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Variations in Leaf Functional Traits Across Ecological Scales in Riparian Plant Communities of the Lijiang River, Guilin, Southwest China

Runhong Liu[1,2], Shichu Liang[1,2], Wenxing Long[3], and Yong Jiang[1,2]

Abstract

Knowing plant functional trait variation is integral to understanding species coexistence and biodiversity maintenance. To explore how variations in a given trait vary across different spatiotemporal and ecological organizational scales, we performed a linear mixed model and *varcomp* function to partition the variance in four key functional traits (specific leaf area [SLA], leaf area [LA], leaf thickness [LTH], and leaf chlorophyll content [CHL]) from 5,418 individuals of 51 species across four nested ecological scales (plot, species, individual, and leaf) in riparian plant communities of the Lijiang River, Guilin, southwest China. We found that the relative contribution of all traits is similar: species (0.51–0.70) > individual (0.21–0.27) > leaf and error (0.09–0.20) > plot (0–0.07). For all traits, interspecific variability was higher than intraspecific variability and the plot level accounted for only a minute percentage of the total variance, despite relatively high species turnover between plots. These results suggest that the variation of leaf functional traits is dominated by interspecific variation, but data also showed a substantial amount of intraspecific trait variability. Thus, intraspecific variation of functional traits should be taken into account if assembly rules in plant communities are to be properly understood. The low, or even lack of, functional trait variance at plot level provides substantial support for the idea that trait-based habitat filtering could play a central role in plant community assembly.

Keywords

plant functional traits, trait variation, scales, riparian plant communities, Lijiang River

Introduction

Plant functional traits, defined as any morphological, physiological, or phenological features that impact fitness indirectly via their effects on growth, reproduction, and survival (the three components of individual performance), link environmental factors, individual plants, and ecosystem structures, processes, and functions (Cornelissen et al., 2003; Violle et al., 2007). The most favored traits are those that are also relatively easy and inexpensive to measure for large numbers of plant species. Recent evidence of variations in plant functional traits, from intra-individual to community scale, suggest that trait-based approaches are highly effective for addressing contemporary ecological questions (e.g., M. Kang, Chang, Yan, & Wang, 2014; Messier, McGill, & Lechowicz, 2010). A core assumption of trait-based ecology is that trade-offs and constraints have shaped phenotypic variations in different trait dimensions across ecologically relevant spatial and temporal scales (Messier, McGill, Enquist, & Lechowicz, 2017). Indeed,

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many ecologists are now persuaded that functional trait approaches are the best available approach for research ranging from studies of organisms to studies of ecosystems.

Variations in plant functional traits are the product of evolutionary and environmental drivers that operate at different scales, which are challenging to differentiate among them (Pierce, Luzzaro, Caccianiga, Ceriani, & Cerabolini, 2007; Reich, Wright, et al., 2003). However, in most previous studies, trait-based approaches tend to rely on a tacit assumption that intraspecific trait variability is negligible compared to interspecific variability, and that species can be characterized by mean trait values, regardless of environmental or genetic context (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Auger & Shipley, 2013; Lichstein, Dushoff, Levin, & Pacala, 2007). We believe that variance within species is dependent on a consideration on all factors (i.e., genetic, developmental, and environmental factors) (Bolnick et al., 2011; Fu et al., 2013; Violle et al., 2012). In evolutionary biology, it has been established that intraspecific variation is a necessary condition for species to adapt to environmental change (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011). For instance, intraspecific trait variability enhances mean plant responses to environmental variation as well as to niche partitioning and is especially important in enabling species to establish in a larger area of the environmental gradient (Carlucci, Debastiani, Pillar, & Duarte, 2015). On the other hand, there is growing evidence that high levels of trait disparity are being observed within communities, indicating that the environmental filtering is the primary driving force shaping optimal trait values, which then select an appropriate species mixture. For example, Messier et al. (2010) studied trait variation across ecological scales in lowland tropical rainforests, and the results of their study showed a lack of variance at the plot level, which lends substantial support to the idea that trait-based environmental filtering plays a central role in plant community assembly. Therefore, identifying which ecological scales account for the greatest variation in traits can help focus research efforts on patterns and processes at the spatiotemporal scales that are ecologically most important (McGill, 2008).

