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Authors: Jiang, Yong, Chen, Xingbin, Ma, Jiangming, Liang, Shichu, Huang, Jing, et al.

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Interspecific and Intraspecific Variation in Functional Traits of Subtropical Evergreen and Deciduous Broadleaved Mixed Forests in Karst Topography, Guilin, Southwest China

Yong Jiang^{1,2}, Xingbin Chen³, Jiangming Ma^{1,2,4}, Shichu Liang^{1,2}, Jing Huang^{1,2}, Runhong Liu^{1,2}, and Yuanfang Pan^{1,2}

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Abstract

Interspecific variation in plant functional traits is the basis of species coexistence in natural ecosystems. However, intraspecific variation is extremely important to community assemblage as well. Here, we quantify leaf trait variation within and across 32 dominant shrub species within two different leaf forms (16 evergreen species and 16 deciduous species) in subtropical evergreen and deciduous broadleaf mixed forest in the Karst topography of Guilin, southwest China. Results showed that leaf area (LA) and leaf thickness (LT) of evergreen species were significantly lower than those of deciduous species, whereas specific leaf areas (SLA) and leaf dry matter content (LDMC) showed the opposite pattern. For SLA and LA, the majority variance was found among species (50.82% vs. 65.01%) and little was found within species (22.98% vs. 27.89%), whereas the largest variation was within species (44.87% vs. 48.2%) with little among species (40.73% vs. 43%) for LDMC and LT. The large variability of LDMC and LT within species may reflect niche differentiation and the importance of intraspecific variation on species coexistence. Our results will help design conservation strategies for this unique subtropical evergreen-deciduous broadleaved forest ecosystem.

Keywords

functional traits, variation coefficient, interspecific variations, intraspecific variations, evergreen and deciduous plants

Introduction

Functional traits have been extensively used to describe, group, and rank species according to their functions (Baraloto et al., 2010). The study of a plant's functional traits is becoming a high priority area of research in the field of plant ecology because of its offering a promising path to understanding and predicting how species properties and composition change along geographical gradients (Díaz, Noy-Meir, & Cabido, 2001; McGill, Enquist, Weiher, & Westoby, 2006; Westoby & Wright, 2006). Aspects such as plant morphology, function, and the diversity of a community can be partially assessed by determining variation in plant traits (Díaz et al., 2007; Westoby, Falster, Moles, Vesk, & Wright, 2002). While broad interspecific comparisons invariably focus on the mean with little or no attention to within-species

¹Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Ministry of Education, Guangxi Normal University, Guilin, Guangxi, China

²College of Life Sciences, Guangxi Normal University, Guilin, Guangxi, China

³Jiangxi Provincial Key Lab for Plant Biotechnology, Jiangxi Academy of Forestry, Nanchang Jiangxi, China

⁴University Key Laboratory of Karst Ecology and Environmental Change of Guangxi Province, Guangxi Normal University, Guilin, Guangxi, China

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Corresponding Authors:

Jiangming Ma, College of Life Sciences, Guangxi Normal University, Guilin, Guangxi 541004, China.

Email: mjming03@gxnu.edu.cn

Shichu Liang, College of Life Sciences, Guangxi Normal University, Guilin, Guangxi 541004, China.

Email: gxlsc@sina.com



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variation among co-occurring individuals (Preston, Cornwell, & DeNoyer, 2006), there is now growing evidence that intraspecific functional variability, as well as interspecific variability, can have significant effects on ecosystem functioning (Albert et al., 2010).

The growing interest in the intraspecific variability of plant functional traits can be explained by at least three factors. First, factors shaping trait coordination may differ within- and between-species, which could result in dissimilarities between trait relationships at these two levels, the need for caution when interpreting such correlations as true functional tradeoffs (Cianciaruso, Batalha, Gaston, & Petchey, 2009). Second, the mean value as well as the overall variability in functional traits is likely to vary within species, with important implications for their response to changes in climate or other environmental factors (Laforest-Lapointe, Martínez-Vilalta, & Retana, 2014). Finally, underlying mechanisms driving both within- and among-species trait variation have frequently been linked to the regeneration niche (Cornwell, & Ackerly, 2009) or resource partitioning (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Stubbs & Bastow Wilson, 2004). As such they need to be considered when exploring within- and among-species trait variation in diversity maintaining mechanisms of plant ecology.

