Abiotic factors, such as soil nutrient content and nitrogen-phosphorus content, directly affected the beta component, while biotic factors, such as tree height variation, had a direct and stronger effect on the alpha component. Our results demonstrate that alpha and beta components, as independent differentiation axes among coexisting species, have different sensitivities to different environmental factors and traits in different ecological strategies and spatial scales. Trait gradient analysis can more clearly reveal the variation patterns of species traits in communities, which will help to understand the scale effects and potential mechanisms of trait relationships.

Keywords: Functional traits; Intra-specific variation; Environmental filtering; Dispersal limitation; Community assembly.

Forest communities rely on competition and allocation of resources such as space, time, and biotic factors, which are crucial in driving species coexistence and ecological niche differentiation (Lamprecht et al., 2018; Midolo et al., 2019; Staude et al., 2022). However, solely considering interspecific trait variation may underestimate the overlap of species' ecological niches and functional traits, potentially biasing our understanding of species coexistence, community function, and dynamics (Violle et al., 2007). Increasing evidence shows that intraspecific trait variation is more likely to determine the competitive interactions of individual species and community-level responses to global environmental change (Bassar et al., 2017; Henn et al., 2018; Midolo et al., 2019; Thomas et al., 2020; Rixen et al., 2022; Staude et al., 2022).

Several studies have found that intraspecific trait variation explains a significant portion of the total trait variation within and between communities, having strong predictive power in predicting ecological processes, community-building mechanisms, and ecosystem function (Benavides et al., 2021; Violle et al., 2012). Siefert et al. (2015) found that intraspecific trait variation explained 25% of the total trait variation within a community and 32% of the trait variation between communities. Albert et al. (2010) found that nearly 30% of trait variation came from intraspecific variation, with the highest intraspecific variation in leaf nitrogen and carbon content. Intraspecific trait variation has been found to promote species coexistence through biotic and abiotic filtering (Jung et al., 2010) and can help plants cope with environmental changes (Laforest-Lapointe et al., 2014). Studies of grassland communities on the Qinghai-Tibet Plateau also found that intraspecific trait variation dominated the functional diversity changes in response to inter-annual climate fluctuations, buffering the impacts of climate on community stability (Chen et al., 2019). Intra-specific trait variation also affects the functional trait diversity and the functional diversity components of alpha and beta diversity (Bello et al., 2017; Thomas et al., 2020) The presence of intra-specific variation can also influence community building by affecting the distribution pattern of functional trait beta diversity which has implications for nutrient cycling, crop disease resistance, and community building (Cornwell et al., 2006;Lecerf and Chauvet, 2008; Garrett et al., 2011; Thomas et al., 2020).

Species that are screened in a local environment are theoretically able to adapt to the small habitat, which results in functional convergence among species within the community (de Bello et al., 2021). However, interactions among the community's biota lead to competition and exclusion of similar species, known as limiting similarity, which limits the similarity among coexisting species. Both individual environmental filtering and limiting similarity contribute to community structure and maintain biodiversity (Violle et al., 2012). Trait gradient analysis (TGA) provides a better understanding of interactions among communities at different levels (Cornwell et al., 2006). Intraspecific trait variation can be divided into alpha and beta components. The alpha component represents the differences between the mean attributes of a species and the community's mean attributes at its location, reflecting differences in adaptive strategies of coexisting species in the same community environment (Swenson, 2013; Yao et al., 2020a). The beta component represents a species' position on this trait gradient, reflecting the strength of the response signal of functional traits among species along environmental gradients. This helps to explain the relative roles of dispersal limitation and environmental filtering in community assembly (Yao et al., 2020a,b). By studying the functional similarity between alpha and beta components within species (Swenson, 2013), it is possible to directly reveal whether species coexistence is due to strong environmental filtering or processes such as limiting similarity.

