

INTER- AND INTRASPECIFIC LEAF TRAIT VARIATION INDUCED BY THE LOCAL ENVIRONMENT IN A MONTANE BROAD-LEAVED FOREST IN WESTERN CHINA

ZHAO, A. J.¹ – CHEN, X. H.^{1*} – XIAN, J. R.²

¹*College of Forestry, Sichuan Agricultural University, Chengdu 611130, China*

²*College of Environment, Sichuan Agricultural University, Chengdu 611130, China*

**Corresponding author*

e-mail: xiaohong_chen@sicau.edu.cn; phone: +86-181-2346-3625

(Received 27th Apr 2020; accepted 13th Aug 2020)

Abstract. Understanding how forest communities respond to environmental factors via intra- and interspecific variation in leaf functional traits is a fundamental challenge in forest ecology. Especially, little is known about the degree to which trees respond to environmental factors at the forest community level. To fill this gap, an experiment across 34 plots was conducted in a subtropical montane broad-leaved forest in western China. Based on 327 trees of 27 species, intra- and interspecific variations in leaf morphological and chemical traits were measured, and their relationship with environmental factors was determined. Canonical correlation analysis (CCA) was used to assess the relationships between the local environment and trait variation. Our results show that leaf morphological traits are related to chemical traits. The contribution of interspecific variability was dominant between species and communities, but intraspecific variability explained a large amount of variation (35.9%–56.2%) in chemical traits, despite the fact that high levels of species turnover were observed at the forest community level. Leaf traits showed responses to local environmental variables, with tree size being most strongly correlated. Our findings emphasize that leaf functional traits are correlated with environmental gradients. Therefore, to study the ecological process in subtropical forests using traits-based approaches, researchers need to account for their considerable intraspecific variability.

Keywords: *leaf morphological traits, leaf chemical traits, interspecific and intraspecific variability, tree size, soil properties, community ecology*

Introduction

Leaf functional traits including morphological traits, chemical traits, physiological traits, and symptoms, balance leaf construction costs against growth potential, reproduction and survival (Violle et al., 2007; Diaz et al., 2016). Foliar morphological traits reflect structural and physical characteristics, mainly including leaf mass, size, morphology and water status (Bussotti and Pollastrini, 2015). For instance, specific leaf area (SLA) is positively related to relative growth rates, leaf turnover rates, foliar nutrient concentrations and photosynthetic capacities in plant community assembly (Wright et al., 2004). Leaf dry matter content (LDMC) in particular has been regarded as an important component of the evolutionary history of species (Shipley et al., 2007; Messier et al., 2010). Foliar chemical traits, characterizing the mineral nutrition status, have been used as important parameters to recognize critical ecological processes of community assembly and species coexistence, and ecosystem structure and function (Aerts and Chapin, 2000; Wright et al., 2004). For example, leaf nitrogen content (LNC) is an extremely relevant ecological index, which is connected to photosynthesis, nutrient cycling, belowground diversity and water quality (Niinemets, 2010). By working with functional traits and their variation within and among communities,

researchers shed generalisable light on community assembly and ecosystem processes, one example is that three quarters of trait variation is captured in a two-dimensional global spectrum of plant form and function by analyzing variation in six major traits with the largest sample of global vascular plant species (Diaz et al., 2016). Traditionally, most previous studies operating on the mean values of species traits, focused on interspecific differences more between co-occurring species than within species (Wright et al., 2004; McGill et al., 2006; Cornwell et al., 2008). However, to date there is now growing evidence that intraspecific variability, can have significant effects on many ecological and evolutionary processes (Violle et al., 2012), moreover, sometimes the extent of intraspecific trait variation is similar to or greater than interspecific variation within and among plant communities. For example, many studies have demonstrated the importance of intraspecific variability for the maintenance of species coexistence, the dynamics of communities and the ecosystem properties in tropical forest, subtropical forest and grass ecosystems (Albert et al., 2010a; Messier et al., 2010; Bolnick et al., 2011). As such we need to consider that moving beyond the species mean approach by focusing on individual traits may improve our predictive ability of community ecology (Violle et al., 2012).

Trait-based community assembly rules have shed light on that environmental variation (or environmental filter) plays in shaping plant community functional trait composition (Albert et al., 2010a; Auger and Shipley, 2013). As the matter of fact, many studies have examined correlations in leaf traits with environmental variables like regional climate, local soil conditions and biotic interactions (Santiago and Wright, 2007; Atkin et al., 2008; Ordoñez et al., 2009), which can influence plant functional diversity and ecosystem function through primary production, carbon sequestration, trophic transfer and litter decomposition (Cornwell et al., 2008; Sedjo and Sohngen, 2012). To our knowledge, along environmental gradients the variation of many popular indices (e.g. aggregated trait averages) reflecting the functional characteristics of locally dominant species in ecological communities can be as a consequence of both species turnover and intraspecific trait variability (Lepš et al., 2011). In other words, not only can trait values among species vary in response to the environment (i.e., niche breadth) via phenotypic plasticity (Ashton et al., 2010), but intraspecific variability can also display different idiosyncratic responses (Albert et al., 2011). Especially, recent work also shows that an increasing interest in accounting for intraspecific functional trait variability on a regional to global scale, the response of functional, ecophysiological or demographic traits to environmental gradients (McGill et al., 2006; Hausch et al., 2018; Li et al., 2018). For instance, most studies dealing with intraspecific functional variability have focused on indirect gradients (e.g., altitude, latitude or longitude), which are unknown combinations of multiple direct environmental gradients that impact plant physiology (e.g., temperature, nutrient availability) (Cordell et al., 1998; Albert et al., 2015). Moreover, Violle et al. (2012) reported that the relative contribution of intraspecific trait variation to shifts in community-average trait values along environmental gradients reflects the importance of within-species trait responses to environmental stress. However, Lajoie and Vellend (2015) suggested that the relative contribution of intraspecific variation and species turnover to total trait variation along environmental gradients is poorly understood. For example, on account of the scale of environmental heterogeneity relative to the size of individual plants, the potential for individuals to express genetic and plastic trait differences across different environments, thus the relationship

between spatial grain (plot or sampling unit size) and the relative extent of intraspecific trait variation within communities is more difficult to predict (Siefert et al., 2015). Therefore, how intraspecific variation is influenced by environmental gradients, this issue might be dependent on the functional traits measured, the spatial scale of observation, and the study habitat type (Luo et al., 2016).

Montane broad-leaved forests in the southwest Sichuan are known for their high biodiversity. Because of the complicated geomorphological features and climate conditions, they shape abundant tree species and large habitat heterogeneities. Moreover, these forest communities appear tremendously diverse ecological characteristics of their spatial structure, functions and dynamics, with wide ranges in growth rates and shade tolerance (Zhao et al., 2009). But to date little is known about the ecological processes of structural and functional features of these broad-leaved forests and their effects of large range of environmental factors in this region (Zhao et al., 2009). Therefore, this study centered on leaf functional traits and its responses to environmental gradients (especially local soil properties and stand structures) in forest communities. As we now know foliar morphology correspond to the fundamental tradeoff in leaf construction costs vs. light-intercepting surface area and foliar chemical compounds influence the nutrient cycling and photosynthetic machinery of forest ecosystems (Wright et al., 2004). Hence, in this study from two aspects of foliar morphology and foliar chemistry we discuss the following questions: (1) How variable are the leaf morphological and chemical traits across individuals and communities? (2) Whether the contribution of intraspecific variation is lower than that of interspecific variation, and whether these relative contributions would differ among traits? (3) Whether differences and relationships between leaf functional traits and environmental gradients had existed among communities, and how do leaf traits vary in response to environmental gradients (i.e., soil properties and stand structures)? To address these questions, we measured leaf functional traits, soil properties and stand structures of 34 plots collected from the montane broad-leaved forest in western China.

Materials and methods

Study site

This study was conducted in Shangli town of Ya'an City (30°11'N, 103°5'E, 900-1800 m a.s.l., *Fig. A1*), within the montane broad-leaved forest region. The area is a geomorphologic complex located in southwest Sichuan, western China. The study area is characterized by a subtropical humid monsoon climate. The mean annual temperature is 16.1 °C and the mean annual precipitation is 1772.2 mm (Zhao et al., 2009; Zhou et al., 2018). Annual average sunshine is 1019.9 h, with an average of 289 frost free days. The soils are derived from sandy mudstone and mudstone substrates and contain >5% organic matter and >2% nitrogen (N) content. Local conditions for plant growth are strongly P-limiting, with soil total phosphorus (P) and available P of 0.5 g/kg and 12.5 mg/kg, respectively. The dominant tree species in this region include *Machilus pingii*, *Machilus ichangensis*, *Phoebe zhennan*, *Castanopsis fargesii*, *Quercus serrata* and *Photinia beauverdiana*. Dominant shrub species include *Camellia oleifera*, *Dichroa febrifuga*, *Eurya groffii*, *Eurya glaberrima* and *Ficus heteromorpha*. Herbaceous species were represented by *Setaria plicata*, *Iris japonica*, *Hosta plantaginea*, *Pilea notate*, *Pteridium aquilinum* var and *Latiusculum* (*Table A2*).

Field survey and leaf traits measurements

Data of forest communities were collected in forest plots from May to August 2017. According to the distributed characters of this study forest, 34 plots (20*20 m) were randomly sampled (*Fig. A1; Table A3*), with a minimum distance of 100 m from the outer forest margins, and a minimum distance of 250 m relative to one another. At each plot, each tree with a diameter at breast height (DBH) > 3 cm was recorded, overall, 2067 trees of 76 species were identified to the species level in total sampling areas. The procedure of leaf trait collection and measurements is described and explained below. One species was randomly selected in a plot with three mature and unshaded individuals based on DBH > 15 cm, of the 76 species in the survey data, sufficient trait data were collected for 327 trees of 27 species. In the field, leaves from these three individuals per species were assessed for chlorophyll content with a SPAD-502 meter (Konica Minolta, Tokyo, Japan), averaging five measurements taken on different parts of the leaf lamina. Next, we collected 10 in-tact leaves per individual tree for other trait measurements. In the laboratory, the fresh mass of each leaf was measured immediately with an SE202F electronic balance (Ohaus Corp., Parsippany, NJ, US). Leaves were scanned with a scanner (CanonScan LiDE 210, Canon Inc., Tokyo, Japan) and leaf area was calculated by using Image J (Pérez-Harguindeguy et al., 2013). An electronic digital caliper was used to measure leaf thickness (mm) at the center of the lamina by avoiding the major leaf veins. Leaves were dried to a constant weight at 70 °C for at least 3 days and then weighed. Specific leaf area (SLA), leaf dry matter content (LDMC), and leaf density (LD) were also calculated. Leaf N content (LCN) was determined with the Kjeldahl method and leaf P content (LCP) with spectrophotometry (Bao, 2000). Foliar N concentrations per unit leaf area (N_{area}) and foliar P concentrations per unit leaf area (P_{area}) were also obtained. All the leaf traits are described in *Tables A1* and *A2*.