Evergreen broadleaved forests are a major forest type in the subtropical region of China and are a globally distinct forest ecosystem at latitudes of 25°N to 35°N. With increasing altitude and decreasing temperature, subtropical evergreen-deciduous broadleaved forests become the dominant vegetation type. Evergreen and deciduous species typically have distinct morphological and functional features (Huang et al., 2015), which are an ideal for studies focusing on the mechanisms of species coexistence and trait variation. The topography of Karst landscape is unique, shaped by the dissolution of one or more layers of soluble bedrock, usually carbonate rock such as limestone or dolomite (Fan et al., 2011). The Karst area in southwestern China is distinct to other Karst areas at similar latitudes because of abundant precipitation there. Rainfall is concentrated in the growing seasons, from April to September. Meteorological data show that two consecutive rainfall events normally occur 7 to 10 days apart during the growing season (Wu, Tong, & Yang, 2003). Plant species with different leaf life spans (e.g., deciduous and evergreen trees) usually occupy different habitat types. Several hypotheses have been proposed for the advantages of having a longer or shorter leaf life span (Aerts, 1995; Chabot, & Hicks, 1982; Kikuzawa, 1991). For example, deciduous woody species show higher potential growth rates, higher specific leaf areas (SLA) and higher photosynthetic rates than evergreen species (Antúnez, Retamosa, & Villar, 2001; Cornelissen, Diez, & Hunt, 1996; Reich, Walters, & Ellsworth, 1992). In subtropical forests, SLA illustrates the differences

between evergreen and deciduous leaf phenology type (Cornelissen et al., 2003; Kröber, Böhnke, Welk, Wirth, & Bruehlheide, 2012). Leaf dry matter content (LDMC) is a better predictor of location on an axis of resource capture, usage, and availability. It correlates negatively with potential relative growth rate, and positively with leaf lifespan (Cornelissen et al., 2003). Leaf area (LA) has important consequences for leaf energy and water balance. Leaf thickness (LT) reflects to species' strategies for resource acquisition and use (Vile et al., 2005). For example, the amount of light a leaf absorbed and the diffusion pathway of CO₂ through its tissues depends on its thickness (Syvertsen, Lloyd, McConchie, Kriedemann, & Farquhar, 1995; Westoby et al., 2002). The main objective of this study was (a) to test the difference of traits (i.e., through comparing the means of traits) and trait variations (i.e., through comparing the coefficients of the variation of traits) between deciduous and evergreen trees of Karst habitats in China and (b) to determine the relative contribution of the variability of each trait within species and interspecific levels between deciduous and evergreen trees in Karst habitats. Our hypothesis was the relative contribution of the variability of each trait within species is prominent and important.

Methods

Study Sites

The study was conducted in the Karst topography of Guilin, southwest China (109°36'–111°29' E, 24°15'–26°23' N; Figure 1). The study location is characterized by a typical middle subtropical moisture and monsoon climate, with warm and abundant rainfall at 100 to 500 m elevation. The mean annual precipitation is 1926 mm, and the evaporation capacity change ranges from 1490 to 1905 mm. Rainfall distribution is uneven during the year with the total from April to July accounting for 62% of the annual rainfall. The mean annual air temperature is 19°C followed by a frost-free period of 309 days during which much of the vegetation type is shrub. We selected 32 species for our study, which are numbered on the Boxplot in Figure 2 (Appendix: Table A1). Numbers 1 to 16 were evergreen shrub trees: *Tarenna depauperata*, *Rapanea neriifolia*, *Decaspermum esquirolii*, *Ligustrum tenuipes*, *Ilex bioritsensis*, *Loropetalum chinense*, *Secamone sinica*, *Pyracantha fortuneana*, *Rhamnus kwangsiensis*, *Wikstroemia indica*, *Elaeagnus glabra*, *Salacia sessiliflora*, *Ligustrum lucidum*, *Viburnum propinquum*, *Murraya paniculata*, and *Xylosma controversum*. Numbers 17 to 32 were deciduous shrub trees: *Rhamnus leptophylla*, *Rhamnus lamprophylla*, *Alchornea trewioides*, *Spiraea cantoniensis*, *Paliurus ramosissimus*, *Mallotus repandus*, *Ficus erecta* var. *beeheyana*, *Grewia biloba* var. *parviflora*, *Ligustrum quihoui*, *Flueggea*

