Differences in Leaf Functional Trait Responses to Heterogeneous Habitats Between Canopy and Understory Dominant Species in South Subtropical Evergreen Broad-Leaved Forests (Postprint)

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Date: 2021-07-20T00:00:00+00:00

Abstract

Plants can adapt to environmental changes by modifying functional traits; how different plant types adjust their phenotypes to cope with environmental variation has long been a focal research topic in ecology. To investigate the ecological response mechanisms of different growth forms to heterogeneous habitats in lower subtropical forests, this study examined 5 dominant tree species (including 2 canopy species and 3 understory species) across 27 quadrats (20 m × 20 m) at varying elevations and convexities along three mountain slopes within a 20 hm^2 plot of lower subtropical evergreen broad-leaved forest in Dinghushan, Guangdong, measuring the diameter at breast height (DBH) of each individual and 8 leaf functional traits, comprising 4 structural traits (leaf thickness, length-to-width ratio, leaf dry matter content, and specific leaf area) and 4 stoichiometric traits ($ $13C, $ $15N, leaf nitrogen content, and leaf phosphorus content), to conduct a comparative analysis of how dominant tree species of the two growth forms respond to heterogeneous habitats characterized by elevation and convexity from the perspective of leaf functional traits. The results indicated: (1) Each tree species displayed significant correlations between several leaf functional traits and elevation; regarding convexity, only the specific leaf area of Cryptocarya chinensis exhibited a positive correlation with convexity, while the leaf nitrogen content of Blastus cochinchinensis showed a negative correlation with convexity. (2) Traits such as specific leaf area, leaf thickness, and $ $15N demonstrated more universal responses to elevation, whereas leaf length-to-width ratio and leaf dry matter content exhibited lower responsiveness. (3) Significant differences in specific leaf area, leaf dry matter content, and leaf nitrogen content between canopy and understory dominant species were consistently observed across all habitat types; compared to canopy species, understory species possessed relatively lower leaf thickness, leaf dry matter content, and

$ $13C values. Moreover, the responsiveness of leaf functional traits to elevation and convexity differed between canopy and understory species, with understory species exhibiting a greater number of functional traits that varied significantly across different habitat types. In summary, these results demonstrate that dominant tree species from different strata (canopy and understory dominant species) in the lower subtropical evergreen broad-leaved forest of Dinghushan exhibit substantial differences in their degree of response to heterogeneous habitats, manifested as understory species displaying greater phenotypic plasticity in response to environmental variation in heterogeneous habitats, thereby adapting to more diverse environmental conditions. Furthermore, specific leaf area, leaf thickness, and $ $15N represent important and effective traits for indicating how tree species in lower subtropical evergreen broad-leaved forests respond to heterogeneous habitats.

Full Text

Differences in Leaf Functional Trait Responses to Heterogeneous Habitats Between Dominant Canopy and Understory Tree Species in a Lower Subtropical Evergreen Broad-Leaved Forest

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Abstract

Plants can adapt to environmental changes through modifications in functional traits, and how different plant types adjust their phenotypes to cope with environmental heterogeneity has long been a central topic in ecology. To investigate the ecological response mechanisms of different growth forms to heterogeneous habitats in south subtropical forests, we measured eight leaf functional traits in five dominant tree species (two canopy and three understory species) across 27 quadrats (20 m × 20 m) distributed along three mountain ridges with varying elevations and convexities within a 20 hm^2 lower subtropical evergreen broad-leaved forest plot in Dinghu Mountain, Guangdong Province. The measured traits included four structural traits (leaf thickness, length/width ratio, dry matter content, and specific leaf area) and four stoichiometric traits (δ^{13}C, δ^{15}N, leaf nitrogen content, and leaf phosphorus content), along with diameter at breast height (DBH) for each individual. Our objective was to compare and analyze differences in how these two growth forms respond to heterogeneous habitats characterized by elevation and convexity.

