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Distribution Pattern of Trait-Based Community Assembly for *Cyclobalanopsis Glauca* in the Guilin Karst Mountainous Areas, China

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Abstract

Cyclobalanopsis glauca is one of the most dominant species in the late succession stage of plant communities in the Guilin karst mountainous areas of China. In order to explore its role in community assembly and adaptation strategies, we quantified three continuous traits (LA, SLA and WD) for 52 woody species and documented community composition for 20 plots across different habitat conditions. We performed a trait-gradient analysis to partition species trait values between alpha and beta components within and between communities. Alpha trait components consistently varied more widely than beta components, which suggests that much of the trait variation between species was associated with different functional strategies within a shared environment. The different correlation structures for alpha and beta components reflects community assembly processes at different scales. The alpha components were largely uncorrelated with the exception of SLA and WD, while the beta components showed significant correlations along the environmental gradient. There is a significant positive correlation between LA and SLA and significant negative correlations between both LA and WD as well as between SLA and WD. These results demonstrate that slow-growing species with high resource-use efficiency gradually became the dominant species in the late successional stage for *Cyclobalanopsis glauca* forest and co-occurring species in the same community employ different trait assemblies.

Keywords

alpha and beta components, community assembly, functional traits, *Cyclobalanopsis glauca* forest, trait correlation, trait-gradient analysis

Plant functional traits, which refer to any measurable property at the individual level that affect overall plant fitness directly or indirectly (Lavorel et al., 1997; Violle et al., 2007), are increasingly used to understand and predict how species properties and composition change along multi-dimensional environmental gradients. The measurement of functional traits may uncover essential aspects of species' ecophysiology, morphology and life-history strategy, as well as offer a pivotal link between fundamental biological processes and community dynamics (McGill et al., 2006; Westoby & Wright, 2006). Furthermore, because traits offer a common, taxon-independent method for species comparisons, trait-based approaches have the potential to reveal

generalizable, synthetic and predictive relationships in response to increasing environmental change (Harley, 2011; Harmon et al., 2009; Tylianakis et al., 2008).

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One of the most ambitious goals of the trait-based approach is to understand how traits mediate ecological strategies, community assembly and functional diversity and how to unify these contrasting viewpoints (e.g., Suding et al., 2005). Our objective is to use this quantitative, trait-based analysis to integrate two opposing community assembly processes operating on functional trait variation along an environmental gradient.

A variety of morphological traits that covary in plants can be used to infer important strategy dimensions (Enquist et al., 2007; Westoby et al., 2002; Wright et al., 2004). Leaf area (LA), as an independent dimension of trait variation, is mainly linked to the size of the contact area between leaves and the environment; this measure affects the balance between gas and energy exchange, with small and thick leaves generally observed in the exposed region of canopy. Specific leaf area (SLA) refers to the amount of light-capturing area per unit of biomass invested in leaf tissue and is a good predictor of plant performance in tropical forests and subtropical forests. Plants with high SLA tend to have higher growth rate, lower nutrient utilization efficiency, less “defensive” investment, and shorter leaf life (Wright et al., 2004, 2005). Wood density (WD) is also regarded as an important component of plant life history strategies (Poorter, 2009; Wright et al., 2004) and refers to the plant’s investment in biomass per unit of wood volume. Plants with denser wood have more carbon and energy content per unit volume as well as lower growth rates compared to lighter woods (King et al., 2005, 2006; Poorter & Rozendaal, 2008). Wood density also determines hydraulic conductivity and mechanical strength (Zanne et al., 2010). These traits were chosen in this study because of their potential to influence the structure, dynamics and assembly of communities (Ackerly et al., 2002; Cornwell et al., 2006).

Ecologists have long been interested in the role of functional traits in structuring communities and in sorting species along environmental gradients (Ackerly, 2003, 2004; Clark et al., 1999; Cowles, 1899; Grime, 2006; Lavorel & Garnier, 2002; McGill et al., 2006; Mouillot et al., 2007; Phillips et al., 2003; Schimper, 1898; Westoby & Wright, 2006). Traits reflect the combination of ecological and evolutionary processes of community assembly (Cavender-Bares et al., 2009). This study uses trait gradient analysis (TGA), an improved approach to the question of how to partition each species trait means (within-site (alpha) and between-site (beta) components) and how these correlations may be structured among traits at different scales. The alpha trait value is a measure of how the traits of each species differ from those of co-occurring taxa. The beta trait value, on the other hand, is a species’ position along a gradient and it has been proposed as a measure of niche position. Habitat processes cause beta values to

converge in ecological strategy among species that share a site, whereas species coexistence through limiting similarity leads to alpha values diverging to alleviate competition for finite resources within a site. The trait correlation arises because different traits need to be coordinated for functional effectiveness at different scales; this is dependent on the extent and strength of trait correlations in relation to both environmental gradients and interactions between co-occurring species. Exploring the key roles in these relationships may help us better understand the ecological strategies as well as the contribution of trait variation to patterns of community assembly under different environmental conditions.