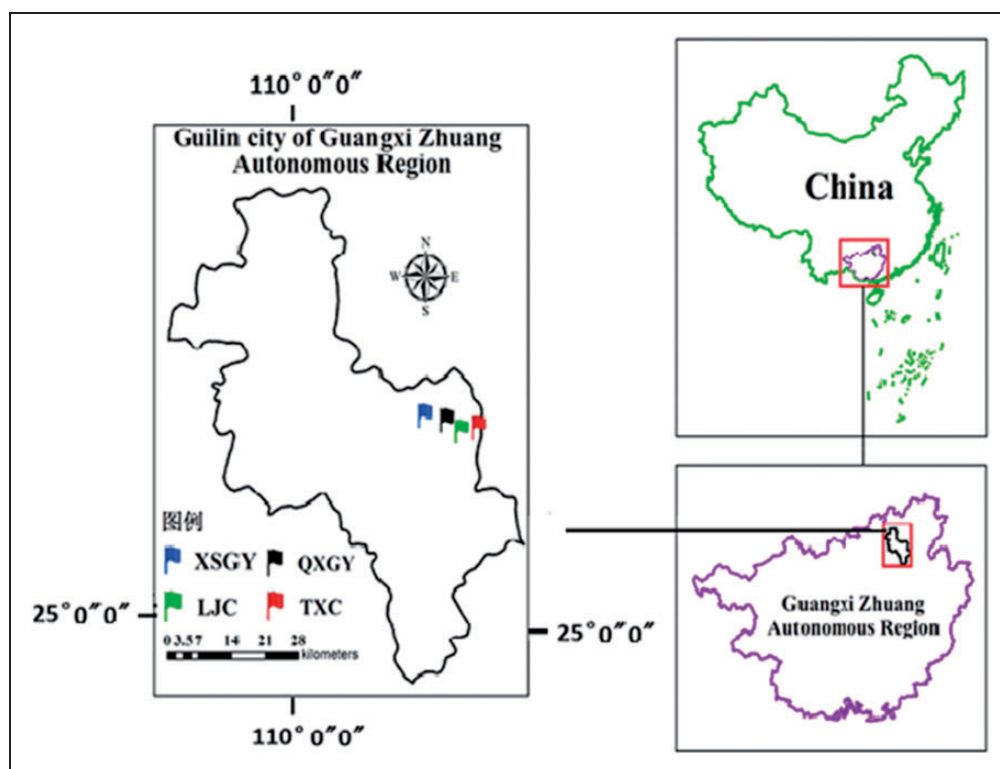


Figure 1. Sketch map of the four sampling sites in Guilin city, Guangxi Zhuang Autonomous Region, China. The flags indicate the locations of the plots.