The results revealed three key patterns. First, each tree species exhibited several leaf functional traits that were significantly correlated with elevation. Regarding convexity, only the specific leaf area of *Cryptocarya chinensis* showed a positive correlation, while leaf nitrogen content of *Blastus cochinchinensis* displayed a negative correlation. Second, specific leaf area, leaf thickness, and δ^{15}N were more responsive to elevation, whereas leaf length/width ratio and leaf dry matter content showed weaker responses. Third, significant differences in specific leaf area, leaf dry matter content, and leaf nitrogen content between canopy and understory species were observed across all habitat types. Compared with canopy species, understory species had relatively lower leaf thickness, leaf dry matter content, and δ^{13}C values. Moreover, canopy and understory species differed in their responsiveness to elevation and convexity, with understory species showing more functional traits that varied significantly across different habitat types.

These findings demonstrate that dominant tree species from different vertical strata (canopy vs. understory) in the Dinghu Mountain lower subtropical evergreen broad-leaved forest exhibit substantially different degrees of response to heterogeneous habitats. Understory species demonstrate greater phenotypic plasticity in response to environmental variation, enabling them to adapt to more diverse conditions. Additionally, specific leaf area, leaf thickness, and δ^{15}N emerge as important and effective indicators of how tree species in lower subtropical evergreen broad-leaved forests respond to heterogeneous habitats.

Keywords: functional traits, canopy species, understory species, elevation gradient, topographical factors

Introduction

Ecosystems worldwide are experiencing varying degrees of disturbance, leading to continuous changes in plant population dynamics and distribution ranges (Parmesan, 2006; Zhou et al., 2013). Functional traits can reflect species' adaptive processes to environmental conditions and characterize physiological and ecological information from different perspectives. Therefore, understanding the physiological and ecological mechanisms underlying plant-environment relationships requires integrating plant functional traits into research frameworks (Chapin, 2003; Wright et al., 2004; McGill et al., 2006). However, consistent patterns regarding the plasticity and spatiotemporal variation of functional traits have yet to emerge, leaving plant adaptation mechanisms under climate and environmental change in need of further exploration (Anderson & Gezon, 2015). A typical approach to address this knowledge gap involves using heterogeneous mountain habitats to investigate how plant traits respond and adapt to different habitat types.

Elevation gradients influence multiple environmental factors including water, air, temperature, and soil conditions. Temperature, atmospheric pressure, and carbon dioxide concentrations all decrease with increasing elevation (Kao & Chang, 2001), while both elevation and convexity can increase light intensity (Schindler, 2003; Enoki & Abe, 2004). Combined with weathering and soil leaching processes, these topographic factors also affect soil moisture and nutrient availability (Poorter et al., 2008; McEwan et al., 2011). Previous studies have documented various responsive changes in functional traits at both population and community levels along habitat gradients in heterogeneous environments (Korner et al., 1988; Tsujino et al., 2006; Hernandez-Calderon et al., 2014). Consequently, research integrating functional traits with elevation and convexity can provide analytical samples for predicting and extrapolating plant adaptation processes under environmental change (Korner, 2007). As dynamic vegetation models receive increasing attention, incorporating plant functional trait data can enhance predictions of biosphere responses and feedbacks to climate change, making the exploration of functional trait response mechanisms critically important (Sakschewski et al., 2015).

In recent years, numerous studies have examined variation in plant functional traits across different elevations and convexities to explore underlying response mechanisms (Rasmann et al., 2014; Read et al., 2014; Zhou et al., 2016; Midolo et al., 2019). These studies have primarily focused on leaf structural and nutrient functional traits, analyzing plant phenotypic adaptation strategies at community, population, and individual levels along convexity and elevation gradients. When environments change temporally and spatially, species' traits and growth strategies also shift accordingly (Moran, 1992; Alpert & Simms, 2002; Baythavong & Stanton, 2010). Research indicates that different types of functional traits show both shared and distinct response patterns to elevation and convexity. For example, specific leaf area consistently shows significant negative correlations with elevation (Bao, 2009; Baythavong & Stanton, 2010; Li et al., 2012; Torres-Dowdall et al., 2012), while conclusions regarding leaf stoichiometric traits vary across studies (Chen et al., 2021). Plants growing in concave habitats typically exhibit larger specific leaf area and adopt fast-growth strategies, while plants across different convexity positions show distinct water use efficiency differences (Garten & Taylor, 1992). However, few studies have explicitly stratified canopy and understory species to compare and analyze differences in their trait responses along environmental gradients.