Cyclobalanopsis glauca species found in the Guilin karst mountain region of China were chosen for this study because they are dominant evergreen broad-leaved tree species with strong adaptability in the climax community of karst ecosystems. Furthermore, karst topography exhibits a special landscape (the dissolution of one or more layers of soluble bedrock), which results in alluvial terraces, shallow soil and mogotes with low anti-interference ability. These fragile habitats contain species with extremely limited growth and diversity. To our knowledge, few studies have included trait data for all individuals and species found in the climax community in karst geology of *Cyclobalanopsis glauca* forests for the purpose of exploring the role of trait variation in community assembly. Most of the evidence to date has been gathered using the species diversity found in tropical ecosystems.

In this paper, we measured three functional traits (LA, SLA and WD) for 3459 individuals (dbh \geq 1 cm) spanning 52 species in the *Cyclobalanopsis glauca* forest. First, we extend the use of the TGA and explicitly compare patterns of alpha and beta trait variation within and between communities for three traits. Then we discussed how correlation structures among these three traits at discrete spatial scales and the presence of habitat filtering may result in strong correlations between the beta components of trait variation and weak correlations between alpha trait values for pairwise trait combinations. Identifying how the distribution of trait variation may influence processes of community assembly is an important question for advancing ecological theory.

Material and Methods

Study Area

The study site is located in the Guilin karst mountainous area (18°53′–19°20′N, 108°58′–109°53′E) in the Guangxi Zhuang Autonomous Region, China. Karst topography is a special landscape characterized by the dissolution of one or more layers of soluble bedrock in soil substrate.

The soil, mainly composed of black and yellow lime soil, has a thin soil layer and exposed carbonate rocks at the floor surface of mountain areas. The climate of this area is sub-tropical with monsoons and abundant rainfall concentrated in the growing season. The annual average temperature is 19°C with the warmest days occurring in August and the coldest days occurring in January when the average temperature is 8°C followed by a frost-free period of 309 days (the China Meteorological Data Service Center; <http://data.cma.cn>). Due to these heterogeneous conditions, tree species richness in this area is limited. The representative dominant species are *Cyclobalanopsis glauca*, *Alchornea trewioides*, *Alchornea davidii*, *Pittosporum planilobum*, *Radermachera sinica*, *Cyclobalanopsis glauca*, *Fordia cauliflora*, *Celtis sinensis*, *Mallotus philippensis*, *Elaeagnus pungens*.

Field Sampling

Field surveys were carried out from July to September 2017 and were done randomly within the woody plant *Cyclobalanopsis glauca* dominated areas. We selected four sampling locations: the BeiTou village site (BT, 24°44'42.93"N, 110°25'19.87"E), the ZhangJia village site (ZJ, 25°18'19.43"N, 110°15'49.34"E), the YanPo mountainous site (YP, 25°19'10.08"N, 110°15'19.06"E), and the BaiSha town site (BS, 24°49'52.99"N, 110°22'43.74"E). A total of twenty 20 m × 20 m plots were established in BT (7 plots), ZJ (3 plots), YP (6 plots) and BS (4 plots). In this study, we included all of the woody plants with a diameter at breast height (dbh) ≥ 1 cm and the height of each individual plant was measured from the base to the highest point within each plot. We also obtained information on altitude, topographic position and field observations at a scale of 20 m × 20 m using the JRBP Geographic Information System (GIS). The nomenclature of species follows Flora of China (English edition; <http://www.efloras.org>) and expert identification. Site environmental conditions and species richness in BT, ZJ, YP and BS are listed in Table 1.

Measurement of Environmental Factors

At each 20 m × 20 m plot location, soil samples were collected from five points, including each of the four corners and the center of each plot. A core of the top 20 cm of soil was taken at each point. Soil samples were air-dried, then sieved (2 mm) to remove bulky organic material. Soil water content (SWC, %) was calculated by subtracting the dry weight from the water saturated weight of each sample. After taking this moisture value, the five samples were thoroughly mixed prior to analyses in order to represent the soil properties of each

20 m × 20 m plot. The analyses of soil properties were determined using methods that have been described in soil agricultural and chemical analysis (Bao, 2008). Available phosphorus (AP, mg·kg⁻¹) was measured using the molybdenum blue colorimetric method after samples had been extracted with 0.5 M Na₂CO₃. Total phosphorus (TP, g·kg⁻¹) was analyzed by acid digestion with an H₂SO₄+HClO₄ solution. Total potassium (TK, g·kg⁻¹) was digested by the HF-HClO₄-HNO₃ acid mixture and determined by the flame photometric method. Available potassium (AK, g·kg⁻¹) was shaken for 30 min with 1 M ammonium acetate solution (1:10 w/v) and then analyzed by flame photometry, and soil organic matter (SOM, g·kg⁻¹) was tested by using the dichromate oxidation method.