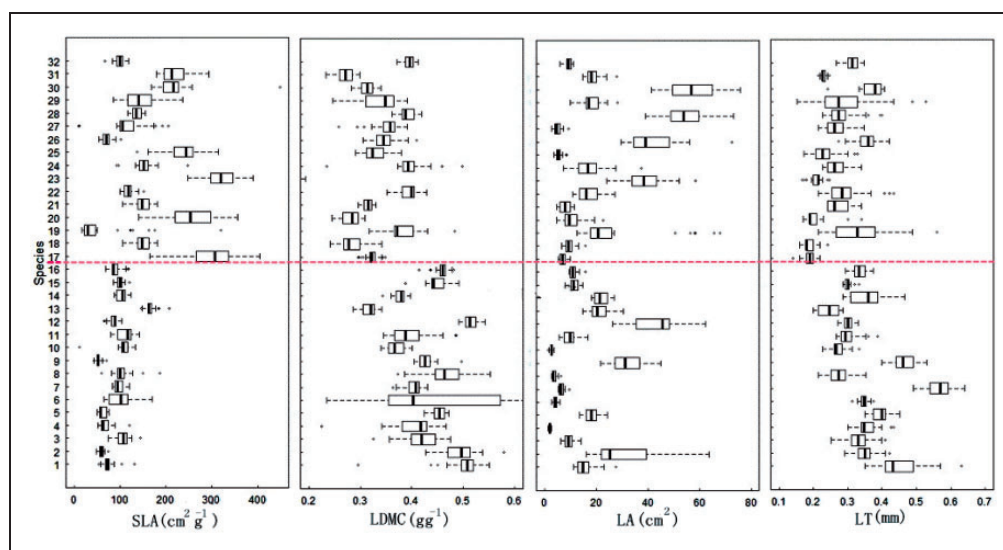


Figure 2. Boxplot of the four plant functional traits of evergreen and deciduous trees among the 32 tree species. Number 1 to 16 were evergreen shrub trees: *Tarenna depauperata*, *Rapanea nerifolia*, *Decaspermum esquirolii*, *Ligustrum tenuipes*, *Ilex boriensis*, *Loropetalum chinense*, *Secamone sinica*, *Pyracantha fortuneana*, *Rhamnus kwangsiensis*, *Wikstroemia indica*, *Elaeagnus glabra*, *Salacia sessiliflora*, *Ligustrum lucidum*, *Viburnum propinquum*, *Murraya paniculata*, *Xylosma controversum*, and numbers 17 to 32 were deciduous shrub trees: *Rhamnus leptophylla*, *Rhamnus lamprophylla*, *Alchornea trewioides*, *Spiraea cantoniensis*, *Paliurus ramosissimus*, *Mallotus repandus*, *Ficus erecta* var. *beecheana*, *Grewia biloba* var. *parviflora*, *Ligustrum quihoui*, *Flueggea suffruticosa*, *Lagerstroemia indica*, *Cephalanthus tetrandrus*, *Croton tiglium*, *Carpinus viminea*, *Cudrania cochinchinensis*, *Glochidion puberum*.

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Leaf Trait Measurement

During June 2012, we selected 30 individuals for each of the 32 species at four sampling sites, which were all in the subtropical evergreen and deciduous broadleaf mixed forest of the Karst topography of Guilin, southwest China (Figure 1). Our sample selection was based on the following principles: (a) The species were sufficiently dominant in a given community and (b) the species were truly site- or habitat-specific, that is, only found only in a particular community. The individuals selected were randomly collected from location distant from one another to reduce the likelihood of collecting genetically similar individuals. We collected three fully expanded, nonsenescent leaves from three branches of each individual. All individuals within a species were collected on the same day within a 1-h period, and all leaves from all species were collected during a 4-day period.

In total, 32 species (960 individuals) were collected from the four sampling sites. SLA ($\text{cm}^2 \text{g}^{-1}$) was calculated as LA divided by leaf dry mass (LDMC; after drying for 72 h at 70°C). LDMC ($\text{g} \cdot \text{g}^{-1}$) was the oven-dried mass divided by the fresh mass (Poorter et al., 2008). LA (mm) was measured for each fresh leaf using a CI-203 Portable Laser Area Meter (CID Inc., Camas, WA, USA). LT (mm) was measured at an average of about 0.25 cm on each side of the main vein, but avoiding the main vein, using a vernier caliper with an accuracy of 0.02 mm.