Strata (or layers) refer to species assemblages distributed along vertical gradients in a community, where species share certain physiological and ecological similarities and experience relatively consistent environmental conditions within the stratum (Gleason, 1936). Canopy species directly interact with external environments, experiencing stronger precipitation wash, wind pressure, and light radiation (Akihiro et al., 2017), and are more susceptible to drought stress due to their longer water transport pathways (Zhou et al., 2013). Compared with canopy species, understory species receive less photosynthetically active radiation and thus require stronger light capture capabilities (Weerasinghe et al., 2014). Consequently, different growth forms likely exhibit differential responsiveness to heterogeneous environments. Particularly under anthropogenic disturbance and climate change, the canopy layer faces greater stress and survival pressure (Ozanne et al., 2003), with some forest ecosystems reportedly undergoing retrogressive succession (Zhou et al., 2013; Ibanez et al., 2017). Therefore, comparative studies on environmental response patterns of tree species from different strata are essential for revealing ecological adaptation strategies across vertical layers in forest communities.

To investigate the response and adaptation strategies of canopy and understory species to heterogeneous environments, we selected five dominant tree species from a 20 hm^2 plot in the lower subtropical evergreen broad-leaved forest in Dinghu Mountain, Guangdong Province (hereafter referred to as the Dinghu Mountain plot), including two canopy species and three understory species. We measured DBH of all individuals with DBH $\geq$ 1 cm, along with eight leaf functional traits: four morphological-structural traits (leaf thickness, length/width ratio, dry matter content, and specific leaf area) and four stoichiometric traits (δ^{13}C, δ^{15}N, nitrogen content, and phosphorus content). This approach allowed us to address three scientific questions: (1) Do plant functional traits respond to elevation and convexity factors? (2) If so, which functional traits more generally respond to elevation and convexity? (3) Do canopy and understory species differ in their adaptation to elevation and convexity?

1.1 Study Area Overview

The Dinghu Mountain plot was established in 2005 within the Dinghu Mountain National Nature Reserve in Guangdong Province (23°09 21 -23°11 30 N, 112°30 39 -112°33 41 E). The region has a mean annual temperature of 20.9°C, mean annual precipitation of 1,927 mm, and mean annual relative humidity of 85% (Ye et al., 2008). The plot features complex topography with three ridges and four valleys, with elevation ranging from 230 to 470 m, substantial terrain undulation, and slope gradients of 30°–50° (Wang et al., 2012). The forest has a natural growth history of over 400 years. Since 2005, community surveys have been conducted every five years, recording species names and coordinates of individuals with DBH $\geq$ 1 cm, and measuring DBH, crown width, and tree height (Shen et al., 2014).

1.2 Sample Plot Setup and Species Selection

Within the 500 quadrats of 20 m × 20 m in the Dinghu Mountain plot, we selected 27 quadrats representing three elevation levels and three convexity types based on relative elevation and convexity variation. Specifically, along three mountain bodies, we chose nine quadrats for each of three elevation levels (low, medium, and high; range: 308.4–413.4 m, maximum relative elevation difference: 105 m) and three convexity types (ridge, slope, and valley; -6.16 to 6.71 m). For each habitat type across the three mountain bodies, we selected the three quadrats with the highest Jaccard community similarity index (Zhou et al., 2016).

We followed two principles when selecting dominant canopy and understory species. First, selected species had to rank among the most abundant canopy and understory species in the 27 quadrats. Second, because comparative studies across different habitats were required, selected species had to be present with adequate abundance in all six topographic types. Based on these criteria, we identified five dominant species: canopy species *Castanopsis chinensis* and *Cryptocarya chinensis*, and understory species *Aidia canthioides*, *Cryptocarya concinna*, and *Blastus cochinchinensis*. Overall, the distribution of these dominant species was relatively uniform and consistent among the three quadrats for each habitat type .

1.3 Environmental Factor Measurement

We used elevation and convexity as environmental factors. Elevation for each quadrat was determined by averaging elevation measurements at the four corners using an electronic total station (Legendre et al., 2009). Additionally, we calculated the elevation at each tree’ s coordinate position using Kriging interpolation and derived convexity from elevation data obtained via total station measurements, classifying plots as ridge, slope, or valley. Detailed methods for convexity measurement are described in Zhou et al. (2016).