Characterization of the stand structures and soil properties

The local environmental conditions of these 34 plots were focused on diameter at breast height (1.3 m, DBH), tree height, forest crown and stem density, and so on. In this study, we employed terms of forest stand structure to describe plot structures characteristics, which convey much information about the size distribution of trees, forest stand structure is the capital importance for understanding forest ecosystem structure and function. In each 20*20 m plot, censuses of all living trees with DBH > 3.0 cm were performed and the following parameters were recorded. DBH was measured using a caliper, height was measured with a vertex hypsometer; crown projection was inventoried in four cardinal directions. The basal area (BA), Shannon–Weaver’s index of diversity (SHI) (Shannon and Weaver, 1949) and Pielou’s evenness index (EVE) (Pielou, 1975) were computed for all sampled plots.

One soil sample per plot was taken using an auger, soil water content (here refers to actual water content, was calculated as (wet soil weight - dry soil weight)/dry soil weight) was quantified using the gravimetric method (Bao, 2000). An additional five profiles of the top 20 cm of depth were also collected in each plot and further mixed to make a combined soil sample per plot using this for chemical analysis. For each plot, soil samples were pooled, homogenized, air-dried and sieved (2 mm) for further analyses in the laboratory. Soil organic matter was determined by the Walkley and Black method and total N was determined by Kjeldahl digestion. Available P was estimated by the Olsen method; total K was extracted with 1 M ammonium acetate and

determined by atomic absorption spectrophotometry (Bao, 2000). The characters of stand structures and soil properties are described in *Tables A1* and *A3*.

Statistical analyses

Linear mixed models were used to analyze single-traits among individual species. Models were calibrated for each functional trait using individual trait measurements and included either no fixed effects (written as fixed ~1, m0) or a species fixed effect (fixed ~Species, m1) (Bolker et al., 2009; Albert et al., 2010b), to reflect interspecific, intraspecific variance, then we calculated a measure of explained variation based on the variances for the different models following (Xu, 2003): $R^2 = 1 - (\sigma_{m1})^2 / (\sigma_{m0})^2$, where σ_{m1} and σ_{m0} are the estimated error standard deviations under models m1 and m0 respectively. Variances were estimated by maximizing the restricted log-likelihood (REML).

According to Dodélec and Chessel (1991) and Albert's method (Albert et al., 2010a), we conducted the principal component analysis (PCA) to disentangle multidimensional structure within the leaf trait space at individual and community level. The relationships between leaf morphological traits and chemical traits were also explored by standardized major axis (SMA) regressions, a statistical tool highly recommended for allometric studies (Warton et al., 2006), using the PCA axis of morphological or chemical traits. There is an interest in knowing the slopes, which are fitted by minimizing the sums of squares of errors in X and Y dimensions, indicating the magnitude of the scaling between the variables. SMA regressions were performed using SMATR software (Falster et al., 2006).

To examine functional trait variations at the forest community level, all leaf traits were weighted by the relative abundance of each species to calculate the community weighted means (CWM) according to Lepš et al.'s (2011) method. We calculated three types of CWM parameters: (1) specific average trait values were calculated for each plot using the trait average of each species measured overall individuals of that species in that specific plot, which reflects the effect of both species' inter- and intraspecific trait variation; (2) fixed trait values were calculated for each plot using the single trait average of each species measured overall individuals of that species in the study, which changes in value among plots that are only due to interspecific trait variation; (3) intraspecific variability trait values were calculated from the differences between specific and fixed average traits and permit an estimation of the pure effects of the intraspecific variability. Specifically, to quantify how much intra- and interspecific variability, this can be employed three community parameters (fixed and specific averages and their difference) to run three parallel ANOVAs for each functional trait. Then, from outcomes of the preceding analyses, we partitioned inter- and intraspecific trait variability effects on plot-level traits values among plots, and used the method that the sum of squares of species trait variance for all plots (SS_{specific}) was decomposed into three different components which include fixed (SS_{fixed}) effects, intraspecific ($SS_{\text{intraspecific}}$) effects and covariation (SS_{cov}) effects, the equations as following: $SS_{\text{cov}} = SS_{\text{specific}} - SS_{\text{fixed}} - SS_{\text{intraspecific}}$ (Lepš et al., 2011). Where, SS_{specific} was the 'total' variation of community trait averages originating from the specific averages. SS_{fixed} and $SS_{\text{intraspecific}}$ came from fixed averages, intraspecific trait variability above-mentioned ANOVAs respectively. SS_{cov} was Covariations of the species turnover (SS_{fixed}), intraspecific variability ($SS_{\text{intraspecific}}$) (more details in Lepš et al., 2011; Carlucci et al., 2015; Luo et al., 2016).

Finally, we used canonical correlation analysis (CCA) to quantify correlations between two sets of multidimensional variables (Tabachnick and Fidell, 2012). As leaf traits and environmental factors are multivariate in nature, an analytic approach that allows for multiple independent variables is thus preferred (Bajorski, 2012). The use of the canonical correlation for this study enabled a more in-depth analysis of the relationships between stand structure, soil factors, and leaf traits than would have been possible with univariate statistical procedures such as multiple regressions. Therefore, we can assume that two sets of random variables, X (leaf traits) with p variables and Y (environmental factors) with q variables, have means of zero. Let n be the number of observations, and let m be $n-1$. Then, we use two aggregate variables U and V to express X and Y in new linear combinations as $U = aX$, $V = bY$. Using PCA's idea, we will try to find the coefficient sets a and b , which lead to the maximum covariance of $\text{cov}(U,V)$. The main steps includes (1) getting the covariance matrix $\text{cov}(U,V)$, (2) employing Lagrange Multiply Method to maximize $\text{cov}(U,V)$, and (3) getting U , V , a , b and their corresponding eigenvalues. From CCA, we can obtain the key values such as canonical correlation coefficients, explanation proportion, and significance testing value (Tabachnick and Fidell, 2012). Linear mixed analyses was conducted using the packages 'ape' (Paradis et al., 2004), the principal component analysis was performed using the packages 'FactoMinerR' (Lê et al., 2008) and the canonical correlation analysis was performed using the packages 'vegan' (Dixon, 2003) in the R (R 3.5.3 version).

Results

Leaf traits variations of the individuals of all species

Principal component analysis on individual data produced variation and structure of the leaf morphological and chemical trait space. Morphologic traits were positively correlated among themselves (Table A4). The data set was structured by a strong first axis (58.6% of the variance) that was primarily correlated with LDMC and SLA (Fig. 1a). The second axis explained 28.6% of the variance and to some extent was correlated weakly with the leaf area (LA) and LD (Fig. 1a). Multi-trait variation of chemical traits representing the first PCA component (43.2% of the variance) was mainly driven by leaf chlorophyll (LChl), and the second axis (36.5% of the variance) was driven by leaf N content (LCN), and they were both positively correlated among themselves (Fig. 1c).

The SMA regressions between morphological traits and chemical traits were largely significant relationships ($R^2 = 0.51$, $F = 284.3$, $P < 0.0001$, Fig. 2a). In addition, the morphological traits were significantly correlated with chemical traits such as LChl, LCN, leaf N content per area (N_{area}), and leaf P content per area (P_{area}) (Fig. 3). They were negatively related to leaf morphology, except for LCN. Similarly, the chemical traits were significantly correlated with the morphology related traits such as LA, SLA, LDMC, and LD (Fig. 3).

Leaf morphological and chemical traits led to similar results, with a partition around 80% vs. 20% for interspecific vs. intraspecific variability (Fig. 4). There were small differences between traits, with LD (up to 24.7%, Fig. 4) and P_{area} (up to 24.9%, Fig. 4b) showing relatively more intraspecific variability. Total variances are about 60% for leaf morphological and chemical traits, except for leaf thickness (LT) (up to 97.7%, Fig. 1a), LA (up to 79.7%, Fig. 1a) and LChl (up to 73.7%, Fig. 4).

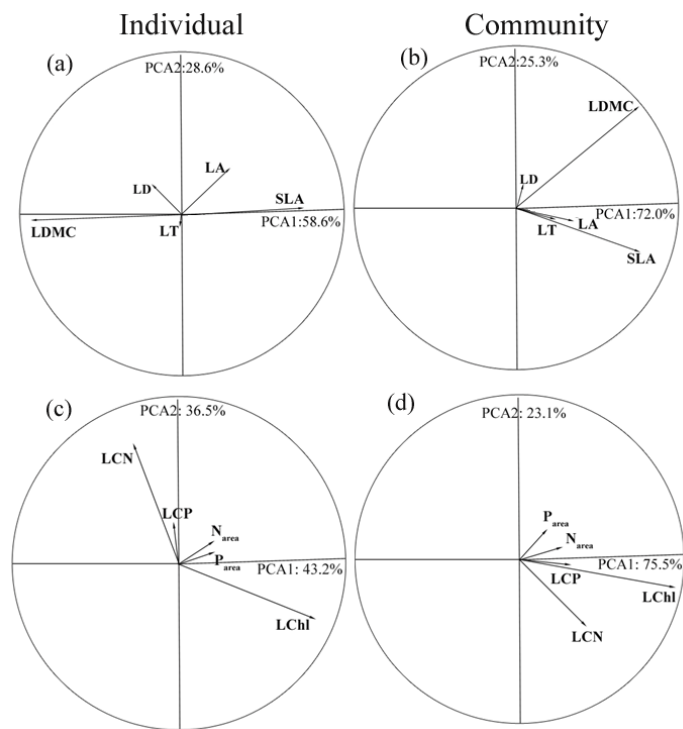


Figure 1. Multidimensional structure within the trait space showing (a) leaf morphology trait at individual level, (b) leaf morphology trait at community level (c) leaf chemistry trait at individual level, (d) leaf chemistry trait at community level. Variables (leaf traits) used for the PCA are displayed with their vector. See Table A1 for abbreviations of traits