Several previous studies have already addressed functional trait variation within a single organism (e.g., Piersma & Drent, 2003), within a species (e.g., Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Bolnick et al., 2011; Clark et al., 2011; Fajardo & Piper, 2011; Jung et al., 2014; Laughlin, Joshi, Bodegom, Bastow, & Fulé, 2012; Mitchell & Bakker, 2014; Violle et al., 2012), among species (e.g., Comas & Eissenstat, 2009; Fajardo & Siefert, 2016; Hättenschwiler, Aeschlimann, Coûteaux, Roy, & Bonal, 2008; Reich, Buschena, et al., 2003; Weedon et al., 2009; Westoby, Falster, Moles, Vesk, & Wright, 2002), and among communities (Ackerly & Cornwell, 2007; Baraloto et al., 2010). These analyses assume that variance in functional traits can focus on only one biological organizational level, albeit with several traits, and therefore a quantification comparison of trait variation across different scales is still limited. It is urgent that researchers begin to view variance in plant functional traits separately across different biological organizational levels of comparison.

Riparian zones are an important buffer zone between aquatic and terrestrial ecosystems for exchanging materials, energy and information and have unique biotic, biophysical and landscape characteristics (Qin, Xin, Wang, & Xiao, 2017). Riparian vegetation is an essential part of riparian ecosystems and has crucial ecological functions, such as providing food and habitats for terrestrial organisms, maintaining ecosystem stability, and providing a buffer zone that filters sediment, controls nutrients, and stabilizes riverbanks (Alahuhta, Heino, & Luoto, 2011; Richardson et al., 2007). They are greatly affected by fluvial processes such as flooding and the deposition of alluvial soil and form a distinctive flora in structure and function from adjacent terrestrial vegetation (Richardson et al., 2007). Typical trees in these forests tend to be malformed (i.e., twisted and misshapen), and species are more adaptable to habitats within a matrix of vegetation that is less specialized and less frequently disturbed (Lyon & Gross, 2005). Several studies have found that individuals of species in riparian zones increase their leaf gas exchange in response to submergence stress so as to cope with oxygen limitation (Huang, Wang, Ren, Qin, & Wu, 2017; Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Mommer, Lenssen, Huber, Visser, & de Kroon, 2006). Thus, riparian zones are particularly important for studying the role of plant functional trait variations in community ecology.

In this study, we applied a linear mixed model and *varcomp* function to partitioning the variance of four key functional traits (SLA, LA, LTH, and CHL) across four hierarchically structured ecological scales (plot, species, individual, and leaf) in riparian plant communities of the Lijiang River, Guilin, southwest China. Specifically, we asked the following three questions: (a) What are the relative contributions of four nested ecological scale variabilities in driving functional trait responses to riparian zone habitats of the Lijiang River? (b) What are the dominant sources of variation for different traits across different spatial scales? (c) Is intraspecific functional trait variability negligible compared to interspecific variability? Answering these questions will show whether or not we are justified in believing that functional mean trait values can adequately represent all populations and individuals of a species in multi-species studies.

Methods

Study Area

The study was conducted in the upper reaches of the riparian zones of the Lijiang River, southwest China (110°18′–110°27′ E, 25°18′–25°32′ N; Figure 1). The Lijiang River belongs to the upper reaches of the Guijiang River in Xijiang River of the Pearl River Basin and originates from the northeast side of Mao'er Mountain, which is the highest peak in South China (2,141.5 m). Lijiang River flows through five cities or counties (Xing'an, Lingchuan, Guilin, Yangshuo, and Pingle) from north to south. It can be divided into upper, middle, and lower reaches according to precipitation, topography, and runoff characteristics, and the part between headstream and Guilin is the upper reaches. The Lijiang River riparian zones lie in low latitudes and are affected by a typical middle subtropical moist monsoon climate: hot and wet in summer and cold and dry in winter. Annual temperatures range from 17.8 to 19.1°C and annual precipitation is between 1,500 and 2,600 mm (1960–2010). The average annual evaporation is between 1,377 and 1,857 mm (Duan, Wang, Zhang, Li, & Huang, 2014). The Lijiang River is recharged by rain, and the water level changes quickly in response to precipitation. The mean annual total runoff is $41.8 \times 10^9\,\mathrm{m}^3$, but it is extremely uneven throughout the year. The flood season is between March and August, and the runoff then accounts for nearly 80% of the total annual runoff, while September to February is the dry season only accounting for 2% of the annual runoff (Y. Li, Wang, & Xin, 2013). The soil of the Lijiang River riparian zone is dominated by coarse textured red loam, with a high gravel content, high humidity, gravel-type substrates, and a shallow soil layer (Huang et al., 2017; Q. S. Li, Wang, Xin, Li, & Ren, 2014). The dominant woody species include *Ficus abelii* Miq., *Boehmeria formosana* var. *Formosana*, *Celtis biondii* Pamp., *Pterocarya stenoptera* C. DC., *Rubus rosaefolius* Smith, *Combretum alfredii* Hance, *Cinnamomum burmanni* (Nees et T. Nees) Blume, *Callerya championii* (Benth.) X. Y. Zhu, *Flueggea virosa* (Roxb. ex Willd.) Voigt, *Alangium chinense* (Lour.) Harms, and *Urena lobata* var. *lobata*.