1.4 Functional Trait Measurement

We measured leaf functional traits of the five dominant species in the 27 quadrats [TABLE:1, TABLE:2]. In each quadrat, for species with more than 10 individuals, we randomly selected 10 individuals for DBH and leaf functional trait measurements; for species with fewer than 10 individuals, we measured all individuals. We used a carbon fiber high-branch pruner (maximum reach: 14 m) to cut outer branches from the middle canopy, then collected mature, intact leaves from these branches for analysis. A total of 1,058 individual trees were sampled, with at least three branches and six fully expanded, mature, sun-exposed leaves collected per plant. We measured leaf area (LA, cm^2), leaf length, and width using a leaf area meter; leaf thickness (mm) using a spiral micrometer; and fresh leaf weight before oven-drying at 70°C for at least 72 hours to obtain dry weight. Specific leaf area (SLA, cm^2 g^{-1}) was calculated as the ratio of leaf area to dry weight, and leaf dry matter content (LDMC) as the ratio of fresh to dry weight. Detailed methods are described in Zhou et al. (2016). Leaf nitrogen content (N) was determined using an elemental analyzer, leaf phosphorus content (P) by molybdenum resistance colorimetry (Shen et al., 2014), and δ^{13}C and δ^{15}N by mass spectrometry analysis of isotope ratios.

1.5 Data Analysis

All statistical analyses were performed in Python (version 3.6.11) (Sanner, 1999), with statistical significance set at $P < 0.05$. We used Pearson correlation from the SciPy package (Swami & Jain, 2013) to analyze linear relationships between elevation/convexity and traits for each species and for both growth forms combined. We employed the Kruskal-Wallis test from SciPy (Kruskal & Wallis, 1952) to detect statistical differences among groups, with higher Z-values indicating greater between-group differences. This method does not require homogeneity of variance and can accommodate unequal group sizes.

We conducted Pearson correlation analyses between each individual' s functional traits and local elevation/convexity, and used Kruskal-Wallis tests to analyze intraspecific variation in functional traits across the three convexity types and three elevation gradients for each species. We repeated these analyses after combining the two canopy species and three understory species as respective groups. Finally, we used Kruskal-Wallis tests to examine whether functional traits differed significantly between canopy and understory species across the six habitat types. Notably, because abundance and sampling numbers differed substantially between canopy and understory dominant species, we used the Kruskal-Wallis method, which allows for unequal sample sizes between groups.

2.1 Intraspecific Variation in Leaf Functional Traits and Responses to Elevation and Convexity in Dominant Canopy and Understory Species

Along elevation gradients, canopy species showed several significant relationships: δ^{15}N in *Castanopsis chinensis* increased significantly with elevation; *Cryptocarya chinensis* exhibited negative correlations between specific leaf area (SLA) and leaf phosphorus content (P) with elevation, and a positive correlation between leaf dry matter content (LDMC) and elevation. Among understory species, leaf thickness (LT) decreased with elevation in all three species, while δ^{15}N increased with elevation. SLA decreased with elevation in *Aidia canthioides* and *Cryptocarya concinna*. Additionally, leaf nitrogen content (N) showed opposite relationships with elevation in *Aidia canthioides* (positive) and *Blastus cochinchinensis* (negative). Regarding convexity, only SLA in the canopy species *Cryptocarya chinensis* showed a positive correlation, while N in the understory species *Blastus cochinchinensis* showed a negative correlation. No other significant correlations were detected .

2.2 Differences in Within-Stratum Variation of Leaf Functional Traits Between Canopy and Understory Species in Response to Elevation

When analyzing both growth forms combined, understory species showed more functional traits significantly correlated with elevation compared to canopy species. Understory species exhibited significant negative correlations between elevation and DBH, LT, LDMC, N , and δ^{13}C, and positive correlations between elevation and SLA and P . In contrast, canopy species only showed significant negative correlations between elevation and DBH and N , and a positive correlation between δ^{13}C and elevation. Variance analysis indicated that understory species' DBH, LT, SLA, LDMC, and P differed significantly across convexity habitats. Understory species also showed more traits with significant differences across elevation and convexity categories, including DBH, LT, SLA, LDMC, and P , whereas canopy species only showed significant differences in N across convexity habitats .