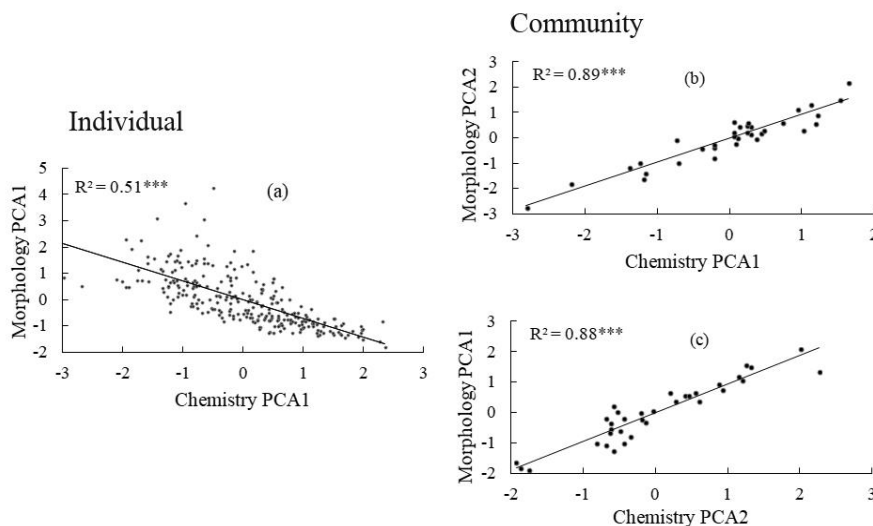


Figure 2. Standardized major axis (SMA) regressions between leaf morphological traits and chemical traits at the between-species and communities. (a) Species analyses, only morphology PCA1 and chemistry PCA1 showed significant relationships which R^2 was 0.51, $P < 0.0001$. (b) Community analyses morphology PCA2 and chemistry PCA1 showed significant relationships which R^2 was 0.89, $P < 0.0001$. (c) Community analyses morphology PCA1 and chemistry PCA2 showed significant relationships which R^2 was 0.88, $P < 0.0001$. Squared correlation coefficient (R^2) is given and SMA regression line is plotted when significant. ** $P < 0.01$, *** $P < 0.001$

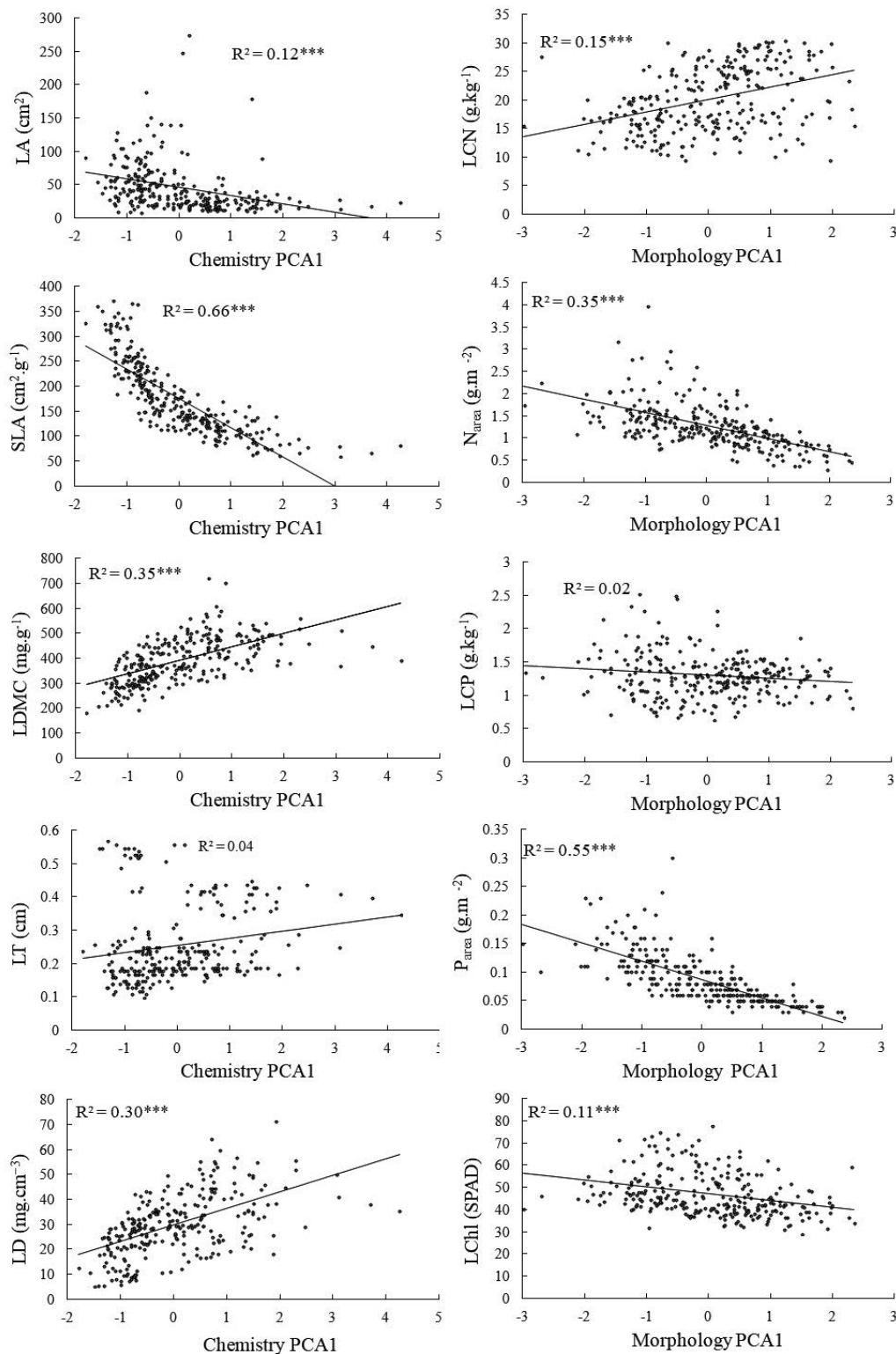


Figure 3. Relationships at the between-species are morphology related traits (LT, LA, SLA, LDMC and LD) and chemical traits (chemistry PCA1) (left column), and chemistry related traits (LChl, LCN, N_{area}, LCP, P_{area}) and morphological traits (morphological PCA1) (right column) using standardized major axis (SMA) regressions. Squared correlation coefficient (R^2) is given and SMA regression line is plotted when significant. $^{**}P < 0.01$, $^{***}P < 0.001$. See Table A1 for abbreviations of traits

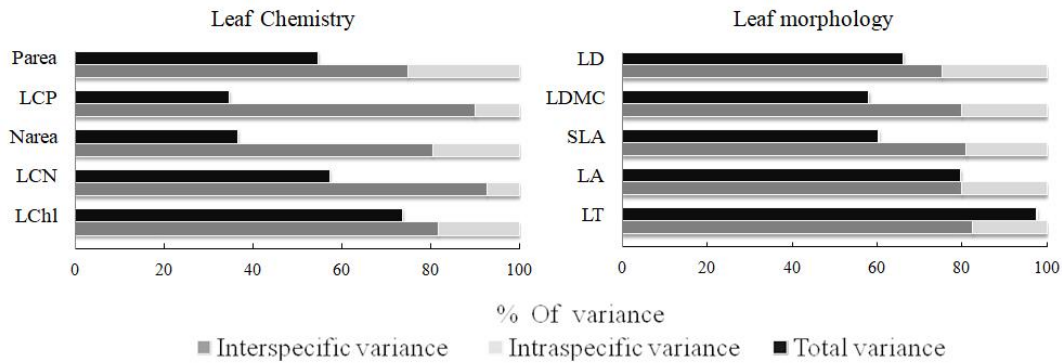


Figure 4. Variance decomposition in interspecific and intraspecific contributions for single-trait of between-species. Leaf morphological traits analyses (left) and leaf chemical traits analyses (right) resulting from mixed models, the black bars are the total variance resulting from general line mixed models. See Table A1 for abbreviations of traits

Leaf traits variations of the communities

At the community, PCAs of variation and structure of the leaf morphological and chemical trait were similar to PCA results at the species level. For the morphological traits, PCAs results showed that the data set was structured by a strong first axis (72.0% of the variance) that was mainly explained by LDMC and SLA. A second axis (25.3% of the variance) was explained largely by LA and LD (Fig. 1b). Multi-trait variation of chemical traits represented the first PCA component (75.5% of the variance) and was mainly driven by LChl and LCN (Fig. 1d).

The SMA regressions indicated that morphology PCA2 was significantly correlated with chemistry PCA1 (Fig. 2b, R^2 was 0.89, $P < 0.0001$), and morphology PCA1 was significantly correlated with chemistry PCA2 (Fig. 2d, R^2 was 0.88, $P < 0.0001$). Chemistry PCA1 was significantly correlated with LDMC and LD, and chemistry PCA2 was significantly correlated with LT, LA, and SLA (Fig. 5, left column). Similarly, morphology PCA1 was significantly correlated with LChl and LCN, and morphology PCA2 was significantly correlated with LCN, N_{area}, LCP, and P_{area} (Fig. 5, right column).

Interspecific variability contributed to a greater proportion of explained variation to the functional shift than did intraspecific variability for leaf morphological and leaf chemical traits. For LT and LChl, the CWM trait variation was almost completely generated by interspecific variation, which accounted for 98.3% and 93.8% of the total variation, respectively. However, the contribution of intraspecific variation was greater than interspecific variation for LCN (56.2% vs. 21.0%), and there was a positive covariation between interspecific and intraspecific variation among the plots (Table 1). This, however, was not the case for LT (-2.3%) and LChl (-7.2%).

Intra- and inter-specific variability of CWM along different environmental axes

A canonical correlation analysis was conducted to evaluate the multivariate shared relationship between the leaf traits and the environmental groups, which yielded the first canonical variables with squared canonical correlations (Canonical R^2) and Wilks' Lambda values (Table 2). To total variability and interspecific variability, the full model across the first canonical variables was statistically significant except for leaf chemistry and soil properties. Meanwhile, for intraspecific variability, leaf morphology was

significantly correlated with soil properties ($F = 5.29$, $p < 0.0001$), and leaf chemistry were significantly correlated with stand structures ($F = 1.63$, $p = 0.02$).