Subtropical evergreen broad-leaved forests are highly diverse and play critical roles in maintaining biodiversity and ecosystem functions. Although facing habitat loss and threats from human activities, the species composition, structure, and function of subtropical evergreen secondary forests are significant for biodiversity conservation, climate regulation, soil and water conservation, and prevention of land degradation (Zhang et al., 2022). To gain insights into species' functional traits and community dynamics, we conducted a study of 30 fixed monitoring plots of subtropical evergreen secondary forests in Zhejiang Province, with 79 species and 3546 individuals. We collected data on nine functional traits and community data, and the trait gradient method to decompose species functional traits into alpha traits (within-community) and beta traits (between communities) to quantify the effects of environmental gradients and coexisting species on trait variation. We hypothesized that small habitat heterogeneity and few individuals of the same species at the local scale would lead to the high similarity among coexisting individuals and smaller alpha diversity within species, while large habitat heterogeneity among different plots would result in larger beta diversity within species due to significant differences among individuals of the same species growing in different plots.

1 Study Area and Methods

1.1 Overview of the Study Area

Wuchao Mountain National Forest Park is situated in Xianlin Town, Yuhang District, Hangzhou City, Zhejiang Province, China (33◦410 N, 120◦000 E), and is part of the veins of Tianmu Mountain. The park covers a total area of 522 ha and has an average altitude of 264 m, with the highest point reaching 495 m. As a natural forest ecosystem in the suburbs of the city, Wuchao Mountain National Forest Park is located in the central subtropical zone, with superior water resources and heat conditions. The annual average temperature is 16.1 °C, with the coldest month in January (average of 3.6 °C), and the warmest being August (average of 38.4 °C). The park also experiences an annual average of 1970.6 sunshine hours and has a plant growth period of 311 days, and the forest coverage rate is approximately 93%, showcasing its rich plant species diversity. The area is mainly characterized by red and yellow soil types, and evergreen broad-leaved forests are the predominant vegetation, featuring trees such as *Cyclobalanopsis glauca*, *Castanopsis chinensis*, *Schima superba*, *Castanopsis sclerophylla*. The park has undergone significant restoration efforts, as it was previously subjected to human interference before the 1970s. In the past 40 years, the forest has been completely closed for afforestation.

1.2 Data Collection and Analysis

From October 2020 to June 2021, we established fifty permanent forest dynamics plots, each covering 0.04 ha, in Wuchao Mountain National Nature Reserve. The plots were located at elevations ranging from 340.1 to 467.4 m, where the forest composition, structure, and habitat were all homogeneous. For each plot, the diameter at breast height (DBH) and height (H) of all woody stems ≥1 cm DBH were recorded and identified to species level with the help of local botanists.

We measured key functional traits including specific leaf area (SLA, mm^2/mg), leaf dry matter content (LDMC, mg/m^2), relative chlorophyll content (SPAD), wood density (WD, g/cm^3), leaf nitrogen content (LNC, mg/g), leaf phosphorus content (LPC, mg/g), leaf potassium content (LKC, mg/g) and leaf nitrogen to phosphorus ratio (N:P, %) separately To obtain these measurements, we collected 10-20 healthy and mature sun leaves for each species and analyzed their morphology, chlorophyll content, and nitrogen to phosphorus content. We used a leaf area meter, an electronic balance, and an oven to measure specific leaf area and leaf dry matter content while a handheld chlorophyll meter (Konica Minolta SPAD-502) was used to measure leaf chlorophyll content. Leaf elemental analysis was conducted in the laboratory on dried leaf samples. In each of the permanent forest dynamics plots, we collected branches and leaves from all individuals with DBH ≥ 10 cm. For individuals with a DBH less than 10 cm, we sampled the five largest individuals of each species. For individuals with a DBH of less than 10 cm, we sampled the five largest individuals of each species. In cases where there were fewer than five individuals of a species in a plot, we sampled all individuals of the species present in that plot. Overall, we measured and sampled 3546 individuals, representing 79 species found in the 50 plots.