Trait Measurement

All woody plants (excluding vines) with a dbh ≥ 1 cm were sampled to measure functional traits. For each individual plant within the plots, three functional traits were measured. For each individual, we collected five well-developed and sun-exposed leaves. Leaf area (LA; cm²) was measured with a Li-Cor 3100 leaf area meter (Li-Cor, Lincoln, Neb) with leaves dried for 48 h at 65°C to determine dry mass. Specific leaf area (SLA; cm²·g⁻¹) for broadleaved species was calculated as leaf area divided by dry mass. To obtain species' wood density (WD; g·cm⁻³), we sampled branches (1 cm ≤ diameter ≤ 2 cm) from one to ten individuals across the species in each plot. We removed the pith, phloem, and bark, measured fresh volume by water displacement and determined dry mass after drying for 72 h at 70°C (Cornwell et al., 2006). We also chose ten species of hardwood and corkwood from locations near our study site and collected branch samples and measured the stem core of ten individuals from each species (Haglof Increment Borer, Sweden). We found that the core density linearly related to the branch density for hardwood ($\rho_{\text{core}} = 1.054\rho_{\text{branch}}$, $R^2 = 0.95$, $P < 0.0001$) and for corkwood ($\rho_{\text{core}} = 1.235\rho_{\text{branch}}$, $R^2 = 0.93$, $P < 0.0001$).

Statistical Analysis

Using the data we collected, we created a dataset for trees that included the name, abundance and a measure of each of the three trait values (LA, SLA and WD) for species sampled at each of our twenty plots. Prior to statistical analyses, data for LA and SLA functional trait were log₁₀ transformed to reduce skew. Then, using trait-gradient analysis to decompose species trait values at two different ecological scales: alpha (within community) and beta (between community) components. The beta component refers to a measure of a

Table 1. Site Conditions and Species Richness in 20 Plots for *Cyclobalanopsis glauca* Forest of the Guilin Karst Mountainous Areas, China.

Site	Sample No	Altitude (m)	Species richness	Rock exposed rate/%	Soil environmental factors					
					SWC (%)	SOM (g·kg ⁻¹)	TP (g·kg ⁻¹)	TK (g·kg ⁻¹)	AP (mg·kg ⁻¹)	AK (mg·kg ⁻¹)
BT	1	173	26	56	10.97	49.33	0.64	6.99	1.90	154.71
BT	2	188	29	50	9.84	75.77	0.57	4.88	1.77	195.07
BT	3	187	28	42	9.70	74.81	0.64	3.83	1.64	191.72
BT	4	198	26	42	12.77	77.80	0.76	2.34	2.47	147.94
BT	5	198	28	36	12.48	73.29	0.58	2.89	3.17	196.14
BT	6	198	24	48	14.33	72.48	0.67	4.11	2.46	166.95
BT	7	208	24	53	18.25	93.58	0.87	1.14	6.13	122.86
ZJ	8	185	14	56	21.39	54.35	0.43	4.62	16.12	130.51
ZJ	9	179	15	72	21.45	65.00	0.44	3.19	17.34	174.90
ZJ	10	193	13	65	19.73	58.15	0.49	3.63	13.84	161.06
YP	11	234	10	51	32.85	196.49	1.35	7.04	7.27	421.70
YP	12	237	17	54	21.66	68.29	0.63	5.81	0.71	196.85
YP	13	237	13	76	21.73	58.10	0.49	3.98	11.31	177.60
YP	14	240	11	67	24.02	69.18	0.39	4.66	0.61	180.18
YP	15	254	15	60	19.83	59.72	0.26	4.17	0.59	155.27
YP	16	268	13	58	33.50	71.81	0.38	4.55	0.36	211.80
BS	17	257	19	50	27.17	62.34	1.06	1.73	25.49	128.53
BS	18	241	19	60	34.03	72.97	1.28	1.25	20.79	107.53
BS	19	244	17	45	22.18	50.78	1.03	1.20	11.04	98.64
BS	20	240	19	56	24.46	41.19	0.79	1.42	15.08	108.95

Notice: BT, BeiTou village; ZJ, Zhangjia village; YP, Yanpo mountain; BS, Baisha town; SWC, soil water content; SOM, soil organic matter; TP, total phosphorus; TK, total potassium; AP, available phosphorus; AK, available potassium.

species position based on average trait values for the species found in plots along a gradient, forming the x-axis of Figure 1 (the ‘trait-gradient’ of TGA). Also, it has been proposed as a measure of niche position. While, the alpha components refer to the difference between a species trait value and its beta value, (i.e. a measure of how the traits of each species differ from those of co-occurring taxa). These analyses can be expressed using the following four equations (Ackerly & Cornwell, 2007):

$$p_j = \frac{\sum_{i=1}^s a_{ij} \times t_{ij}}{\sum_{i=1}^s a_{ij}} \quad (1)$$

$$t_j = \frac{\sum_{j=1}^n a_{ij} \times t_{ij}}{\sum_{j=1}^n a_{ij}} \quad (2)$$

$$\beta_i = \frac{\sum_{j=1}^n a_{ij} \times p_j}{\sum_{j=1}^n a_{ij}} \quad (3)$$

$$\alpha_i = t_i - \beta_i \quad (4)$$

In the equations, P_j is abundance-weighted plot mean trait values (i.e. the mean of trait values weighted by the relative abundance of each species in the plot); t_i is species mean trait values; a_{ij} is the abundance or weighed for species i in plot j ; t_{ij} is species i trait value in plot j ; s is the total species found within the plots; and finally, n is the total number of plots in the study.