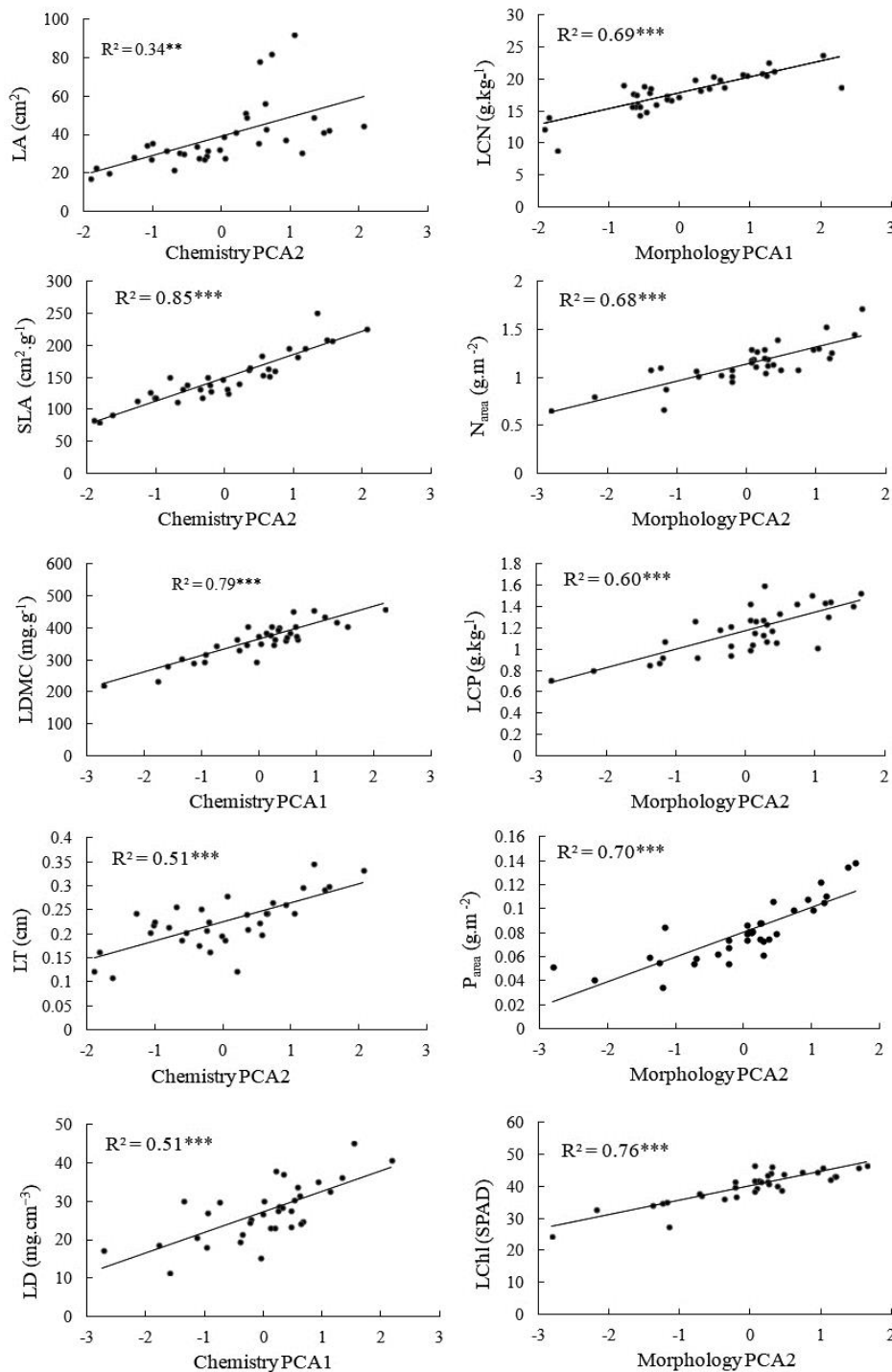


Figure 5. Relationships in community are morphology related traits (LT, LA, SLA, LDMC and LD) and chemical traits (chemistry PCA1 or PCA2) (left column), and chemistry related traits (LChl, LCN, N_{area} , LCP, P_{area}) and morphological traits (morphological PCA1 or PCA2) (right column) using standardized major axis (SMA) regressions. Squared correlation coefficient (R^2) is given and SMA regression line is plotted when significant. ** $P < 0.01$, *** $P < 0.001$. See Table A1 for abbreviations of traits

Table 1. The proportion of interspecific variation, intraspecific variation and covariation effects contributing to the variance in community weighted mean trait values (unit: %). See Table A1 for abbreviations of traits

Group	Traits	Interspecific variation effect	Intraspecific variation effect	Covariation effect
Leaf morphology	LT	100.26	4.02	-4.28
	LA	59.67	15.33	25
	SLA	63.22	22.29	14.49
	LDMC	82.23	16.16	1.61
	LD	67.41	21.41	11.18
Leaf chemistry	LChl	93.84	13.32	-7.16
	LCN	21.03	56.19	22.78
	N _{area}	49.74	42.78	7.48
	LCP	40.29	36.16	23.55
	P _{area}	46.55	35.91	17.54

Table 2. Canonical correlation between leaf trait functions (morphology and chemistry) and environmental variables (stand structures and soil properties) for their first canonical variables

	Leaf traits	Environmental variables	Proportion	Canonical R ²	Wilks' Lambda
Total variability	Morphology	Stand structures	0.64	0.83 ***	0.023
		Soil properties	0.71	0.99***	0.0001
	Chemistry	Stand structures	0.34	0.69 ***	0.021
		Soil properties	0.58	0.41	0.380
Interspecific variability	Morphology	Stand structures	0.60	0.77 **	0.043
		Soil properties	0.83	0.76 ***	0.137
	Chemistry	Stand structures	0.56	0.72 **	0.062
		Soil properties	0.68	0.57	0.259
Intraspecific variability	Morphology	Stand structures	0.58	0.72	0.066
		Soil properties	0.99	0.99 ***	0.0002
	Chemistry	Stand structures	0.54	0.69 **	0.074
		Soil properties	0.45	0.22	0.560

***P < 0.01, **P < 0.001. Canonical R² is squared canonical correlations, Wilks' lambda is Wilks' lambda (likelihood ratio) statistic

Stand structures and soil properties significantly influenced leaf morphology and leaf chemistry (Tables 3, 4, 5). For instance, the total variation in LA, LDMC, and LCN were all significantly correlated with soil properties, which were mostly explained by soil water and soil P content (Table A5). Meanwhile, SLA, LD and all variables of leaf chemistry were significantly correlated with stand structures, which were mainly supported by tree sizes (e.g. H and DBH) (Tables 3 and A5). Furthermore, soil properties explained 29.3% of the total variance in leaf morphology and stand structures explained 19.6% and 30.2% of the total variance in leaf morphology and chemistry (Fig. 6). In the same situation, the interspecific variation of LA and LCN were all

significantly correlated with soil properties, which were mainly supported by soil water and soil P content (Table A6). Specific leaf area, LChl, LCN, and LCP were significantly correlated with stand structures that mainly contributed by BA and DBH (Tables 4 and A6). Soil properties explained 18.4% of the interspecific variance in leaf morphology, stand structure explained 26.89% and 31.7% of the interspecific variance in leaf morphology and chemistry (Fig. 6). For intraspecific variance, LA, LDMC, and LCN were all significantly correlated with soil properties, and SLA, LD, LCN, LCP, and Parea were significantly correlated with stand structures defined by stand tree height (Tables 5 and A7). 40.7% of intraspecific variation of leaf morphology was explained by soil properties, and 20.9% of leaf chemistry was explained by stand structures (Fig. 6).

Table 3. Univariate multiple regressions of community-weighted mean traits values in total variability by soil properties and stand structures in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits

Variables		Soil properties			Stand structures		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Leaf morphology	LT	0.41	1.4	0.30	0.34	1.35	0.26
	LA	0.90	17.35	0.00	0.37	1.56	0.18
	SLA	0.44	1.57	0.25	0.52	2.86	0.02
	LDMC	0.98	109.52	<.0001	0.40	1.80	0.12
	LD	0.30	0.85	0.55	0.51	2.77	0.02
Leaf chemistry	LChl	0.11	0.71	0.62	0.64	4.84	0.00
	LCN	0.36	3.08	0.02	0.66	5.12	0.00
	N _{area}	0.03	0.19	0.97	0.46	2.29	0.05
	LCP	0.09	0.57	0.72	0.58	3.70	0.00
	P _{area}	0.07	0.42	0.83	0.47	2.37	0.04

Table 4. Univariate multiple regressions of community-weighted mean traits values in interspecific variability by soil properties and stand structures in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits

Variables		Soil properties			Stand structures		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Leaf morphology	LT	0.11	0.71	0.62	0.37	1.57	0.18
	LA	0.62	8.96	<.0001	0.41	1.84	0.11
	SLA	0.31	2.49	0.05	0.54	3.17	0.01
	LDMC	0.11	0.72	0.62	0.45	2.22	0.06
	LD	0.12	0.75	0.59	0.42	1.95	0.09
Leaf chemistry	LChl	0.18	1.25	0.31	0.66	5.15	0.00
	LCN	0.54	6.51	0.00	0.47	2.39	0.04
	N _{area}	0.08	0.50	0.77	0.43	2.00	0.08
	LCP	0.12	0.78	0.57	0.47	2.34	0.05
	P _{area}	0.13	0.80	0.56	0.39	1.73	0.14

Table 5. Univariate multiple regressions of community-weighted mean traits values in intraspecific variability by soil properties and stand structures in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits

Variables		Soil properties			Stand structures		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Leaf morphology	LT	0.31	0.90	0.52	0.31	1.18	0.35
	LA	0.67	4.05	0.03	0.24	0.86	0.58
	SLA	0.61	3.14	0.06	0.37	1.56	0.19
	LDMC	0.99	144.19	<.0001	0.30	1.12	0.38
	LD	0.31	0.89	0.53	0.55	3.30	0.01
Leaf chemistry	LChl	0.09	0.55	0.74	0.22	0.75	0.66
	LCN	0.16	1.06	0.41	0.53	3.00	0.02
	N _{area}	0.16	1.10	0.38	0.34	1.35	0.26
	LCP	0.07	0.42	0.83	0.58	3.69	0.01
	P _{area}	0.08	0.46	0.81	0.49	2.60	0.03