1.3 Trait Gradient Analysis

The community was sorted according to the weighted average trait values of the species (the trait values of the species were weighted by species abundance). The functional traits of the species were further divided into two trait values, alpha, and beta. The position of a species on the gradient of this trait is called the beta trait, which reflects the response of the species to environmental change in the community. The difference between the average properties of the species and the community averages for where they are located is called an alpha trait. This reflects the difference in the adaptation strategies of coexisting species to the same community environment (Cornwell et al., 2006). These were calculated with the formulas of Ackerly and (Cornwell et al., 2006):

$$\overline{p_j} = \frac{\sum_{i=1}^{S} a_{ij} t_i}{\sum_{i=1}^{S} a_{ij}} \quad \text{…………(1)}$$

$$\beta_i = \frac{\sum_{j=1}^{P} \overline{p_j} a_{ij}}{\sum_{j=1}^{P} a_{ij}} \quad \text{…………(2)}$$

$$t_i = \alpha_i + \beta_i \quad \text{…………(3)}$$

The process of Trait Gradient Analysis (TGA) involves breaking down traits into various components. Firstly, the abundance of each species in a given sample is denoted by aij. The average trait of a sample, pj, is then calculated by weighing the abundance of each species in that sample (Formula 1). All samples are then arranged in order of their average trait (pj), thus creating the trait gradient. The beta trait value of a given species (i) is determined by calculating the average trait of that species across all samples, with each value being weighted by the abundance of that species (Formula 2). The average range of a given species (i) is referred to as the ti value. Finally, the difference between the average range (ti) and the beta trait (as per Formula 3) is known as the alpha trait value of species i.

1.4 Analysis Method

In this study, we employed a range of statistical methods to analyze the functional traits of different species. First, we used the TGA method to partition functional traits and assess variation between alpha and beta values. Next, the skewness analysis method was used to explore the distribution of alpha and beta values, identifying whether the distribution was skewed to the right or left, symmetrical or uniform. To compare functional traits among species, we used chi-square tests (*p < 0.05; **p < 0.01; ***p < 0.001) and transformed the SLA, LA, LNC, LKC, and N:P values using a log10 transformation, as these traits did not follow a normal distribution. To identify the main influencing factors, we conducted separate principal component analyses on the alpha component, beta component, soil nutrients, and biotic factors. We then used structural equation modeling (SEM) to examine the direct and indirect effects of soil nutrients and biotic factors on intraspecific trait variation through the alpha and beta components. The maximum likelihood method was used to fit the SEM. The goodness of fit was evaluated using comparative fit index (CFI), root mean square error of approximation (RMSEA), significance probability value (P), and Akaike's information criterion (AIC). A good fit was indicated by CFI > 0.9, RMSEA < 0.08, P > 0.05, and a smaller AIC value. Statistical analysis and plotting were performed in R 4.2.1.

Result

2.1 Functional trait variation in evergreen broad-leaved secondary forest communities

The evergreen broad-leaved secondary forest community displays some degree of functional trait differentiation among its nine functional traits. Species traits such as SLA, LA, and CHL have the highest mean values, whereas LDMC and LKC have the lowest mean values. LPC and LA exhibit the greatest range of variation in mean values, while CHL and WD exhibit the least. Additionally, the range of alpha values is greater than the beta values, with LPC and LKC having the highest range of variation in alpha values, and CHL and WD having the lowest. LPC and LA exhibit the largest range of variation in beta values, while CHL and N:P exhibit the smallest range of variation.

Ecologically, LA and LPC possess the broadest niche width, whereas CHL, WD, and N:P exhibit the narrowest niche width. The functional traits with the largest mean values in the plot are SLA, CHL, and LA, while LDMC and LPC have the smallest mean values. The functional traits with the largest range of variation in plot mean values are LPC and LA, while CHL and WD have the smallest range of variation.