In order to investigate the correlation between functional traits at comparable scales (the plot mean, species mean, alpha and beta levels), we calculated correlation coefficients (r) using Pearson product-moment method for each pairwise combination of the three traits. We then performed a Mantel test in the “vegan” package based on the matrix of species composition dissimilarity values and the matrix of environmental factors distances among the three field samples including 20 plots. Finally, we compared site mean trait values for species with 6 soil environmental factors. This step allowed us to arrange sites in relation to underlying environmental gradients and indicate whether trait gradients for species are aligned with particular abiotic factors (Appendix S1 of Supporting Information). All analyses were carried out in R version 3.3 (R Development Core Team, 2015) and were considered significant at the 0.05 a-level.

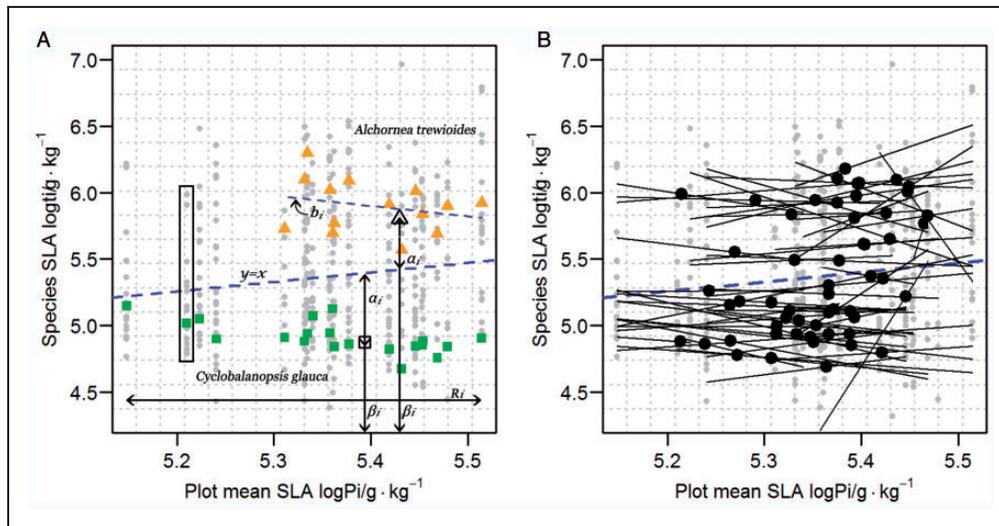


Figure 1. A: Scatterplot of species trait values (t_{ij}) vs. abundance-weighted plot mean trait values (P_j) for log₁₀ SLA ($\text{cm}^2 \cdot \text{g}^{-1}$) in *Cyclobalanopsis glauca* forest vegetation of Guilin karst mountainous areas. B: Distribution of trait means and regression lines for all 52 woody plant species in study. Value for two species are highlighted for illustration: *Cyclobalanopsis glauca* (green square) and *Alchornea trewioides* (yellow triangles). For each species, the large open square or triangle shows the mean position of occupied plots in which it occurs. The y-axis value for open shapes provides the mean trait value while the x-axis value provides the Beta component for the species along the trait gradient. The range of occupied plots on the x-axis is the species niche breadth (R_i), and it expresses the degree of intraspecific variation relative to the overall shift in trait values at the plot level. Alpha components reflect the deviation of each species from co-occurring taxa with regard to the trait, and α_i means the distance from the $Y=X$ line ($Y=X$ line, slope 1 and intercept 0 by definition). Regression line shows abundance-weighted least squares regression of species trait values relative to plot mean trait values, with slope β_i . For log SLA, t_{ij} varied from 2.65 to 6.96 (range = 4.31) across the entire study, while P_j ranged from 5.14 to 5.51 (range = 0.37). Each species (grey solid points) at each plot has a point-location. The vertically arranged points at a particular value of P_j represent the species that occur together in one plot.