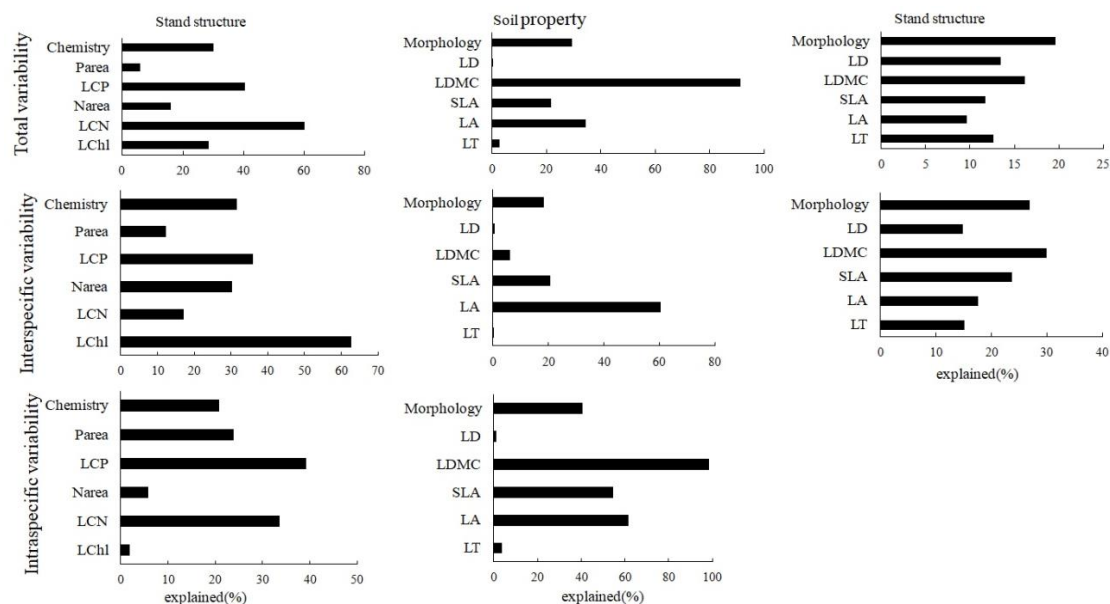


Figure 6. The relative contribution of total, interspecific and intraspecific variability of CWM trait values along different environmental axes. (According to canonical correlation analysis, the results showing the significance level is listing, seeing Table 2). See Table A1 for abbreviations of traits

Discussion

Intra- and interspecific variability of leaf traits

Our findings indicate that leaf morphology traits of the between-species for two independent axes of trait covariation together accounted for approximately 87% of the variance. Likewise, at the communities, roughly 97% of the variance was explained in multidimensional trait space (Fig. 1). The first axis alone accounted for 58.6% of

variance at between-species and 75% of variance at the community, which depicted light capture dimension of the plant strategy spectrum and light availability (LDMC and SLA) (Wright et al., 2004; Lusk et al., 2008), and the second axis accounted for 28.6% of variance at between-species and 25.3% of variance at the community, which described investment physical attributes (LA and LD) (Chauvin et al., 2018).

For chemical trait spaces of the between-species and communities, the first axis reflected the chemical attributes, which is integral to the proteins of the photosynthetic machinery. The second axis represents an investment in foliar nutrition, which is essential to many of the chemical compounds involved in leaf structure and metabolism (Wright et al., 2004). Other results from The SMA regression analysis demonstrated that morphological traits were reciprocally correlated with chemical traits (*Figs. 2, 3, 5*). In fact, these traits are often found to be strongly correlated with each other across species and communities. For example, evergreen leaves are often sclerophyllous and associated with a lower SLA, lower leaf N content, and lower mass-based photosynthetic capacity (Curtis and Ackerly, 2010; Kröber et al., 2015). This trend is in line with the leaf economics spectrum (LES) that characterizes ecological strategies with quick to slow payback of investments of nutrients and dry mass (Wright et al., 2004; Osnas et al., 2013). At the leaf level, SLA, leaf dry matter content, and leaf N concentration has been employed to predict accurately the maximum photosynthetic rates of a wide range of species (Reich et al., 1997). At the plant level, all three traits have been found to be involved in a fundamental tradeoff between a rapid production of biomass and efficient conservation of nutrients (Poorter and Jong, 1999). And SLA (or related leaf traits) and LCN significantly impacted on primary productivity and nutrient cycling at the ecosystem level (Aerts and Chapin, 2000).

The importance of intraspecific variance has been neglected in community ecology for a long time (Bolnick et al., 2011). Recently, however, there has been greater attention paid to intraspecific variability, which has underlined the developments to integrate variation in both the intraspecific as well as interspecific levels in trait-based community ecology (Violle et al., 2012). Despite this increase in attention, understanding how intraspecific variation influences such functional shifts is not well understood in montane broad-leaved forests. Our results show that intraspecific variability of both leaf morphological and chemical traits account for roughly 20% of the variation, and interspecific variability explained 80% in functional turnover (*Fig. 4*). These findings illustrate that most of the variance in raw trait values was explained by differences between species. Intraspecific variance accounted for a smaller part of the total variance, resulting in either from genetic variation or phenotypic plasticity (Albert et al., 2011), in line with the growing consensus that intraspecific trait variation is not negligible (Albert et al., 2010b). This result could reflect the dissimilarity in high species turnover in montane broad-leaved forests (Luo et al., 2016).

Based on community-weighted mean traits values, the interspecific variation of leaf morphologic traits was the main contributor to functional trait change (*Table 2*). For chemical traits, intraspecific variability of LCN, N_{area} , LCP, P_{area} accounted for 56.2%, 42.8%, 36.2% and 35.9% variation, respectively. This was in accordance with previous results that intraspecific effects are often comparable to, and sometimes stronger than, species effects. These effects tend to be larger for direct ecological responses, whereas intraspecific effects and species effects tend to be similar for indirect responses; intraspecific effects are especially strong when indirect interactions alter community composition (Des Roches et al., 2018). Chemical functional traits are associated with

photosynthetic rate and nutrient cycling (Wright et al., 2004; Pérez-Harguindeguy et al., 2013), high variability in leaf chemical trait responses to stress or environmental gradients has been reported in previous studies (Auger and Shipley, 2013; Siefert et al., 2015). Finally, chemical traits are typically greater than leaf morphologic traits in broad-leaved forests, indicating that the relative contribution of intraspecific variation largely influences local functional composition, the maintenance of species coexistence, and the dynamics of communities (Lichstein et al., 2007; Bolnick et al., 2011; Courbaud et al., 2012; Violle et al., 2012; Luo et al., 2016).

Influence of environmental factors on intra- and interspecific trait variability

We found that soil properties significantly showed relationships with leaf morphology in total variance, interspecific variance, and intraspecific variance (Table 2). Soil properties accounted for 29.3%, 18.4% and 40.7% of the variation in these variables, respectively (Fig. 6). This result is interesting given that soil nutrient conditions (i.e., total soil N and total organic C) are the most important explanatory factors for SLA variation at both intra- and interspecific levels (He et al., 2018). In particular, LDMC of intraspecific variance was more significant than SLA with soil properties, and soil properties explained roughly 98% of variation intraspecific variance (Fig. 6). In other words, LDMC was a better predictor than SLA for describing the relationships between leaf morphologic traits and soil properties. Though LDMC and SLA were both correlate with nutrient availability, LDMC varied independently from leaf thickness and was also strongly correlated with resource availability and with relative growth rate (Garnier et al., 2004; Roche et al., 2004; Fortunel et al., 2009).

Leaf dry matter content has been recommended as a more reliable correlate of soil fertility in biomes not subject to severe water limitation (Vendramini et al., 2002). Another reason is that in montane broad-leaved forests, the shaded leaves have high SLA that results in the optimization of light capture rather than being associated with high soil fertility (Hodgson et al., 2011). Likewise, abundance-weighted LDMC, as opposed to SLA, was the superior predictor of aboveground net primary production (Smart et al., 2017). In addition, leaf area (LA) of inter- and intraspecific variance was related to soil attributes (Tables 4, 5), this indicated increasing in LA had greater access to light, leading to take advantage of increased soil resource availability, especially for tall species (Siefert and Ritchie, 2016), in line with the dominant plasticity mechanism, which predicts that competitive species have strong phenotypic plasticity to maximize resource capture and competitive ability (Ashton et al., 2010).

With regard to the relationships between leaf chemical traits and soil properties, our finding was that two categories showed inconspicuous relevance for the first canonical variable (Table 2). This result hints at the idea that soil properties had no systematic effect on foliar nutrient status, which might be because plants are able to constrain the flexibility of nutrient concentrations (Sistla et al., 2015). Namely, a change in soil nutrient availability did not necessarily imply a change in foliar nutrient status, especially when deficiencies were moderate (Luiro et al., 2009). Another explanation is that gradients of nutrient availability in soils were generally narrow, making investigations of the role of soil fertility in nutrient remobilization difficult (Achat et al., 2018). Additionally, their relationships were directly or indirectly affected by soil properties, soil types, parent materials, and climate gradients, even though their gradients were not very wide in our study sites (Augusto et al., 2017; Achat et al., 2018).

From a stand structural perspective, we suggest that leaf traits in interspecific and intraspecific variance were significantly correlated with stand characteristics. Previous studies on height and crown-related changes in leaf morphological, chemical and photosynthetic traits between and within species (Chmura and Tjoelker, 2008; Burgess and Dawson, 2010; Kenzo et al., 2016). For instance, mass- and area-based leaf N decreased, and specific leaf area (SLA) increased with increasing canopy depth, and SLA and leaf N -trait gradients showed variations between loblolly pine and slash pine (Kenzo et al., 2016). The intraspecific variance of leaf traits (e.g., LDMC, SLA) may also be related to aboveground biomass, which was potentially driven by the functional identity of tree height at different forest strata as well as at whole-community (Ali and Yan, 2018). In general, plant life history strategies suggest that taller species respond more strongly to leaf photosynthetic capacity (e.g. SLA, N and P content) because they potentially experience increasing light levels as they grow to the canopy. In contrast, small-statured species may remain in the shaded understory for their whole life cycle, and those results are supported by studies of the effect of light, nutrients and other environmental factors on plant leaf traits and their relationships (Santiago and Wright, 2007; Mao et al., 2017).

Our study showed that leaf N content per area (N_{area}) and leaf P content per area (P_{area}) (high values for acquisitive strategies) are strongly related to stand height and DBH in their intra- and inter-specific variance (Tables A5, A6, A7). Leaf density (LD) and dry matter content (LDMC) (high values for conservative strategies) are strongly in their interspecific variance responses to different stand height and DBH (Tables A5, A6, A7). Those findings that leaf traits consistently represent inter- and intraspecific variations in the studied forest have important implications in the individual plant strategies, community assembly and ecosystem function (Siefert et al., 2015). In addition, LDMC showed high contributions of interspecific variance to the changes along the stand structural gradient (Fig. 6). Those results hint at the fact that leaf traits and bivariate leaf trait relationships are modified by plant size, although their positive correlations generally remain invariant. However, a plant size effect on leaf traits relationships has scarcely been examined, although it may be critical to understanding plant life history strategies, especially for subtropical forests (Liu et al., 2010).