2.3 Differences in Leaf Functional Traits Between Canopy and Understory Species Across Different Habitats

Canopy and understory species differed significantly in DBH, SLA, LDMC, and N across all three elevation levels and three convexity types. Leaf length/width ratio (except in valley habitats) and δ^{13}C (except at high elevation) showed significant differences between canopy and understory species across environmental gradients. Leaf thickness, leaf phosphorus content, and δ^{15}N differed only in specific topographies such as low elevation. In terms of trait values, canopy species generally had higher DBH, LT, LDMC, leaf length/width ratio, N , P , δ^{13}C, and δ^{15}N, but lower SLA compared to understory species .

3.1 Leaf Functional Trait Responses to Elevation and Convexity

Our study found that specific leaf area (SLA) and leaf thickness (LT) in multiple dominant tree species decreased with increasing elevation, consistent with previous research (Bao, 2009; Li et al., 2012). Elevation is closely related to soil water content and nutrients, with higher elevations experiencing stronger light intensity. This correlation between elevation and leaf structural traits was detectable even across small elevation gradients. Liu et al. (2017) found that despite only a 70 m elevation difference among their plots, specific leaf area in different growth forms showed highly significant negative correlations with elevation due to differential soil moisture distribution. As relative elevation increases, soil moisture and nutrient content gradually decrease, leading to reduced SLA and increased LT. This allows leaves to invest more resources in secondary metabolites and thicker cell walls to prevent water loss and adapt to environmental changes. Pfennigwerth et al. (2017) reported similar patterns, showing that SLA and LT are sensitive to environmental changes and exhibit substantial variation with temperature, precipitation, and light intensity.

Plant δ^{15}N reflects environmental characteristics such as high temperature and drought and is closely related to nitrogen utilization, absorption, and water use efficiency (McLauchlan et al., 2006). Plants typically have higher δ^{15}N in hot and dry climates (Amundson et al., 2003; Craine et al., 2009). δ^{15}N in *Castanopsis chinensis*, *Aidia canthioides*, *Cryptocarya concinna*, and *Blastus cochinchinensis* all showed significant correlations with elevation, similar to conclusions by Anderson & Gezon (2015) regarding altitudinal differences in δ^{15}N in high-elevation mountainous regions. These patterns likely result from reduced soil nutrient utilization and intensified drought stress with increasing elevation.

Regarding stoichiometric traits, only leaf phosphorus content (P) in *Cryptocarya chinensis* showed a significant negative correlation with elevation, while leaf nitrogen content (N) in *Aidia canthioides* and *Cryptocarya concinna* showed opposite trends with elevation, and N and P in other species did not change significantly with elevation. Previous studies have reported inconsistent relationships between stoichiometric traits and elevation. Van de Weg et al. (2009) found significant negative correlations between N and elevation, while other studies found no significant relationships (Fisher et al., 2013), likely indicating that different species have distinct response mechanisms to nitrogen and phosphorus. For instance, herbaceous plants tend to show higher responsiveness in N compared to woody plants, indicating stronger resource acquisition capacity (Midolo et al., 2019).

Our study found significant positive correlations between leaf thickness and specific leaf area with relative elevation, and significant negative correlations with δ^{15}N. These stoichiometric and morphological-structural traits mutually support the hypothesis that heterogeneous distribution of functional traits along elevation gradients is likely associated with water and nutrient availability. These similar trends also suggest that different species may share comparable response patterns to environmental heterogeneity (Poorter et al., 2009). However, leaf nitrogen and phosphorus contents showed no consistent response patterns to elevation. Furthermore, only specific leaf area in *Cryptocarya chinensis* and leaf nitrogen content in *Blastus cochinchinensis* showed significant relationships with convexity, suggesting that convexity may more broadly have non-linear relationships with leaf functional traits.