Table1 Mean and range of plant functional traits parameters

Parameter	Species characteristics									Plot characteristics		
Traits	Ti, mean	Ti	Range of Ti	beta	Range of beta	alpha	Range of alpha	Rs, mean	Rs	Pj, mean	Pj, min − max	Range of Pj
SLA	2.21	1.71 2.50	0.79	2.08 2.27	0.19	-0.45 0.39	0.84	0.07	0.00 0.19	2.13	2.08 2.27	0.19
LDMC	0.43	0.14 1.12	0.98	0.34 0.47	0.13	-0.20 0.65	0.85	0.06	0.00 0.15	0.41	0.34 0.49	0.15
WD	0.97	0.66 1.14	0.48	0.93 1.06	0.13	-0.35 0.11	0.46	0.05	0.00 0.13	1.02	0.92 1.06	0.14
LA	1.76	1.01 2.20	1.19	1.39 1.97	0.58	-0.46 0.39	0.85	0.25	0.00 0.58	1.66	1.39 1.97	0.58
CHL	1.74	1.49 1.87	0.38	1.72 1.81	0.09	-0.27 0.09	0.36	0.04	0.00 0.10	1.76	1.71 1.82	0.11
LNC	1.23	0.81 1.67	0.86	1.12 1.36	0.24	-0.36 0.39	0.75	0.08	0.00 0.25	1.16	1.11 1.36	0.25
LPC	0.96	0.14 1.51	1.37	0.62 1.20	0.58	-0.28 0.69	0.97	0.20	0.00 0.58	0.75	0.61 1.20	0.59
LKC	0.95	0.29 1.46	1.17	0.86 1.00	0.14	-0.65 0.54	1.19	0.06	0.00 0.14	0.91	0.85 1.00	0.15
N:P	1.28	0.75 1.45	0.7	1.24 1.35	0.11	-0.54 0.16	0.7	0.05	0.00 0.14	1.31	1.24 1.39	0.15

2.2 Functional trait differentiation and correlation of evergreen broad-leaved secondary forest community

There are significant differences in the correlations among different functional traits in the evergreen broad-leaved secondary forest community. There is a strong correlation ($p < 0.001$, $r > 0.84$) between Ti (the mean value of functional traits for each species) and alpha for all traits except LKC and N: P. There is a weak significant correlation ($p < 0.001$, $r > 0.84$) between Ti and beta for all traits except LKC and N: P. There is no significant correlation between Ti and Rs (species richness). Only LDMC, WD, LA, and LNC show weak significant correlations between alpha and beta ($p < 0.05$, $r > 0.24$), while there is no significant correlation between other functional traits. There is no significant correlation ($p > 0.05$) between Rs and the differentiation of functional traits (Ti, alpha, and beta) for each trait.