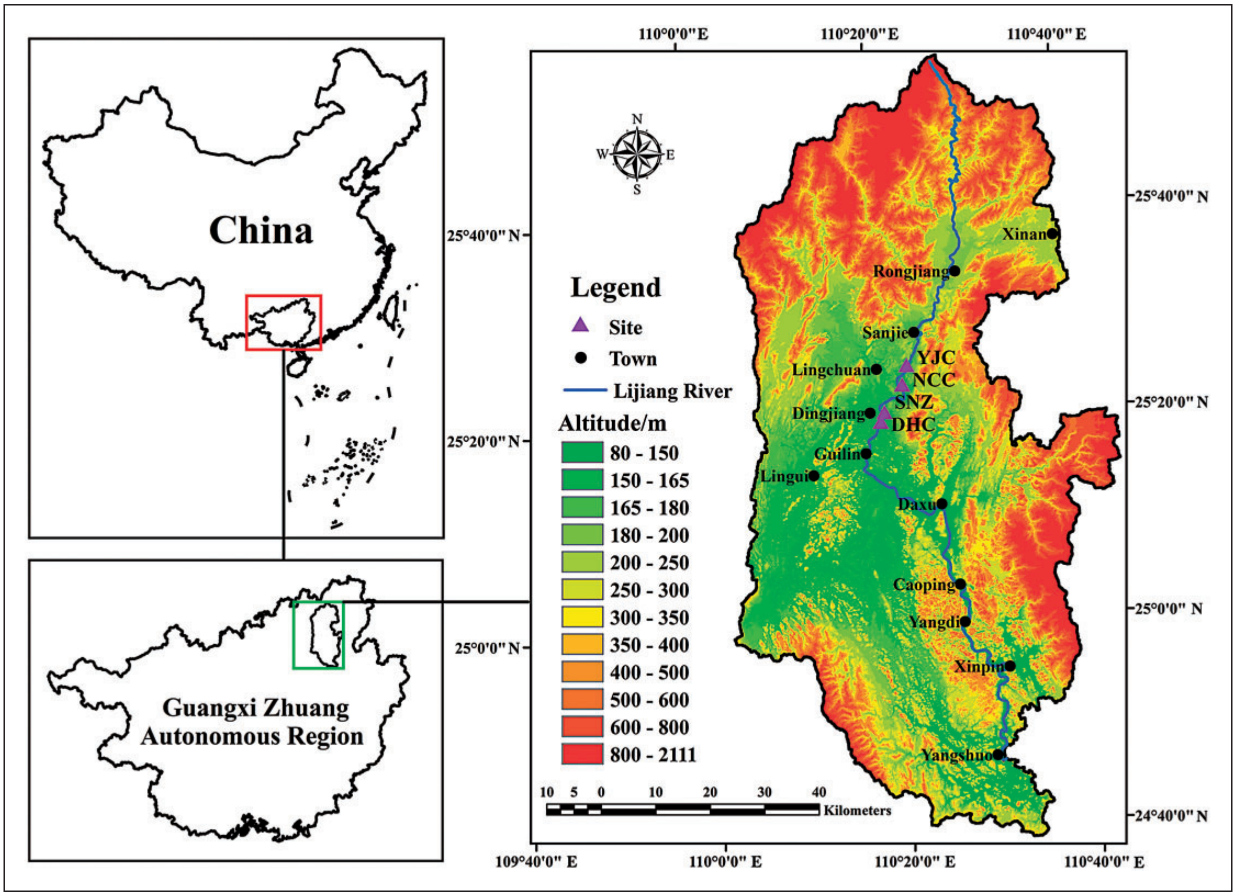

Figure 1. Location of the sampling sites in riparian plant communities of the Lijiang River, Guilin, southwest China. The four sites are indicated by purple triangles. They are Yangjiangcun (YJC), Nancangcun (NCC), Shangnanzhou (SNZ), and Dahecun (DHC).