Results

The Description of Parameters Characterizing

Figure 1A shows *Cyclobalanopsis glauca* and *Alchornea trewioides* as examples to illustrate the meaning of the parameters characterized in this analysis. *Cyclobalanopsis glauca* is a typical dominant evergreen tree species in karst mountainous areas, and occurs in almost all plots across all gradients in our study (with $t_i = 4.87$ and spans a range of P_j from 5.14 to 5.51) while *Alchornea trewioides* is a typical dominant deciduous shrub species that lives in a shaded understory in karst mountainous areas, which accounts for 14 plots of 20 plots (with $t_i = 5.79$ and spans a range of P_j from 5.31 to 5.51). *Cyclobalanopsis glauca* has low β_i and negative α_i values, reflecting the fact that it has a lower SLA than most of the other species with which it occurs (Figure 1). Species with low SLA and dense wood, like those with long-lived leaves tend to have higher survival rates because they tolerate stress from shade, wind, drought and herbivores in relatively resource-poor habitats (Chave et al., 2009). *Alchornea trewioides* is high β_i and positive α_i values, towards the upper of the gradient, indicating different plant life-history strategies compared with *Cyclobalanopsis glauca*, and reflecting an advantage in the form of a rapid acquisition of growth rate with

low construction costs and rapid leaf turnover. A potential explanation for this shift towards higher SLA in *Alchornea trewioides* is that reduced carbon investment in structural support alters allocation patterns and allows deciduous species to dedicate a higher proportion of carbon and nutrient resources to leaf turnover. For *Cyclobalanopsis glauca*, $R_i = P_i$; for *Alchornea trewioides*, $R_i = 5.51 - 5.31 = 0.20$ and $\beta_i = -2.41$. Figure 1B shows the distribution of trait means and regression lines for all 52 woody plant species in study. For each species the slope of β_i was calculated by t_{ij} versus P_j and expresses the degree of intraspecific variation relative to the overall shift in trait values at the community level (Ackerly & Cornwell, 2007).

Correlations Between Functional Traits

Plant functional traits had different relationships within and between communities. Plot means were significantly negatively correlated between SLA and WD (Figure 2A, $P < 0.01$, $r = -0.67$). The correlation between LA and SLA was weakly positive. The species mean between SLA and WD traits showed a negative significant correlation while the correlation between LA and SLA and between LA and WD was positive (Figure 2B). For the relationship between beta components among the three