Data Analysis

First, we assessed differences in the four plant functional traits (SLA, LDMC, LA, and LT) between evergreen and deciduous tree species using Wilcoxon tests, as all the trait variables checked did not have normal distribution. Second, we applied the conventional coefficients of variation formula ($\text{CV} = \text{traits (SD)} / \text{traits (mean)} \times 100\%$) to calculate the CVs' values, where traits (SD) is the sample standard deviation and traits (mean) is the sample mean. The coefficient is usually presented as a percentage by multiplying it by 100 (Sokal, & Braumann, 1980). We compared the coefficients of variation of the four studied traits at interspecific and intraspecific scales between evergreen and deciduous tree species. We used mixed-effects models to divide the variance of these four leaf traits into leaf phenology, and interspecific and intraspecific scales, using a restricted maximum likelihood method with the functions of "lme" and "varcomp" in R v.2.11.1 environments (R Foundation for Statistical Computing, Vienna, AT), in which the trait in question

was the dependent variable. Leaf phenology, at interspecific and intraspecific levels, was included as random effects, and no predictor variables were used. The variance attributable to each hierarchical level was expressed as a percentage of the total variance.

Results

The Difference in Plant Functional Traits Between Evergreen and Deciduous Trees

The Wilcoxon tests showed significant differences among the four plant functional traits (SLA, LDMC, LA, and LT) between evergreen and deciduous trees (Figure 2, $p < .01$). For SLA and LA, deciduous trees had, on average, relatively higher values than evergreen trees. However, for LDMC and LT, evergreen trees showed relatively higher values than deciduous trees.

Coefficients of Variation in Leaf Functional Traits Between Evergreen and Deciduous Trees

Figure 3 shows substantial intraspecific and interspecific variability among the four plant functional traits between evergreen and deciduous trees, with coefficients of variation (CV) ranging from 11.55% to 30.10% at intraspecific level and 2.44% to 56% at interspecific level. For SLA, the CV at intraspecific level was higher than at interspecific level in evergreen trees, but the trend was the inverse in deciduous trees. For LDMC, CVs in both evergreen and deciduous trees showed that interspecific level was significantly higher than intraspecific level. LA and LT showed a consistent pattern in CVs in both evergreen and deciduous trees, but their CVs at intraspecific level were higher than at interspecific level.

Variance in Decomposition of Leaf Habit, Interspecific and Intraspecific to Different Kinds of Leaf Functional Traits

There was a distinct pattern in the variance in decomposition of leaf phenology, interspecific and intraspecific, of four plant functional traits (see Table 1). For SLA and LA, the majority of variation was interspecific variability rather than intraspecific, with very little variation of the leaf phenology. LDMC and LT exhibited the largest variation at intraspecific scale and a relative low percentage of the total variance at interspecific scale and still the less leaf phenology scale.

Discussion

Significant differences were found among the four leaf functional traits (SLA, LDMC, LA, and LT) of evergreen and deciduous trees, indicating that the driving traits of