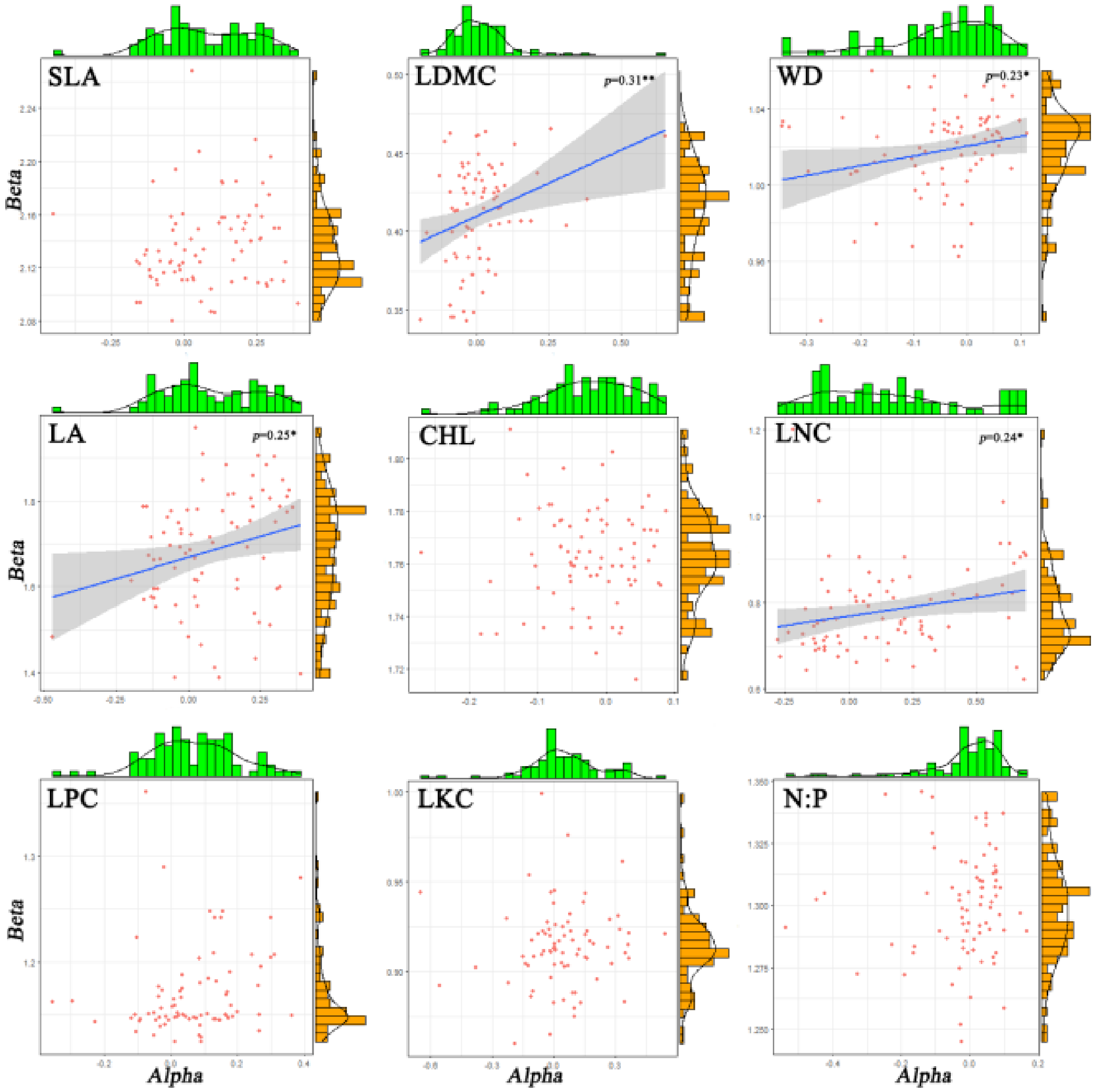


Figure 1 Scatter plot and distribution plot of alpha and beta components for functional traits of evergreen broad-leaved secondary forest communities