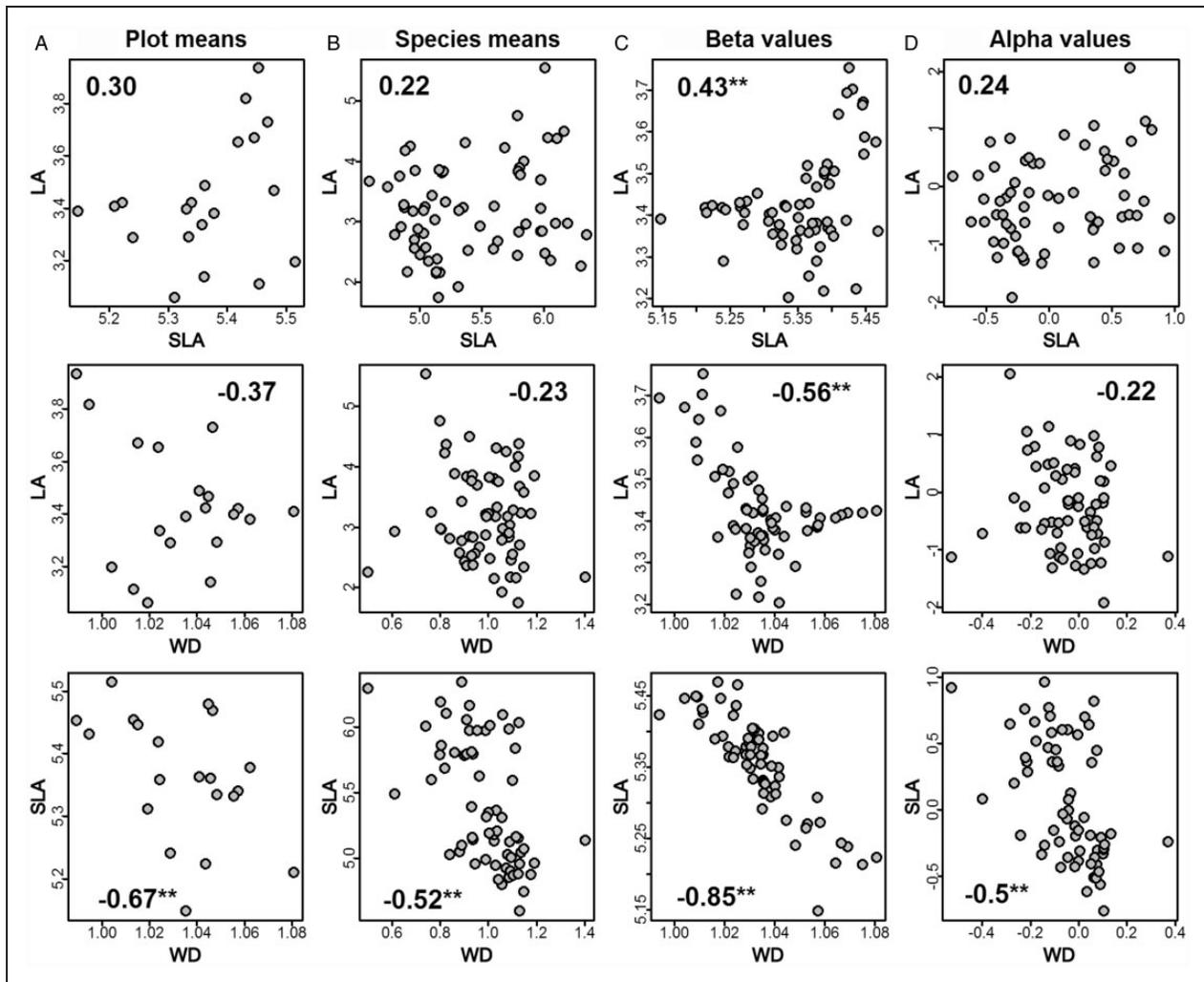


Figure 2. Scatterplots of (A) plot-mean trait values (P_i), (B) species mean trait values (C) species beta trait values (β_i) and (D) species alpha trait values (α_i) for pairwise combinations of LA, SLA and WD without log transformation. Asterisks indicate significant correlation (r) values across scales (** $P < 0.01$; * $P < 0.05$).

traits across the plot level, they showed significant correlation ($P < 0.05$, $r = 0.43$, -0.56 and -0.85), but LA and SLA are positively correlated while LA compared to WD and SLA compared to WD were negatively correlated. The alpha components showed weaker correlations for LA and SLA when compared across scales (Figure 2D); specifically, LA was positively correlated with SLA and negatively correlated with WD while SLA and WD showed significantly negative correlation ($P < 0.05$, $r = -0.33$).

Discussion

Partitioning of Species Trait Values

Trait variation in plant communities is thought to be constrained by two distinct and random assembly

processes operating at discrete spatial scales: habitat filtering and limiting similarity between coexisting species. Species with similar functional attributes in the regional species pool are screened by the habitat filtering, leading to species with similar function being filtered into the same niche, and causing the under-dispersion of trait values within communities. On the other hand, niche differentiation prevents coexisting species from being too ecologically similar and leads to the over-dispersion of trait values, promoting species coexistence within communities (Grime, 2006). In our study, for three plant functional traits (LA, SLA and WD), the range of alpha and beta values are -1.92 – 2.05 , -0.76 – 0.96 , -0.53 – 0.37 and 3.20 – 3.75 , 5.15 – 5.47 , 0.99 – 1.08 respectively. The range of alpha components was much wider than the range of beta component for the three traits (Figure 2, Table 2), meaning a broader range of

Table 2. Summary Statistics for Three Traits Measured in the *Cyclobalanopsis glaucab* Forest (LA, SLA log 10 Transformed Without WD).

Parameter*	Traits		
	Leaf area (cm ² , log)	Specific leaf area (cm ² .g ⁻¹ , log)	Wood density (g.cm ⁻³)
Species characteristics			
<i>t_i</i> , mean	3.18	5.42	0.99
<i>t_i</i> , min – max	1.74,5.54	4.60,6.34	0.50,1.40
<i>β_i</i> , min – max	3.20,3.75	5.15,5.47	0.99,1.08
<i>α_i</i> , min – max	–1.92,2.05	–0.76,0.96	–0.53,0.37
<i>R_i</i> , mean	0.45	0.45	1.74
<i>R_i</i> , min – max	–0.61,1.09	–0.43,1.08	0.67,3.0
Plot characteristics			
<i>P_j</i> , mean	3.43	5.36	1.03
<i>P_j</i> , min – max	3.06,3.94	5.15,5.51	0.99,1.08

Notice: SLA, specific leaf area; min, minimum; max, maximum. *t_i*, species trait mean; *β_i*, beta trait value; *α_i*, alpha trait value; *R_i*, niche breadth; *P_j*, plot mean trait value.* Units for all variables are same as trait units.

trait variation in co-existing species within shared ecological conditions. This provides a potential explanation for co-coexisting species to occupy distinct positions in multi-dimensional trait space in order to limit their similarity and reduce competition. Next, based on the calculation of LA and SLA alpha components interval (–1.92–2.05, –0.76–0.96), we found both LA and SLA were overall positive values, possibly suggesting that traits vary more within community compared with the shift across communities due to interspecific variation. However, the range of WD at the alpha components level was generally negative (–0.53–0.37), as interspecific variation will show species changing along the environment gradient. These results emphasize that a habitat filter and a limit to the similarity of coexisting species can simultaneously shape the distribution of traits and the assembly of local plant communities. In contrast, we found that a limiting similarity of coexisting species within a shared environment was greater than the habitat filtering in both LA and SLA trait value relatively. While on WD, habitat filtering contributes more to community assemblage relatively in our study.