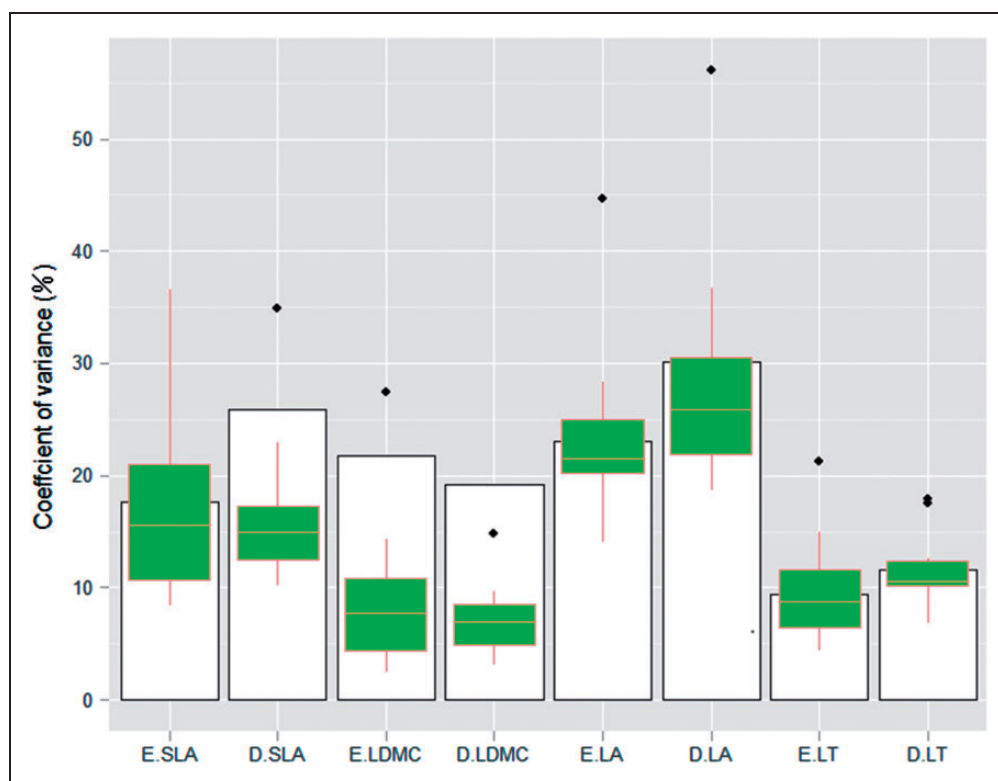


Figure 3. Coefficient of variance among the four plant functional traits between evergreen and deciduous trees. Histograms represent the interspecific coefficient of variation and boxplots represent the intraspecific coefficient of variation. E = Evergreen trees; D = Deciduous trees.

Table 1. Variance Partitioning of Leaf Habit, Interspecific and Intraspecific to Different Kinds of Leaf Functional Traits.

Traits	Percentage of contribution (%)			
	Leaf phenology	Interspecific	Intraspecific	Random error
SLA (cm^2/g)	22.4	50.82	22.98	3.8
LDMC (g/g)	11.9	40.73	44.87	2.5
LA (cm^2)	2.5	65.01	27.89	4.6
LT (mm)	3.1	43.0	48.2	5.7
Mean	9.97	49.89	35.99	4.15

variation may be attributable to the different strategies of evergreen and deciduous species. For SLA, evergreen trees had relatively lower values than deciduous trees but significantly higher values than deciduous trees in LT (Figure 2). Species with a low SLA (or evergreen species) were thought to be relatively higher construction costs and had a slower growing conservative strategy (Villar, & Merino, 2001). They tended to have thicker leaves than species with a high SLA (or deciduous species) with preferential allocation to photosynthesis and growth (Wright et al., 2004). A low SLA signifies a higher leaf weight per LA, which is caused by thicker

leaves (Castro-Díez, Puyravaud, & Cornelissen, 2000). Our results support this notion. For LDMC, deciduous trees showed lower values than evergreen trees but significantly higher ones than evergreen trees in LA. In comparison with evergreen species, deciduous species generally had innately fast growth, which corresponded with their having short-lived leaves of higher SLA, lower leaf dry matter content, lower tensile strength (thinner leaves) and high palatability to generalist invertebrate herbivores. A continuum in carbon storage strategies contributes to a continuum in the growth of LA for deciduous species, thereby obtaining more carbohydrates in the growing season and using acquisitive strategies to overcome a negative impact on growth under more severe environmental conditions. Recently, Tang, Huang, Ding, and Zang (2016) demonstrated that SLA, LDMC, LA, and SSD (stem specific density) functional traits showed significant differences between interspecific and intraspecific scales in subtropical evergreen and deciduous broad-leaved mixed forest in the Hubei province of central southern China (Tang et al., 2016). We found a consistent pattern of variation for SLA, LDMC, and LA between evergreen and deciduous trees in the Karst topography of our study sites. However, plant functional distribution ranges in Karst topography are significantly lower than these of fertile soils in the Hubei province of central