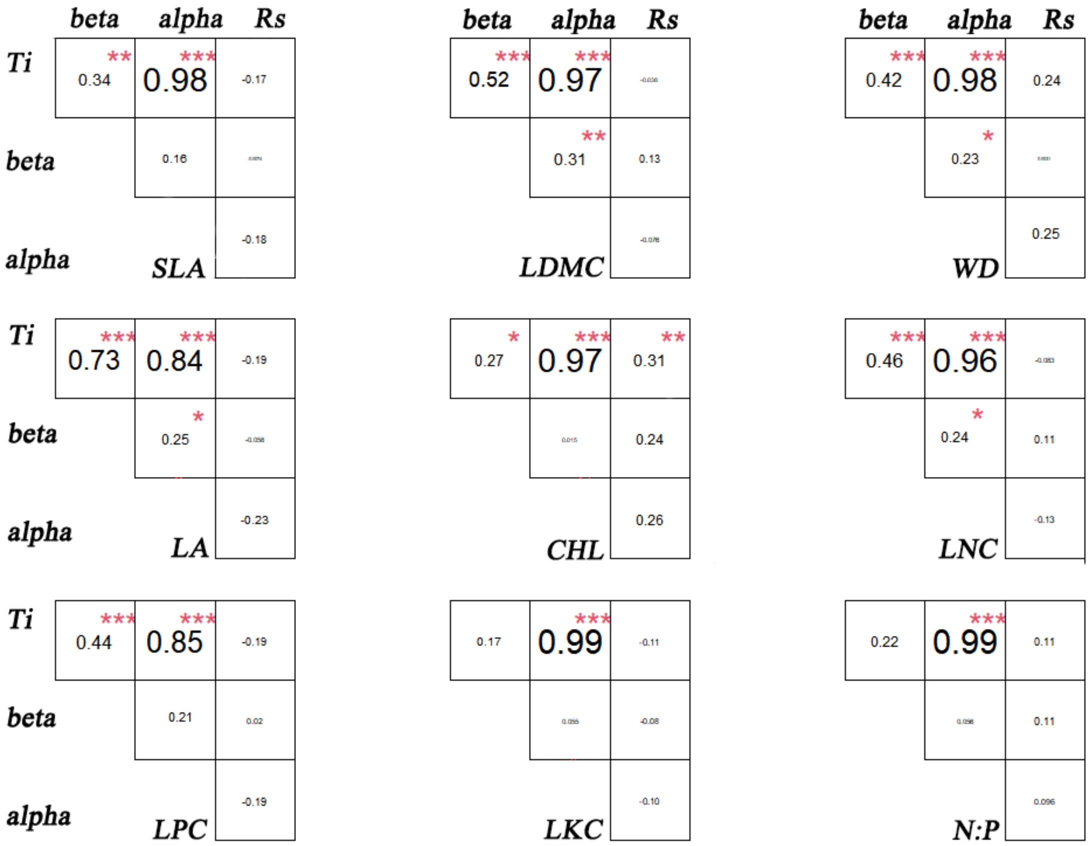
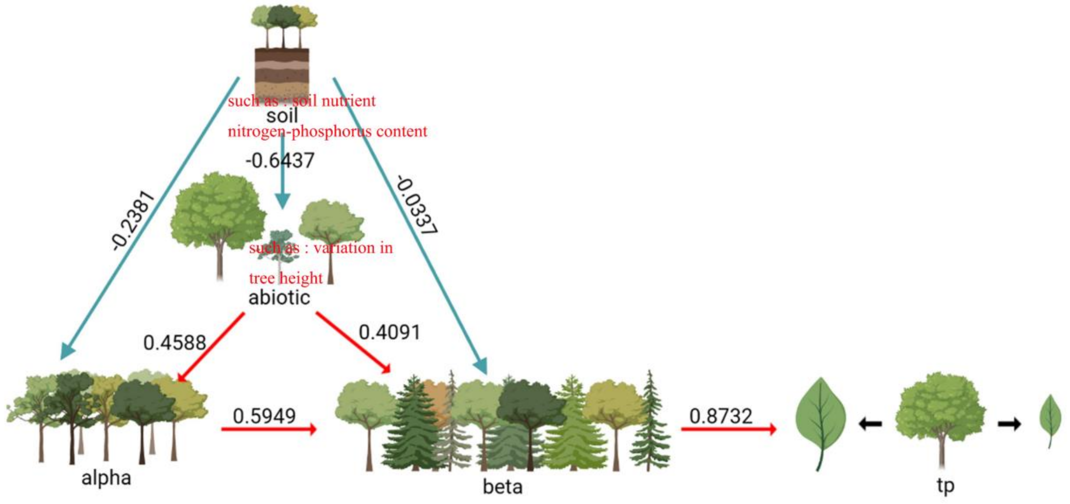


Figure 2

Association of functional traits in evergreen broad-leaved secondary forest communities

2.3 Factors affecting intra-specific trait variation in evergreen broad-leaved secondary forests

The factors influencing the variation of intra-specific traits in the evergreen broad-leaved secondary forests of Wuchao Mountain in Zhejiang are relatively complex. As shown in Figure 3, the variables explain 37% of the observed variation. The alpha and beta components were found to have a significant direct effect on intra-specific trait variation ($P < 0.05$), with path coefficients of 0.58 and 0.19, respectively. Abiotic factors, such as soil nutrients and nitrogen-phosphorus content, have a direct effect on the beta component ($P < 0.001$, path coefficient of 0.72). Biotic factors, such as variation in tree height, have a direct effect on the alpha component ($P < 0.001$, path coefficient of 0.46). Abiotic factors have a direct effect on biotic factors ($P < 0.001$, path coefficient of 0.28). Overall, these results demonstrate that multiple factors contribute to intra-specific trait variation in the evergreen broad-leaved secondary forests of Wuchao Mountain in Zhejiang, with both biotic and abiotic factors playing a crucial role.



path coefficients negative $\chi2=5.62$，df=7，p=0.78 positive RMSE=0.00，AIC=33.50

Figure 3 Effect of Biotic and soil factors, alpha components, and beta components on intraspecific trait variation.