Variation and Correlation of Plant Functional Traits at Comparable Scales

The partitioning of species traits into alpha and beta components provides a link between trait variation and coexistence mechanisms evaluated at comparable scales (Ackerly & Cornwell, 2007). Distinguishing between trait variation and coexistence mechanisms for a trait-based strategy is important because it gives us insight into life-history trade-offs that operate within and between environments. In the present study LA, SLA and WD showed inconsistent correlation patterns within and between communities (Figure 2). Between

LA and SLA as well as between LA and WD alpha components were largely weakly correlated or not correlated across species. This appears to be consistent with earlier findings by Ackerly and Cornwell (2007), where LA varied independently from SLA in woody plant communities of coastal California, suggesting that they act as independent dimensions of variation among coexisting species. This indicates that LA and SLA strategy axes are often orthogonal in multivariate space. On the other hand, the lack of correlation in alpha components means any two species that share a site are unlikely to exhibit the same combination of trait values, and will instead exhibit a broader range of trait variation, reflecting the differentiation of niche space along dimensions of varying habitat conditions (Rachael & Michelle, 2012). WD was largely unrelated to the other traits across species except for exhibiting a negative correlation with SLA. However, significant correlations were found at beta components for each other, indicating correlations between these two trait pairs were predominantly driven by their tendency to vary in parallel along wider scale abiotic gradients, though alpha components contributed more variation than beta components (Kooyman et al., 2010). In community ecology, the convergence of trait function in relation to edaphic and climatic conditions is viewed as evidence for habitat filtering (Cornwell et al., 2006; Kooyman et al., 2010). For SLA and WD, there were significant negative correlations (across species, alpha, beta level and plot means). However, evidence for these two traits have been different across species. Santiago et al. (2004) found wood density and photosynthetic capacity (A mass) to be negatively correlated. While two studies found that specific leaf area and wood density were negatively correlated (Bucci et al., 2004; Ishida et al., 2008), another found no correlation (Wright et al., 2007). In our study, the

negative correlations between them are the same with those reported Bucci et al. (2004) and Ishida et al. (2008) across species. Generally, no correlations or weak correlations were found among traits at the alpha level. However, a negative relationship was presented between WD and SLA not only at the alpha level but also at the rest of the scales. This may be related to the specific habitat of our field sampling. Because the samples were carried out in the late of succession for the *Cyclobalanopsis glauca* forest, evergreen species occupied a large proportion compared to deciduous species. Furthermore, we found species with small SLA and higher WD in a large proportion of most plots and species with this combination of traits were more abundant in some plot relative to others. This results in slow-growing species with high resource-use efficiency which gradually became the dominant species in a later successional stage of the *Cyclobalanopsis glauca* forest. An explanation for this may be that species were negatively correlated at comparable scales.

Implications of Conservation

In the present study, the alpha trait component of the three functional traits, LA, SLA and WD, had a larger variation range than the beta trait component. With the exception of LA and WD, the alpha components of traits were largely uncorrelated, while the beta component of traits showed significant correlation along an environmental gradient. There was a significant positive correlation between LA and SLA, while there was a significant negative correlation between LA and WD and between SLA and WD. These phenomena indicate that species adopt different ecological strategies to adapt to the environment within and among communities. We believe that it is of great significance to examine the variation and association of α and β components of species in order to understand community assembly at different scales. The karst mountain ecosystem is extremely fragile, and *Cyclobalanopsis glauca*, as the main tree species for the restoration of Karst degraded ecosystem, plays an important role in maintaining the stability of ecosystem and protecting species diversity. As our research shows, in order to protect the unique biodiversity of the region and the integrity of the forest landscape, we should consider the variation and correlation of the α and β components of the species at different scales. This approach may help us understand the position and difference of environmental screening and biological interaction in community assembly, in order to provide a theoretical basis for species selection, vegetation restoration, and reconstruction in karst areas.

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References

- Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, *10*(2), 135–145. <https://doi.org/10.1111/j.1461-0248.2006.01006.x>
- Ackerly, D. D. (2003). Canopy gaps to climate change—extreme events, ecology and evolution. *New Phytologist*, *160*(1), 2–4. <https://doi.org/10.1046/j.1469-8137.2003.00888.x>
- Ackerly, D. D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, *74*(1), 25–44. <https://doi.org/10.1890/03-4022>
- Ackerly, D. D., Knight, C., Weiss, S., Barton, K., & Starmer, K. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: Contrasting patterns in species level and community level analyses. *Oecologia*, *130*(3), 449–457. <https://doi.org/10.1007/s004420100805>
- Bao, S. D. (2008). *Soil agricultural and chemical analysis*, 3rd ed. China Agriculture Press: Beijing, China.
- Bucci, S. J., Goldstein, G., Meinzer, F. C., Scholz, F. G., Franco, A. C., & Bustamante, M. (2004). Functional convergence in hydraulic architecture and water relations of tropical savanna trees: From leaf to whole plant. *Tree Physiology*, *24*(8), 891–899. <https://doi.org/10.1093/treephys/24.8.891>
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693–715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Clark, D. B., Palmer, M. W., & Clark, D. A. (1999). Edaphic factors and the landscape-scale distributions of tropical rain