The dominant herbaceous species include *Cynodon dactylon* var. *dactylon*, *Polygonum hydropiper* L., *Humulus scandens* (Lour.) Merrill, *Alternanthera philoxeroides* (Martius) Griseb., and *Setaria plicata* var. *plicata*.

Ecological Scales and Sampling Design

We assessed the variation of four key plant functional traits (SLA, LA, LTH, and CHL) across four nested ecological scales. These were (a) among leaves within an individual, (b) among individual plants within a species, (c) among species within a plot, and (d) among plots within a site. These four hierarchical ecological scales contain a mixture of taxonomic (species) and spatial factors with no immediately obvious environmental gradient (leaf, individual, and plot). Plots within our four sites were established at distances (60 m, 65 m, and 70 m) away from one another to ensure spatial interspersion of sampling, were within the same habitat, and were subject only to local topographic variations.

From September to October 2016, we randomly carried out fieldwork in the four sites which were all in the upstream area of the riparian zones. They were Yangjiangcun (YJC: 110°22′30.08″ E, 25°24′48.87″ N), Nancangcun (NCC: 110°21′ 54.17″ E, 25°22′57.73″ N), Shangnanzhou (SNZ: 110°19′49.48″ E, 25°20′23.83″ N), and Dahecun (DHC: 110°19′21.76″ E, 25°19′29.30″ N), respectively (Table S1 and Figure 1). The distance between any two randomly chosen sites was between 1.39 km and 10.19 km. To test trait variation among plots, we systematically set up a total of nineteen 20 × 20 m plots (six plots in YJC, three plots in NCC, four plots in SNZ, and six plots in DHC). Moreover, 20 × 20 m plots were used as a 20 × 20 m area which is the smallest reasonable size that can be considered a community for subtropical forests, which represent a forest community in the sense of a set of species coexisting together and interacting in a locality (M. Kang et al., 2014).

To measure variation among species within a plot and among individuals within a species, we sampled at least three newly matured leaves from all individuals of all woody species occurring in the plots for tree individuals with DBH (diameter at breast height) $\geq$1 cm and for shrub and woody vine individuals with basal diameter (BD) $\geq$1 cm. Given that temporal variations in traits change between seasons and years, we collected all data during September and October 2016. Individual functional traits may also vary in relation to the age, size, or developmental stage of a plant, which is another important source of variation that merits future study. Due to some constraints, we were not able to include this component in this study. Instead, to minimize any variability in leaf traits due to leaf age, ontogeny, canopy position, or shading, we sampled leaves that were all fully expanded, mature, and exposed to the sun. For each individual, samples were randomly collected from canopy leaves that were fully exposed to the sun, from adult plants that showed no signs of physical damage from pathogens, herbivory, or other causes. A total of 51 native species were sampled, with species richness ranging from 5 to 24 species per plot. A total of 4 sites, 19 plots, 5,418 individuals, and 16,254 leaf observations make up our data set for the analyses presented.

Trait Selection and Measurement

We chose and measured four key functional traits to characterize the ecological strategies of the studied species across four nested ecological scales: (a) SLA: this is the area of one side of a fresh leaf divided by its oven-dry mass, expressed in $cm^2 \cdot g^{-1}$, indicating a trade-off between an investment in leaf surface area to capture light for photosynthesis and an investment in constructing more protective tissues to avoid dehydration and herbivory (Carlucci et al., 2015; Long, Zang, Schamp, & Ding, 2011). (b) LA (cm^2) is important for leaf energy, water balance, and tolerance to environmental stress, with smaller leaves generally observed in drier and more exposed conditions (Ackerly & Cornwell, 2007; Satdichanh, Millet, Heinimann, Nanthavong, & Harrison, 2015). (c) LTH (mm) reflects species' strategies for resource acquisition and use, especially light, water, and nutrients (Pérez-Harguindeguy et al., 2013; Wright et al., 2004). (d) CHL is a direct indicator of photosynthetic capacity, and plant productivity is linked to leaf nitrogen concentration per mass and hence to the photosynthetic rate (Chaturvedi, Raghubanshi, & Singh, 2011; Jiang et al., 2015).