southern China, especially for SLA with ranges of 100 to 200 cm² g⁻¹, compared with the 300 to 400 cm² g⁻¹ ranges (Tang et al., 2016). SLA has been considered as a useful proxy for the axis of resource capture and utilization (Schamp, & Aarssen, 2009). High SLA leaves work best in resource-rich environments while low SLA leaves work better in resource-poor environments where the retention of captured resources is a higher priority. The Karst topography of our study sites were characterized by the dissolution of one or more layers of soluble bedrock and had shallower soils and poorer soil nutrients. Thus, our study results imply that an observed lower SLA in Karst landscapes reflects alternative predictors in resource-poor environments.

Studies have shown that the variation of leaf phenology at interspecific and intraspecific scales was not consistent among the leaf traits. For example, Roche Diaz-Burlinson, and Gachet (2004) observed 36.5% of intraspecific variability for SLA but only 9% for LDMC in Mediterranean vegetation. Wilson, Thompson, and Hodgson (1999) found 32% (angiosperms) of intraspecific variability for SLA and 14% (angiosperms) for LDMC. Our results showed that SLA and LA varied among species more than within species, whereas leaf traits LDMC and LT exhibited higher variation within species. For SLA and LA, intraspecific variability was found relatively important, suggesting that the leaves might be more plastic and allow changes in individual differences to increase individual variation, thus making full use of sunlight intensity from horizontal time and vertical angle. LDMC and LT exhibited higher variation within species, indicating that this variation pattern might be related to the competitive exclusion of similar individual plants or local niche differentiation. The role of such leaf traits defines fine-scale niche differentiation (Ackerly, Schwilk, & Webb, 2006), and the importance of intraspecific variation for species coexistence (Violle et al., 2012).

This study suggests that the interspecific average variance was 49.89%, while the percentage of intraspecific average variance was 35.99%. Such a difference cannot be ignored. It suggests that variation in leaf traits within species may be important for shaping community assembly and species coexistence across spatial scales. Albert et al. (2010) have similarly reported that intraspecific variability in the functional traits of tree height, SLA, LDMC, leaf carbon, and leaf nitrogen content of herbaceous species in the French Alps was species-specific and trait-specific. Jung et al. (2010) and Bolnick et al. (2011) also noted that species response to biotic and abiotic filters, which influence the population dynamics and the community structure, is highly dependent on intraspecific trait variability. Intraspecific trait variation is believed to play an important role in resistance to disturbances, competition, coexistence, and productivity

(Kang, Chang, Yan, & Wang, 2014; Weiher et al., 1999). Understanding to what extent intraspecific variability mediate species coexistence and plant associations is therefore necessary. However, in most empirical studies, plant traits have been assessed mainly at the interspecific level, while the intraspecific variability has been largely ignored (Bolnick et al., 2011; de Bello et al., 2011). We argue that trait variability should be evaluated at the individual plant level in order to understand patterns of species coexistence and community dynamics. A poor understanding of intraspecific trait variation could be one reason why models predicting plant performance or abundance have low predictability (Albert et al., 2010). In such cases, the residuals of these models may be explained by intraspecific variation (Cianciaruso et al., 2009; Violle et al., 2012).

Implications for Conservation

In this study, SLA and LA leaf traits varied more between species than within species. Leaf traits LDMC and LT, however, showed higher variations within species. Based on variation, partitioning of leaf traits among different ecological scales was not coordinated, and we found that different leaf traits play different roles in plant ecological strategies. The large variability of LDMC and LT within species may reflect niche differentiation, and the importance of intraspecific variation which affects species coexistence. We argue that trait variability should be evaluated at individual plant level in order to understand patterns of species coexistence and community dynamics. Subtropical evergreen-deciduous broad-leaved forests are among the most biodiverse forests in the world and are considered extremely vulnerable to global climate change (Chi et al., 2015). These forests are important habitats for endangered species in the Karst landscapes of Guilin, southwest China. As our study has shown, variability at individual level should be considered in order to conserve the regional endemic biodiversity and the integrity of the forest landscape. A better understanding of intraspecific variation is of central importance to design of conservation areas and to develop conservation strategies for this unique subtropical evergreen-deciduous broadleaved forest and its related ecosystems.