Conclusion

Our results revealed that the contribution of interspecific variability was dominant for leaf morphological and chemical traits at between-species and communities, despite the high level of intraspecific variability for leaf chemical traits (e.g. LCN, N_{area} , LCP, P_{area}) at communities in montane broad-leaved forest, which suggest that intraspecific functional variability should be a concern for ecologists. We also observed that intensely relationships between leaf morphological and chemical traits presented by leaf assemblages at between-species and communities. Traits that are coordinated within plant strategies (leaf economics spectrum) showed that total, intra- and inter-specific variability responses to environmental gradients (stand structures and soil properties) when considered for the communities. Our findings highlight the structure of inter- and intraspecific variability in actual communities acts as a signature of community assembly processes, and alters with environmental gradients. In the future, we need more experiments to better understand the influence of sampling effort and design on the quantification of the absolute and relative amount of intraspecific trait variability

within and among communities, and disentangle the extent and consequences of plastic and genetic trait variation at the community and ecosystem levels. Most importantly, the researchers should perform a more systematic evaluation of the effects of inter- and intraspecific variability on functional diversity indices and their relationships to environmental variables or other community properties on local scales.

Acknowledgments. This study was funded by the National Natural Science Foundation of China (Grant No. 31800352) and the National Major Protection Wild Plants Inventory Project (003Z0305), and was supported by Cooperative Innovation Center of Ecological Security in the Upper Reaches of the Yangtze River.

Author contribution. C. X. H. and X. J. R. performed the leaf morphological and soil measurements; Z. A. J. analyzed the data and wrote the article with substantial collaboration from all authors.

Conflict of interests. The authors declare that there is no conflict of interests.

REFERENCES

- [1] Achat, D. L., Pousse, N., Nicolas, M., Augusto, L. (2018): Nutrient remobilization in tree foliage as affected by soil nutrients and leaf life span. – *Ecological Monographs* 88: 408-428.
- [2] Aerts, R., Chapin, L. F. S. (2000): the mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. – *Advances in Ecological Research* 30: 1-67.
- [3] Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., Lavorel, S. (2010a): A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. – *Funct Ecol* 24: 1192-1201.
- [4] Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. et al. (2010b): Intraspecific functional variability: extent, structure and sources of variation. – *J Ecol* 98: 604-613.
- [5] Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., Violle, C. (2011): When and how should intraspecific variability be considered in trait-based plant ecology? – *Perspectives in Plant Ecology Evolution and Systematics* 13: 217-225.
- [6] Albert, C. H., De Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., Thuiller, W. (2015): On the importance of intraspecific variability for the quantification of functional diversity. – *Oikos* 121: 116-126.
- [7] Ali, A., Yan, E. R. (2018): The mediation roles of intraspecific and interspecific functional trait diversity for linking the response of aboveground biomass to species richness across forest strata in a subtropical forest. – *Ecological Indicators* 85: 493-501.
- [8] Ashton, I. W., Miller, A. E., Bowman, W. D., Suding, K. N. (2010): Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. – *Ecology* 91: 3252-3260.
- [9] Atkin, O. K., Atkinson, L. J., Fisher, R. A., Campbell, C. D., Zaragoza-Castells, J., Pitchford, J. W. et al. (2008): Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. – *Global Change Biol* 14: 2709-2726.
- [10] Auger, S., Shipley, B. (2013): Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. – *Journal of Vegetation Science* 24: 419-428.
- [11] Augusto, L., Achat, D. L., Jonard, M., Vidal, D., Ringeval, B. (2017): Soil parent material. A major driver of plant nutrient limitations in terrestrial ecosystems. – *Global Change Biol* 23: 3808-3824.

- [12] Bajorski, P. (2012): Canonical Correlation Analysis. – John Wiley & Sons, Ltd, Hoboken, NJ.
- [13] Bao, S. D. (2000): Soil and Agricultural Chemistry Analysis. – China Agricultural Press, Beijing (in Chinese).
- [14] Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. et al. (2009): Generalized linear mixed models: a practical guide for ecology and evolution. – *Trends Ecol Evol* 24: 127-135.
- [15] Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M. et al. (2011): Why intraspecific trait variation matters in community ecology. – *Trends Ecol Evol* 26: 183-192.
- [16] Burgess, S. S. O., Dawson, T. E. (2010): Predicting the limits to tree height using statistical regressions of leaf traits. – *New Phytologist* 174: 626-636.
- [17] Bussotti, F., Pollastrini, M. (2015): Evaluation of leaf features in forest trees: methods, techniques, obtainable information and limits. – *Ecological Indicators* 52: 219-230.
- [18] Carlucci, M. B., Debastiani, V. J., Pillar, V. D., Duarte, L. D. S., de Bello, F. (2015): Between- and within-species trait variability and the assembly of sapling communities in forest patches. – *Journal of Vegetation Science* 26: 21-31.
- [19] Chauvin, K. M., Asner, G. P., Martin, R. E., Kress, W. J., Wright, S. J., Field, C. B. (2018): Decoupled dimensions of leaf economic and anti-herbivore defense strategies in a tropical canopy tree community. – *Oecologia* 186: 765-782.
- [20] Chmura, D. J., Tjoelker, M. G. (2008): Leaf traits in relation to crown development, light interception and growth of elite families of loblolly and slash pine. – *Tree Physiology* 28: 729-742.
- [21] Cordell, S., Goldstein, G., Mueller-Dombois, D., Vitousek, P. M. (1998): Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. – *Oecologia* 113: 188-196.
- [22] Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O. et al. (2008): Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. – *Ecology Letters* 11: 1065-1071.
- [23] Courbaud, B., Vieilledent, G., Kunstler, G. (2012): Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns. – *Theoretical Ecology* 5: 61-71.
- [24] Curtis, P. S., Ackerly, D. D. (2010): Introduction to a virtual special issue on plant ecological strategy axes in leaf and wood traits. – *New Phytologist* 179: 901-903.
- [25] Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T. et al. (2018): The ecological importance of intraspecific variation. – *Nat Ecol Evol* 2: 57-64.
- [26] Diaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S. et al. (2016): The global spectrum of plant form and function. – *Nature* 529: 167-173.
- [27] Dixon, P. (2003): VEGAN, a package of R functions for community ecology. – *Journal of Vegetation Science* 14: 927-930.
- [28] Dolédec, S., Chessel, D. (1991): Recent developments in linear ordination methods in environmental sciences. – *Advances in Ecology, India* 1: 133-155.
- [29] Falster, D. S., Warton, D. I., Wright, I. J. (2006): User's Guide to SMATR: Standardised Major Axis Tests and Routines. Version 2.0, Copyright 2006. – <http://www.bio.mq.edu.au/ecology/SMATR/>.
- [30] Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K. et al. (2009): Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. – *Ecology* 90: 598-611.
- [31] Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M. et al. (2004): Plant functional markers capture ecosystem properties during secondary succession. – *Ecology* 85: 2630-2637.

- [32] Hausch, S., Vamosi, S. M., Fox, J. W. (2018): Effects of intraspecific phenotypic variation on species coexistence. – *Ecology* 99: 1453-1462.
- [33] He, D., Chen, Y. F., Zhao, K. N., Cornelissen, J. H. C., Chu, C. J. (2018): Intra- and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest. – *Ann Bot-London* 121: 1173-1182.
- [34] Hodgson, J. G., Montserratmartí, G., Charles, M., Jones, G., Wilson, P., Shipley, B. et al. (2011): Is leaf dry matter content a better predictor of soil fertility than specific leaf area? – *Ann Bot-London* 108: 1337-1345.
- [35] Kenzo, T., Iida, S., Shimizu, T., Tamai, K., Kabeya, N., Shimizu, A. et al. (2016): Seasonal and height-related changes in leaf morphological and photosynthetic traits of two dipterocarp species in a dry deciduous forest in Cambodia. – *Plant Ecol Divers* 9: 505-520.
- [36] Kröber, W., Heklau, H., Bruelheide, H. (2015): Leaf morphology of 40 evergreen and deciduous broadleaved subtropical tree species and relationships to functional ecophysiological traits. – *Plant Biology* 17: 373-383.
- [37] Lajoie, G., Vellend, M. (2015): Understanding context dependence in the contribution of intraspecific variation to community trait-environment matching. – *Ecology* 96: 2912-2922.
- [38] Lê, S., Josse, J., Husson, F. (2008): FactoMineR: an R package for multivariate analysis. – *Journal of Statistical Software* 25: 1-18.
- [39] Lepš, J., de Bello, F., Šmilauer, P., Dolezal, J. (2011): Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. – *Ecography* 34: 856-863.
- [40] Li, T. T., Wu, J., Chen, H., Ji, L. Z., Yu, D. P., Zhou, L. et al. (2018): Intraspecific functional trait variability across different spatial scales: a case study of two dominant trees in Korean pine broadleaved forest. – *Plant Ecology* 1-12.
- [41] Lichstein, J. W., Dushoff, J., Levin, S. A., Pacala, S. W. (2007): Intraspecific variation and species coexistence. – *American Naturalist* 170: 807-818.
- [42] Liu, F. d., Yang, W. J., Wang, Z. S., Zhen, X., Hong, L., Ming, Z. et al. (2010): Plant size effects on the relationships among specific leaf area, leaf nutrient content, and photosynthetic capacity in tropical woody species. – *Acta Oecologica* 36: 149-159.
- [43] Luiro, J., Kukkola, M., Saarsalmi, A., Tamminen, P., Helmisaari, H. (2009): Logging residue removal after thinning in boreal forests: long-term impact on the nutrient status of Norway spruce and Scots pine needles. – *Tree Physiology* 30: 78-88.
- [44] Luo, Y. H., Liu, J., Tan, S. L., Cadotte, M. W., Wang, Y. H., Xu, K. et al. (2016): Trait-based community assembly along an elevational gradient in subalpine forests: quantifying the roles of environmental factors in inter- and intraspecific variability. – *PloS One* 11(5): e0155749.
- [45] Lusk, C. H., Reich, P. B., Montgomery, R. A., Ackerly, D. D., Cavender-Bares, J. (2008): Why are evergreen leaves so contrary about shade? – *Trends Ecol Evol* 23: 299-303.
- [46] Mao, W., Felton, A. J., Zhang, T. (2017): Linking changes to intraspecific trait diversity to community functional diversity and biomass in response to snow and nitrogen addition within an Inner Mongolian grassland. – *Frontiers in Plant Science* 8: 339.
- [47] McGill, B. J., Enquist, B. J., Weiher, E., Westoby, M. (2006): Rebuilding community ecology from functional traits. – *Trends Ecol Evol* 21: 178-185.
- [48] Messier, J., McGill, B. J., Lechowicz, M. J. (2010): How do traits vary across ecological scales? A case for trait-based ecology. – *Ecology Letters* 13: 838-848.
- [49] Niinemets, Ü. (2010): A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. – *Ecological Research* 25: 693-714.
- [50] Ordoñez, J. C., van Bodegom, P. M., Witte, J. P. M., Wright, I. J., Reich, P. B., Aerts, R. (2009): A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. – *Global Ecol Biogeogr* 18: 137-149.