- Forest trees. *Ecology*, 80(8), 2662–2675. [https://doi.org/10.1890/0012-9658\(1999\)080\[2662:EFATLS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2662:EFATLS]2.0.CO;2)
- Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. *Ecology*, 87(6), 1465–1471. [https://doi.org/10.1890/0012-9658\(2006\)87\[1465:ATTFHF\]2.0.CO](https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO)
- Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of lake Michigan. *Botanical Gazette*, 27(5), 361–391. <https://doi.org/10.1086/327840>
- Enquist, B. J., Kerkhoff, A. J., Stark, S. C., Swenson, N. G., McCarthy, M. C., & Price, C. A. (2007). A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, 449(7159), 218–222. <https://doi.org/10.1038/nature06061>
- Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, 17(2), 255–260. [https://doi.org/10.1658/1100-9233\(2006\)17\[255:TCATDI\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2006)17[255:TCATDI]2.0.CO;2)
- Harley, C. D. G. (2011). Climate change, keystone predation, and biodiversity loss. *Science (New York, N.Y.)*, 334(6059), 1124–1127. <https://doi.org/10.1126/science.1210199>
- Harmon, J. P., Moran, N. A., & Ives, A. R. (2009). Species response to environmental change: Impacts of food web interactions and evolution. *Science (New York, N.Y.)*, 323(5919), 1347–1350. <https://doi.org/10.1126/science.1167396>
- Ishida, A., Nakano, T., Yazaki, K., Matsuki, S., Koike, N., Diego, L., Lauenstein, Shimizu, M., & Yamashita, N. (2008). Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia*, 156(1), 193–202. <https://doi.org/10.1007/s00442-008-0965-6>
- King, D. A., Davies, S. J., Tan, S., & Supardi, M. N. N. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, 94(3), 670–680. <https://doi.org/10.1111/j.1365-2745.2006.01112.x>
- King, R. S., Baker, M. E., Whigham, D. F., Weller, D. E., Jordan, T. E., Kazyak, P. F., & Hurd, M. K. (2005). Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecological Applications*, 15(1), 137–153. <https://doi.org/10.1890/04-0481>
- Kooyman, R., Cornwell, W., & Westoby, M. (2010). Plant functional traits in australian subtropical rain Forest: Partitioning within-community from cross-landscape variation. *Journal of Ecology*, 98(3), 517–525. <https://doi.org/10.1111/j.1365-2745.2010.01642.x>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, 16(5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T. D. (1997). Plant functional classifications: From general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, 12(12), 474–479. [https://doi.org/10.1016/S0169-5347\(97\)01219-6](https://doi.org/10.1016/S0169-5347(97)01219-6)
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Mouillot, D., Mason, N. W. H., & Wilson, B. (2007). Is the abundance of species determined by their functional traits? a new method with a test using plant communities. *Oecologia*, 152(4), 729–737. <https://doi.org/10.1007/s00442-007-0688-0>
- Phillips, O. L., Vargas, P. N., Monteagudo, A. L., Cruz, A. P., Zans, M. E. C., Sanchez, W. G., Yli-Halla, M., & Rose, S. (2003). Habitat association among amazonian tree species: A landscape scale approach. *Journal of Ecology*, 91(5), 757–775. <https://doi.org/10.1046/j.1365-2745.2003.00815.x>
- Poorter, L. (2009). Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *The New Phytologist*, 181(4), 890–900. <https://doi.org/10.1111/j.1469-8137.2008.02715.x>
- Poorter, L., & Rozendaal, D. M. A. (2008). Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia*, 158(1), 35–46. <https://doi.org/10.1007/s00442-008-1131-x>
- R Development Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Rachael, V. G., & Michelle, R. L. (2012). Contrasting patterns of trait-based community assembly in lianas and trees from temperate Australia. *Oikos*, 121, 2026–2035. <https://doi.org/10.1111/j.1600-0706.2012.20025.x>
- Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, L. B., Machado, K., Woodruff, D., & Jones, T. (2004). Leaf photosynthetic traits scale with hydraulic conductivity and wood density in panamanian Forest canopy trees. *Oecologia*, 140(4), 543–550. <https://doi.org/10.1007/s00442-004-1624-1>
- Schimper, K. F. (1898). *Plant ecology upon a physiological basis*. Iarendon Press, Oxford.
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional-and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12), 4387–4392. <https://doi.org/10.1073/pnas.0408648102>
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional. *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*, 21(5), 261–268. <https://doi.org/10.1016/j.tree.2006.02.004>
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review*

- of *Ecology and Systematics*, 33(1), 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, 99(5), 1003–1015. <https://doi.org/10.1093/aob/mcl066>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., . . . Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Wright, M., Filatotchev, I., Hoskisson, R. E., & Peng, M. W. (2005). Strategy research in emerging economies: Challenging the conventional wisdom. *Journal of Management Studies*, 42(1), 1–33. <https://doi.org/10.1111/j.1467-6486.2005.00487.x>
- Zanne, A. E., Westoby, M., Falster, D. S., Ackerly, D. D., Loarie, S. R., Arnold, S. E. J., & Coomes, D. A. (2010). Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, 97(2), 207–215. <https://doi.org/10.3732/ajb.0900178>