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Authors' Contributions

Jiangming Ma and Shichu Liang conceived the study and field work. Jing Huang, Runhong Lui and Yuanfang Pan collected the field data and did the morphological identifications. Yong Jiang analyzed the data. Yong Jiang and Xingbin Chen wrote the first

draft of the manuscript. All authors read and approved the final manuscript. Yong Jiang and Xingbin Chen contributed equally to this work.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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Appendix

Table A1. List of the Investigated Species and Their Characteristics in the Subtropical Evergreen-Deciduous Broadleaved Mixed Forest in Guilin city, Guangxi Zhuang Autonomous Region, China.

Species	Leaf habit	Growth Form	Number	Site
<i>Tarenna depauperata</i>	Evergreen	Shrub	30	LJC
<i>Rapanea neriifolia</i>	Evergreen	Shrub	30	LJC
<i>Decaspermum esquirolii</i>	Evergreen	Shrub	30	LJC
<i>Ligustrum tenuipes</i>	Evergreen	Shrub	30	TXC
<i>Ilex bitorisensis</i>	Evergreen	Shrub	30	LJC
<i>Loropetalum chinense</i>	Evergreen	Shrub	30	TXC
<i>Secamone sinica</i>	Evergreen	Shrub	30	QXGY
<i>Pyracantha fortuneana</i>	Evergreen	Shrub	30	TXC
<i>Rhamnus kwangsiensis</i>	Evergreen	Shrub	30	XSGY
<i>Wikstroemia indica</i>	Evergreen	Shrub	30	QXGY
<i>Elaeagnus glabra</i>	Evergreen	Shrub	30	TXC
<i>Salacia sessiliflora</i>	Evergreen	Shrub	30	LJC
<i>Ligustrum lucidum</i>	Evergreen	Shrub	30	XSGY
<i>Viburnum propinquum</i>	Evergreen	Shrub	30	XSGY
<i>Murraya paniculata</i>	Evergreen	Shrub	30	XSGY
<i>Xylosma controversum</i>	Evergreen	Shrub	30	XSGY

(continued)

Table A1. Continued

Species	Leaf habit	Growth Form	Number	Site
<i>Rhamnus leptophylla</i>	Deciduous	Shrub	30	QXGY
<i>Rhamnus lamprophylla</i>	Deciduous	Shrub	30	QXGY
<i>Alchornea trewioides</i>	Deciduous	Shrub	30	TXC
<i>Spiraea cantoniensis</i>	Deciduous	Shrub	30	XSGY
<i>Paliurus ramosissimus</i>	Deciduous	Shrub	30	LJC
<i>Mallotus repandus</i>	Deciduous	Shrub	30	TXC
<i>Ficuserecta</i> var. <i>beeheyana</i>	Deciduous	Shrub	30	XSGY
<i>Grewia biloba</i> var. <i>parviflora</i>	Deciduous	Shrub	30	QXGY
<i>Ligustrum quihoui</i>	Deciduous	Shrub	30	QXGY
<i>Flueggea suffruticosa</i>	Deciduous	Shrub	30	QXGY
<i>Lagerstroemia indica</i>	Deciduous	Shrub	30	TXC
<i>Cephalanthus tetrandrus</i>	Deciduous	Shrub	30	TXC
<i>Croton tiglium</i>	Deciduous	Shrub	30	QXGY
<i>Carpinus viminea</i>	Deciduous	Shrub	30	QXGY
<i>Cudrania cochinchinensis</i>	Deciduous	Shrub	30	QXGY
<i>Glochidion puberum</i>	Deciduous	Shrub	30	QXGY

Note. The nomenclature follows flora of China.