- [51] Osnas, J. L., Lichstein, J. W., Reich, P. B., Pacala, S. W. (2013): Global leaf trait relationships: mass, area, and the leaf economics spectrum. – *Science* 340: 741-744.
- [52] Paradis, E., Claude, J., Strimmer, K. (2004): APE: analyses of phylogenetics and evolution in R language. – *Bioinformatics* 20: 289-290.
- [53] Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013): New handbook for standardised measurement of plant functional traits worldwide. – *Aust J Bot* 61: 167-234.
- [54] Pielou, E. C. (1975): *Ecological Diversity*. – Wiley, New York.
- [55] Poorter, H., Jong, R. D. (1999): A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. – *New Phytologist* 143: 163-176.
- [56] Reich, P. B., Walters, M. B., Ellsworth, D. S. (1997): From tropics to tundra: global convergence in plant functioning. – *Proceedings of the National Academy of Sciences of the United States of America* 94: 13730-13734.
- [57] Roche, P., Diazburlinson, N., Gachet, S. (2004): Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? – *Plant Ecology* 174: 37-48.
- [58] Santiago, L. S., Wright, S. J. (2007): Leaf functional traits of tropical forest plants in relation to growth form. – *Funct Ecol* 21: 19-27.
- [59] Sedjo, R., Sohngen, B. (2012): Carbon sequestration in forests and soils. – *Annual Review of Resource Economics* 4: 127-144.
- [60] Shannon, C. E., Weaver, W. (1949): *The Mathematical Theory of Communications*. – University of Illinois Press, Urbana.
- [61] Shipley, B., Vile, D., Garnier, E. (2007): From plant traits to plant communities: a statistical mechanistic approach to biodiversity. – *Science* 316: 201-201.
- [62] Siefert, A., Ritchie, M. E. (2016): Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. – *Oecologia* 181: 245-255.
- [63] Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A. et al. (2015): A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. – *Ecology Letters* 18: 1406-1419.
- [64] Sistla, S. A., Appling, A. P., Lewandowska, A. M., Taylor, B. N., Wolf, A. A. (2015): Stoichiometric flexibility in response to fertilization along gradients of environmental and organismal nutrient richness. – *Oikos* 124: 949-959.
- [65] Smart, S. M., Glanville, H. C., Blanes, M. D., Mercado, L. M., Emmett, B. A., Jones, D. L. et al. (2017): Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. – *Funct Ecol* 31: 1336-1344.
- [66] Tabachnick, B. G., Fidell, L. (2012): *Using Multivariate Statistics*. 6th Ed. – Allyn and Bacon, Boston, MA.
- [67] Vendramini, F., Díaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K., Hodgson, J. G. (2002): Leaf traits as indicators of resource-use strategy in floras with succulent species. – *New Phytologist* 154: 147-157.
- [68] Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007): Let the concept of trait be functional! – *Oikos* 116: 882-892.
- [69] Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C. et al. (2012): The return of the variance: intraspecific variability in community ecology. – *Trends Ecol Evol* 27: 244-252.
- [70] Warton, D. I., Wright, I. J., Falster, D. S., Westoby, M. (2006): Bivariate line-fitting methods for allometry. – *Biological Reviews* 81: 259-291.
- [71] Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F. et al. (2004): The worldwide leaf economics spectrum. – *Nature* 428: 821.
- [72] Xu, R. H. (2003): Measuring explained variation in linear mixed effects models. – *Statistics in Medicine* 22: 3527-3541.

- [73] Zhao, A., Hu, T., Chen, X. (2009): Multiple-scale spatial analysis of community structure in a mountainous mixed evergreen-deciduous broad-leaved forest southwest China. – *Biodiversity Science* 17(1): 43-50 (in Chinese).
[74] Zhou, S., Huang, C., Xiang, Y., Tie, L., Han, B., Scheu, S. (2018): Effects of reduced precipitation on litter decomposition in an evergreen broad-leaved forest in western China. – *Forest Ecology and Management* 430: 219-227.

APPENDIX

Table A1. List of the leaf functional traits and environmental factors (stand structures and soil properties) considered in this study

Group	Traits	Abbreviation	Unit	Min	Max	Mean	STD	Kurtosis	Skewness
Leaf morphology	Leaf thickness	LT	cm	0.1	0.57	0.25	0.11	1.25	0.58
	Leaf area	LA	cm ²	8.32	274.91	45.56	36.85	2.51	9.47
	Leaf dry matter content	LDMC	mg.g ⁻¹	180.63	719.33	392.09	90.57	0.3	0.1
	Leaf density	LD	mg.cm ⁻³	5.17	71.29	29.7	12.2	0.3	0.07
	Specific leaf area	SLA	cm ² .g ⁻¹	59.33	370.85	174.87	72.29	0.72	-0.18
Leaf chemistry	Leaf chlorophyll	LChl	SPAD	29.2	77.9	47.17	9.66	0.93	0.41
	Leaf nitrogen content	LCN	g.kg ⁻¹	9.38	30.47	20.1	5.63	0.12	-1.12
	Leaf nitrogen content per area	N _{area}	g.m ⁻²	0.3	3.98	1.29	0.5	1.34	3.9
	Leaf phosphorus content	LCP	g.kg ⁻¹	0.63	2.52	1.3	0.33	0.86	1.75
	Leaf phosphorus content per area	P _{area}	g.m ⁻²	0.02	0.3	0.09	0.04	1.36	2.62
Stand structures	Tree height	H	m	5.85	18.64	10.21	2.25	1.26	5.24
	Maximum height	H _{max}	m	11.34	812.5	42.78	136.05	5.82	33.95
	Basal area	BA	cm ²	363	2236.18	1099.37	416.74	0.77	1.62
	Canopy size	CA	m ²	39.6	140.4	67.79	18.05	1.8	6.97
	Diameter at breast height	DHB	cm	7.75	17.84	12.97	2.58	-0.05	-0.53
	Stand density	DEN	N.ha ⁻¹	650	2350	1315.44	418.65	0.4	-0.21
	Shannon index	SHI		1.24	2.47	2.02	0.25	-0.63	1.52
	Evenness index	EVE		0.3	0.67	0.5	0.08	-0.17	0.27
Soil properties	Soil water content	SCW	%	3.94	8.34	6.09	1.2	0.1	-0.66
	Soil nitrogen content	SCN	%	0.62	2.27	1.17	0.45	0.85	-0.15
	Organ matters	OM	%	0.44	6.21	2.89	1.51	0.67	-0.28
	Soil potassium content	SCK	mg.kg ⁻¹	26.57	88.13	51.79	15.45	0.68	0.36
	Soil phosphorus content	SCP	g.kg ⁻¹	0.05	0.14	0.08	0.02	1.03	0.36

Table A2. List of the sampled species and their mean values of leaf functional traits. See Table A1 for abbreviations of traits

Species	Family	Genus	LT	LA	SLA	LD	LDMC	LCN	LCP	LChl	N _{area}	P _{area}
<i>Liquidambar formosana</i>	Hamamelidaceae	Liquidambar	0.14	51.54	233.64	29.23	312.99	27.32	1.40	36.90	1.19	0.06
<i>Acer davidii</i>	Aceraceae	Acer	0.14	98.55	229.46	15.23	307.65	21.56	1.32	43.04	0.97	0.06
<i>Alangium chinense</i>	Alangiaceae	Alangium	0.11	95.04	264.33	18.93	287.79	18.46	1.40	42.00	0.72	0.05
<i>Betula luminifera</i>	Betulaceae	Betula	0.18	36.68	252.47	33.12	318.82	18.05	1.47	44.30	0.72	0.06
<i>Bothrocaryum controversum</i>	Cornaceae	Bothrocaryum	0.18	52.57	197.96	21.84	313.74	19.45	1.21	50.68	1.00	0.06
<i>Camptotheca acuminata</i>	Nyssaceae	Camptotheca	0.27	77.51	264.67	8.99	279.17	21.79	1.24	46.99	0.90	0.05

<i>Castanopsis fargesii</i>	Fagaceae	Castanopsis	0.19	19.87	113.15	87.42	484.14	12.83	1.66	46.58	1.16	0.15
<i>Castanopsis platyacantha</i>	Fagaceae	Castanopsis	0.18	22.59	122.52	80.08	495.95	16.86	1.59	46.81	1.40	0.13
<i>Cinnamomum septentrionale</i>	Lauraceae	Cinnamomum	0.30	45.65	144.42	20.11	408.47	18.04	1.20	48.99	1.47	0.11
<i>Cyclobalanopsis glauca</i>	Fagaceae	Cyclobalanopsis	0.24	93.64	254.03	10.37	342.17	12.86	1.09	35.00	0.56	0.04
<i>Diospyros kaki</i>	Ebenaceae	Diospyros	0.25	58.50	285.65	11.16	244.91	16.33	1.13	39.88	0.67	0.05
<i>Elaeocarpus japonicus</i>	Elaeocarpaceae	Elaeocarpus	0.35	30.90	128.63	24.54	394.40	21.80	1.51	54.63	1.76	0.12
<i>Eurya loquaiana</i>	Theaceae	Eurya	0.40	15.81	113.68	42.17	395.44	20.55	1.31	63.50	1.97	0.12
<i>Ilex chinensis</i>	Aquifoliaceae	Ilex	0.43	14.86	133.41	41.39	398.69	21.91	1.25	53.24	1.92	0.11
<i>Kalopanax septemlobus</i>	Araliaceae	Kalopanax	0.26	216.11	168.16	5.43	448.93	23.49	1.35	41.40	1.41	0.08
<i>Liquidambar formosana</i>	Hamamelidaceae	Liquidambar	0.14	44.56	300.43	27.02	243.76	27.76	1.34	35.10	0.92	0.04
<i>Machilus ichangensis</i>	Lauraceae	Machilus	0.24	53.13	147.53	18.94	362.26	14.90	0.87	47.09	1.04	0.06
<i>Mallotus japonicus</i>	Euphorbiaceae	Mallotus	0.20	123.28	211.56	9.97	363.40	20.57	1.42	49.61	0.99	0.07
<i>Padus wilsonii</i>	Rosaceae	Padus	0.19	45.03	191.08	29.91	377.11	23.53	1.22	37.93	1.29	0.07
<i>Phoebe zhennan</i>	Lauraceae	Phoebe	0.21	24.33	136.88	67.03	519.30	18.48	1.59	41.85	1.38	0.12
<i>Photinia beauverdiana</i>	Rosaceae	Photinia	0.54	36.11	234.93	12.66	368.86	27.02	1.18	41.51	1.21	0.05
<i>Platycarya strobilacea</i>	Juglandaceae	Platycarya	0.17	22.28	216.93	87.16	485.59	21.97	1.22	42.13	1.23	0.06
<i>Quercus serrata</i>	Theaceae	Eurya	0.37	12.53	131.77	48.66	338.43	22.80	1.14	54.80	1.73	0.09
<i>Rhododendron stamineum</i>	Ericaceae	Rhododendron	0.36	29.77	92.48	24.35	391.44	21.86	1.87	73.10	2.32	0.21
<i>Rhus chinensis</i>	Anacardiaceae	Rhus	0.17	56.40	218.40	22.24	319.92	25.20	1.36	37.38	1.30	0.08
<i>Schima superba</i>	Theaceae	Schima	0.43	40.08	220.87	9.55	244.05	19.84	1.53	35.60	0.92	0.07
<i>Symplocos setchuensis</i>	Symplocaceae	Symplocos	0.26	29.75	101.65	30.77	357.04	18.04	1.42	63.80	1.85	0.15