3.2 Differences in Environmental Adaptation Strategies Between Canopy and Understory Species

The 27 sampled quadrats in this study encompassed strong habitat heterogeneity, particularly in soil moisture and nutrients that varied substantially with elevation and convexity (Zhou et al., 2016). DBH, LT, SLA, and leaf dry matter content (LDMC) varied significantly across environmental gradients and effectively indicated phenotypic response processes in each stratum. Canopy and understory species differed significantly in their responsiveness to elevation and convexity. Understory species showed higher responsiveness to elevation gradients and greater intraspecific variation across different convexity habitats compared to canopy species. This likely occurs because understory species experience higher resource heterogeneity, particularly in light availability, than canopy species, necessitating stronger phenotypic plasticity to adjust their adaptation strategies in response to environmental changes. Read et al. (2014) found in a meta-analysis that different life forms have distinct response mechanisms to environmental change, with angiosperm SLA decreasing with elevation while conifers showed no significant altitudinal changes. Our study extends this finding by demonstrating that understory species are more sensitive to environmental changes than canopy species.

Shade-tolerant leaves typically have lower length/width ratios to effectively capture light flecks (Tsukaya, 2006). In our study, canopy species had higher leaf length/width ratios than understory species, indicating that understory species possess relatively higher shade tolerance. This likely reflects adaptation to the understory light environment, where photosynthetically active radiation is partially intercepted by the canopy layer. Under these conditions, understory species have developed traits that facilitate more effective light capture for photosynthesis. Meanwhile, canopy species occupy the outer layer of the forest, directly interacting with external environmental conditions (Akihiro et al., 2017). The forest canopy buffers precipitation wash, reduces light radiation by absorbing and reflecting direct sunlight, and maintains humidity within the canopy (Anhuf & Rollenbeck, 2001), creating microclimatic differences between understory and external canopy environments. Canopy species have higher LDMC and lower SLA, while understory species in low-light, high-humidity environments tend to enhance photosynthetic efficiency. Kenzo et al. (2015) found that tropical rainforest canopy species had lower specific leaf area and higher leaf nitrogen content and δ^{13}C. Weerasinghe et al. (2014) and Ichie et al. (2016) also reported lower specific leaf area in upper canopy species of tropical rainforests. These findings align with our results for lower subtropical evergreen broad-leaved forests. Furthermore, regarding plant hydraulic coordination strategies, canopy species enhance drought tolerance and stress resistance by increasing expression of traits related to water use efficiency, such as δ^{13}C and δ^{15}N, compared to understory species. Thus, under the combined influences of light, internal/external environmental differences, and hydraulic factors, the two strata exhibit differences in leaf functional traits including SLA, LDMC, and δ^{13}C across different habitat types, reflecting distinct adaptive strategies to different microenvironments.

Zhou et al. (2013) reported that canopy species have higher hydraulic transport costs and require greater hydraulic transport safety to avoid xylem embolism. In recent years, the Dinghu Mountain region has experienced increasingly uneven seasonal precipitation distribution, with precipitation becoming more concentrated while total annual precipitation remains unchanged—resulting in drier dry seasons and wetter wet seasons, along with declining water content in deep soil layers that intensifies drought stress (Zhou et al., 2011, 2013). This trend exposes canopy species to greater stress risks. Although our study found that functional traits of multiple dominant species showed similar response patterns to nutrient and water differences along elevation gradients, understory species exhibited more significant trait responses to different elevation and convexity types, demonstrating stronger phenotypic plasticity in response to environmental change. Under such conditions, more plastic species may have stronger adaptive capacity to maintain population sizes during environmental changes, while less plastic species may experience population decline or even extinction risk. Zhou et al. (2013) found that the Dinghu Mountain forest community has shown an increasing trend toward domination by smaller individuals and more species of short-statured trees and shrubs over recent decades. The differences in phenotypic plasticity between canopy and understory species in heterogeneous habitats, combined with environmental differences between canopy and non-canopy layers, may help explain this phenomenon.

In summary, this study compared and analyzed response strategies of dominant canopy and understory species to local heterogeneous habitats in a lower subtropical evergreen broad-leaved forest from the perspective of leaf functional traits. Our results demonstrate that dominant species from different vertical strata exhibit substantial differences in their responsiveness to heterogeneous habitats, with understory species showing more functional traits that differ significantly across habitat types. Consequently, understory species employ stronger phenotypic plasticity to adapt to more diverse environmental conditions in heterogeneous habitats. Furthermore, specific leaf area, leaf thickness, and δ^{15}N are functional traits that more generally respond to elevation factors and thus serve as important and effective indicators of how tree species in lower subtropical evergreen broad-leaved forests respond to environmental heterogeneity.

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