Disccusion

3.1 Functional trait components of evergreen broad-leaved secondary forest communities

The variability of plant functional traits reflects the ability of species to adapt to changes in their environment and is closely linked to community composition and ecological processes such as productivity and litter decomposition (Orwin et al., 2010). Our study found varying degrees of differentiation in the alpha and beta components of nine functional traits in the evergreen broad-leaved secondary forest community. This implies that the differences in the extent of variation in each trait or differences in trait combinations reflect the response of each functional trait to environmental change and species coexistence, ultimately leading to the differentiation of species' ecological niches and ecological strategies. However, the degree of response of different traits varies (Yao et al., 2021) and may be attributed to the allometric relationships between different traits, resulting in inconsistent trait stability. The highest degree of differentiation in alpha components was leaf area. This is likely because leaves are the link through which plants convert and utilize energy through photosynthesis, making them most sensitive to habitat changes (Markesteijn et al., 2011).

Further research confirms that some plant functional traits, such as leaf traits and plant nutrient content, exhibit stronger plasticity in local environments and competition (Kunstler et al., 2016; Thomas et al., 2020). Leaf dry matter content and wood density are relatively stable and have a slower response to environmental change, as they are long-term tree growth results that are related to the plant's support, resistance to pest and disease erosion, and resource acquisition abilities (Choat et al., 2012). However, the range of trait changes across species is larger, possibly because of differences in survival strategies formed by different species adapting to different environments. Both evergreen and deciduous tree species are major dominant species in the secondary forest community of Wuchao Mountain (Yao et al., 2022), and different survival strategies affect trait variation. Conservative species may show lower within-species trait variation while displaying absolute trait values (Rixen et al., 2022). For example, evergreen tree species increase their light resource utilization efficiency through low specific leaf area (negative alpha value) and high leaf dry matter content (positive alpha value), while deciduous tree species acquire light resources rapidly during the growing season through high specific leaf area (positive alpha value) and low dry matter content (negative alpha value). Our study also confirms the existence of obvious trait differentiation phenomena, such as specific leaf area, leaf dry matter content, and leaf phosphorus content, in the subtropical evergreen broad-leaved secondary forest community.

According to Yao et al. (2021), the alpha components of 9 functional traits in the secondary evergreen broad-leaved forest community on Wuchao Mountain exhibit a greater range of variation than the beta components. This suggests that the interactions among coexisting species within each sample community have a stronger influence than the effects of environmental differences between communities. The small geographic area of the study, which consisted of 30 randomly located fixed plots within mid-stage forest communities that had recovered from disturbance, maybe the main reason for this observation. Larger trees are more likely to experience competitive exclusion due to their greater demand for habitat resources. Species dispersal limitations and interactions generally occur at small community scales, while environmental filtering is more prevalent at larger community scales. Additionally, the sample plots in the secondary evergreen broad-leaved forest community on Wuchao Mountain exhibit a larger ecological niche width compared to individual species. This may be attributed to the increased environmental heterogeneity within the community, which expands the ecological niche of the species and increases the niche width of the sample plots. These findings have important implications for understanding the interactions and species distribution patterns of the ecosystem in this region.

3.2 Association of functional trait components in evergreen broad-leaved secondary forest communities

Plants' ability to adapt to the heterogeneous biotic and abiotic environments within a community is enhanced by the interactions between their functional trait components. These interactions deepen the connections between species, communities, and ecosystems (Kraft and Ackerly, 2010; Kunstler et al., 2016; Pérez-Girón et al., 2020). Plant functional trait values are determined by the combined effects of alpha and beta values, and species ecological strategies are determined by the multidimensional trait combinations. The interactions between multidimensional trait combinations indicate that species adopt similar ways to adapt to environmental filtering within a community. Each trait independently defines a functional axis in species strategy, and due to the interactions between coexisting species, independent trait axes may differentiate and couple showing high correlations at regional and global scales but may be uncorrelated at local scales (Webb et al., 2002; Cornwell et al., 2006). Studies have found that the correlations between alpha components are stronger than those between beta components, indicating that multiple plant functional traits exhibit high overall convergent adaptability to the same biotic factor as competition. This may be due to the small sampling area, low number of individuals within the plot, small environmental heterogeneity, and higher genetic correlations among adjacent individuals at the local scale (Albert et al., 2010). This proves that biotic factors, such as competition, led to the convergence of functional traits in species adaptation, and natural selection or environmental stress increases trait differentiation at the local scale (Kunstler et al., 2016). The mid-successional evergreen broad-leaved forest in Wuchao Mountain selectively filters out evergreen and deciduous tree species through inter-specific competition. Species adapt to intra-specific or inter-specific competition within the community by adopting similar ways, such as through the plasticity of one or more functional traits (Diaz et al., 2004).