Table A3. List of main local environmental conditions of the sampled plots. See Table A1 for abbreviations of environmental Variables and X, Y are the GPS positions of the sampling sites

Plot number	X	Y	H	DHB	DEN	OM	SCW
1	606730	3342355	5.89	7.75	2000	1.30	4.42
2	607442	3342433	9.23	12.14	1225	1.88	5.22
3	607117	3342600	18.64	15.14	2050	0.96	5.68
4	606070	3341997	10.85	15.35	1125	4.82	8.34
5	606070	3341997	10.48	16.25	1225	5.50	6.33
6	605797	3343515	9.76	14.83	2350	6.21	6.78
7	605779	3343579	8.58	13.72	1600	5.18	7.62
8	605819	3343656	10.85	14.30	1450	6.05	5.39

9	605310	3343434	9.89	13.92	1600	3.89	6.72
10	605293	3343421	7.62	8.65	950	4.65	4.32
11	605315	3343441	5.85	9.57	1500	4.76	5.34
12	604510	3344733	11.45	13.75	1700	1.51	7.77
13	604465	3344811	9.83	12.70	700	2.69	6.22
14	605603	3342480	8.79	11.00	1075	1.25	3.94
15	606525	3342562	13.23	13.82	1250	2.01	4.74
16	605542	3342588	11.54	10.64	1475	4.24	3.94
17	605418	3342052	9.90	9.81	1325	2.84	6.78
18	605363	3342035	11.85	17.31	675	1.98	5.01
19	605316	3341863	9.21	13.53	650	2.82	5.72
20	605235	3341875	8.08	11.22	975	1.97	5.27
21	605235	3341875	10.61	15.33	1225	2.69	6.05
22	605297	3341338	12.26	17.84	725	2.72	6.79
23	605254	3340746	12.11	15.74	1025	2.34	5.08
24	605286	3340796	12.42	17.53	800	2.96	5.75
25	605396	3340840	10.73	12.86	1050	2.91	8.07
26	605456	3340905	11.53	8.91	1725	3.70	6.99
27	605540	3340871	9.70	10.72	950	2.16	5.45
28	602463	3342556	10.10	12.72	1275	2.45	7.96
29	602454	3342382	9.78	11.10	1075	0.67	7.96
30	602542	3342373	10.55	12.38	1675	0.44	6.39
31	602615	3342629	7.76	13.25	1725	2.13	5.82
32	602582	3342925	9.46	13.84	1825	2.13	6.03
33	602589	3342973	8.85	12.91	1475	2.23	6.53
34	602586	3343161	9.67	10.41	1275	2.34	6.79

Table A4. Pearson correlation coefficients for species data from the PCA analysis (Fig. 1). The significance level is as follows: * $P < 0.05$, ** $P < 0.01$. See Table A1 for abbreviations of traits

		Leaf morphology				Leaf chemistry				
		LA	SLA	LDMC	LD	LChl	LCN	N _{area}	LCP	P _{area}
Leaf morphology	LT	0.3	0.75**	0.12	-0.35*	0.42*	0.74**	0.07	0.21	-0.19
	LA		0.48**	0	-0.3	0.06	0.58**	-0.06	0.21	-0.22
	SLA			-0.12	-0.54**	0.19	0.78**	-0.32	0.18	-0.44**
	LDMC				0.76**	0.77**	0.25	0.79**	0.76**	0.83**
	LD					0.56**	-0.18	0.78**	0.51**	0.92**
Leaf chemistry	LChl						0.52**	0.72**	0.63**	0.58**
	LCN							0.23	0.51**	-0.05
	N _{area}								0.57**	0.83**
	LCP									0.72**

Table A5. Univariate multiple regression statistics for predicting environmental factors from the leaf traits in total variability in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits. The significant factors are specified by bold values (i.e. p -value < 0.05)

Environmental factors		Chemical traits			Morphological traits		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Soil properties	SCN	0.10	0.60	0.704	0.95	27.78	<.0001
	OM	0.13	0.84	0.531	0.96	40.33	<.0001
	SCK	0.06	0.35	0.877	0.72	3.90	0.034
	SCW	0.17	1.18	0.344	0.79	5.75	0.010
	SCP	0.33	2.71	0.041	0.93	20.50	<.0001
Stand structures	H	0.58	7.79	0.000	0.56	5.82	0.001
	H _{max}	0.46	4.73	0.003	0.47	3.91	0.006
	BA	0.44	4.42	0.004	0.28	1.73	0.152
	CA	0.20	1.42	0.249	0.21	1.16	0.354
	DHB	0.40	3.79	0.010	0.45	3.69	0.008
	DEN	0.25	1.84	0.138	0.20	1.10	0.386
	SHI	0.45	4.58	0.004	0.14	0.73	0.631
EVE	0.29	2.24	0.079	0.13	0.66	0.684	

Table A6. Univariate multiple regression statistics for Predicting environmental factors from the leaf traits in interspecific variability in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits. The significant factors are specified by bold values (i.e. p -value < 0.05)

Environmental factors		Chemical traits			Morphological traits		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Soil properties	SCN	0.09	0.55	0.739	0.12	0.63	0.707
	OM	0.06	0.36	0.870	0.07	0.33	0.917
	SCK	0.07	0.45	0.810	0.23	1.38	0.259
	SCW	0.33	2.79	0.036	0.42	3.25	0.016
	SCP	0.40	3.68	0.011	0.35	2.47	0.049
Stand structures	H	0.31	2.57	0.050	0.32	2.09	0.087
	H _{max}	0.13	0.83	0.539	0.09	0.45	0.838
	BA	0.48	5.08	0.002	0.45	3.62	0.009
	CA	0.26	1.98	0.113	0.30	1.93	0.112
	DHB	0.38	3.46	0.015	0.46	3.79	0.007
	DEN	0.25	1.90	0.127	0.23	1.38	0.260
	SHI	0.13	0.84	0.535	0.20	1.12	0.375
EVE	0.14	0.93	0.474	0.17	0.89	0.515	

Table A7. Univariate multiple regression statistics for predicting environmental factors from the leaf traits in intraspecific variability in CCA. R^2 is squared partial correlations, F is approximation or upper bound, and $Pr > F$ is the probability level. See Table A1 for abbreviations of traits. The significant factors are specified by bold values (i.e. p -value < 0.05)

Environmental factors		Chemical traits			Morphological traits		
		R^2	F	$Pr > F$	R^2	F	$Pr > F$
Soil properties	SCN	0.06	0.35	0.876	0.33	0.75	0.624
	OM	0.15	0.99	0.439	0.70	3.45	0.047
	SCK	0.03	0.18	0.969	0.38	0.93	0.517
	SCW	0.15	1.00	0.436	0.43	1.15	0.407
	SCP	0.15	0.95	0.462	0.27	0.55	0.759
Stand structures	H	0.45	4.62	0.003	0.41	3.08	0.020
	H _{max}	0.21	1.48	0.227	0.53	5.12	0.001
	BA	0.16	1.05	0.407	0.29	1.82	0.133
	CA	0.14	0.90	0.496	0.22	1.29	0.297
	DHB	0.22	1.57	0.202	0.08	0.38	0.885
	DEN	0.11	0.71	0.624	0.15	0.80	0.580
	SHI	0.41	3.81	0.009	0.12	0.60	0.727
	EVE	0.29	2.25	0.077	0.11	0.57	0.752

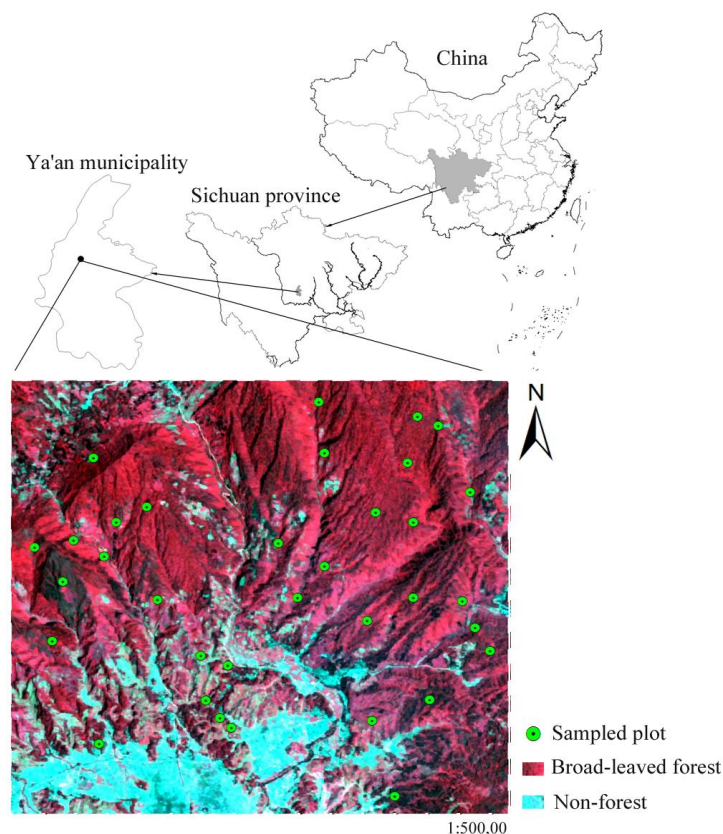


Figure A1. Map of the study site in Shangli town of Ya'an city, southwest Sichuan, western China. 34 plots are shown used green dot. Data obtained from the National Fundamental Geographic Information System (NFGIS, <http://ngcc.sbsm.gov.cn/>), then edited using ArcGIS 10.2 (ESRI, Redlands, CA, USA)