3.3 Factors influencing intraspecific trait variation in evergreen broad-leaved secondary forests

The evolution of species traits is driven by two main factors: limiting similarity and environmental filtering. SEM found that Biotic competition significantly increases trait variation within species in the secondary broad-leaved evergreen forest of Wuchao Mountain. This finding confirms that species interactions and dispersal limitations mainly occur at the small community scale, while environmental filtering occurs at the larger community scale (Thomas et al., 2020). As coexisting species interact more, the deviation of species' alpha traits from the community level increases, indicating stronger differentiation of species' alpha traits and a stronger correlation between species' alpha traits. In a community, species use different combinations of niche differentiation and trait variation to adapt to their environment and reduce competition for resources. Environmental and spatial variables also have a significant impact on the functional trait beta component. Because all plants use similar strategies to utilize resources such as nitrogen, phosphorus, potassium, water, light, and CO_2 in the local environment, species niche differentiation is not very evident when there is limited availability of resources in the habitat. At the regional scale, habitat heterogeneity among different sample sites is large, and individuals belonging to different sample sites may have significantly different genetic structures (Albert et al., 2010). Therefore, environmental filtering reduces within-species variation at the community level, while niche differentiation increases it.

The distribution of plants along environmental gradients is shaped by their functional traits, which also reflect their interactions with coexisting species. Studies have found that trait gradient analysis integrates two different perspectives. Firstly, it emphasizes the role of resource differentiation, interference, and trait variation among coexisting species (referred to as the alpha value) to understand the mechanisms of biodiversity maintenance (Weiher and Keddy, 1995). Secondly, the other emphasizes the impact of environmental heterogeneity on species coexistence by integrating changes along environmental gradients such as soil, climate, and topography (known as beta value) (Wright, 2002). Kooyman et al. (2010) concluded that differences in species traits are essential in determining community stability in similar environmental conditions, indicating that the differences in species traits are an important factor in determining community stability in communities with similar environmental conditions. Intra-specific trait variation can also impact the outcome of species competition, as shown by Flöder et al. (2021) and Kunstler et al. (2016). Habitat filtering plays a crucial role in trait variation, particularly in conditions where environmental gradients differ significantly, such as along latitudinal gradients with marked climate differences. For example, a study on the functional trait differences of plants across North America found that trait differences were strongly correlated with environmental factors, but the impact of species competition intensity on trait variation was small (Šímová et al., 2015).

Conclusion

This study used the trait gradient method to analyze the functional traits of species into alpha (within-community) and beta (between-community) components, revealing trait variation patterns in communities. The basic driving forces behind species coexistence in local communities are the opposing forces of environmental filtering and similarity limitation. We discovered that biotic interactions within plots had a greater impact on trait variation in the evergreen broad-leaved secondary forest community of Wuchao Mountain, while abiotic factors had a relatively weaker influence. In small habitats with limited resources and relatively homogenous conditions, dominant competitive exclusion among species played a significant role in community assembly, with limiting similarity being a key factor. The results of this study will help to understand the essential relationships between species traits, thus providing a better understanding of species coexistence mechanisms and clarifying the instability of evergreen broad-leaved secondary forests during the succession process.

CrediT authorship contribution statement

Liangjin Yao and Bo Jiang conceived the ideas and designed the research. Liangjin Yao, Chuping Wu, Zhigao Wang participated in data collecting. Liangjin Yao analyzed the data and led the writing of the manuscript in close collaboration with Chuping Wu.

All authors commented and approved the final manuscript.

Data availability

The datasets analyzed in the study can be obtained via the corresponding author on reasonable request.

Declaration of competing interest

The authors assert that we have no financial or other non-financial interests that could influence the reported in this paper.

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