Statistical Analyses

All variables were checked for normality and transformed by applying logarithms or square roots where required. To explore the variance components of functional traits across four nested scales (plot, species, individual, and leaf), we fitted a linear mixed model using a restricted maximum likelihood method to quantify the variance of functional traits across four scales nested one into another (i.e., nested analysis of variance [ANOVA] with random effects) in the increasing order of leaf, individual, species, and plot. Next, we used a variance component analysis on this model based on the *varcomp* function of R (R Development Core Team, 2016). The R code conducted to calculate the variance partitioning of the traits across the four nested ecological scales for the full model on SLA was as follows:

$$\text{varcomp.SLA} < -\text{varcomp}\,(\text{lme}\,(\log\,(\text{SLA}){\sim}1,\\ \text{random} = {\sim}1|\text{plot/species/individual},\\ \text{data} = \text{a, na.action} = \text{na.omit}),\ 1).$$

The same model applies to other traits by replacing SLA with the other traits in the R code. Although Bartlett's and Fininger's tests indicate that the hypothesis of homogenous variance between the members of a group (i.e., different species in a plot or different individuals in a species) is not proven, we noted that homoscedasticity only matters in assessing *p* values, not in the calculation of variance fractions—in this case, the variance component across the four scales (Messier et al., 2010). In other words, although heteroscedasticity might prevent us testing for significant differences among groups (e.g., different mean trait values between the plots), it does not affect our calculations of the amount of variance at each of the four scales. We do not specify at which level we did the tests because we believe that the results of heteroscedasticity apply to most or even all levels.

As the variance partitioning analysis does not lend itself to the calculation of *p* values, we applied a nonparametric bootstrapping method of 95% confidence intervals around these values, through extensive computer simulation, to estimate the certainty of the variance component values. It is known that bootstrapping is an effective resampling method for assessing the confidence of a given result as having an unbiased and highly precise measure of repeatability. Thus, based on this method, we first created a random subset from the full data set by randomly selecting 16,254 data points with replacements from the data set. Next, we calculated the variance partitioning analysis for our nested ANOVA on this subset. We repeated this procedure 1,000 times and stored the results of each run. The variance component values resulting from the 1,000 runs were then sorted for each scale, and the values corresponding to the 2.5 and 97.5 percentiles of this bootstrap distribution were identified.

For a nested ANOVA, the variance components are quite general. They can be represented as the variances around the means. Therefore, for any given level (e.g., the individual), each group mean (e.g., the mean value of each individual) was first computed, and then the variance in the group means around the group means of the higher level to which they belong was calculated (e.g., the variance of the individual means around the means of their specie). In this procedure, the portions of variation in the lowest level of the scale (leaf) also include measurement error.

Trait variation between plots may be due to differences either in species composition or in environment. The influence of species composition on trait differences may be greater than environmental influences in riparian zones due to relatively high species diversity. To measure species turnover between plots, we calculated Sorenson's similarity index (C_S) values of species composition based on presence–absence data, which incorporates both true spatial turnover and differences in species richness and abundance (Koleff, Gaston, & Lennon, 2003). The formula is as follows (Baselga, 2010):

$$Cs = \frac{b+c}{2a+b+c}$$

where *a* is the number of species common to both plots, and *b* and *c* are the number of species that occur in the *b* plots but not in the *c* plots and vice versa.

To analyze the variation characteristics of the values of four functional traits for individual leaves for each plot, the frequency distribution and average values of functional traits in each plot and for all samples were compared, using the functional trait values of each individual plant.

Results

The partitioning of variance in four functional traits reveals fairly uneven distributions of variance across four ecological scales. The results for the relative contribution of all traits are similar: species (0.51–0.70)> individual (0.21–0.27) > leaf and error (0.09–0.20)> plot (0–0.07). For all traits, interspecific variability (for SLA, LA, LTH, and CHL, these were 64%, 70%, 51%, and 56%, respectively) was higher than the intraspecific variability (for SLA, LA, LTH, and CHL, these were 34%, 30%, 44%, and 44%, respectively). We also found that the plot scale stands out as containing none, or only a very small percentage, of the total variance in all foliar traits (Table 1 and Figure 2). The Sorenson similarity of species composition between NCC and DHC was 0.47, between SNZ and DHC was 0.37, between SNZ and NCC was 0.37, between YJC and DHC was 0.46, between YJC and NCC was 0.45, and between YJC and SNZ was 0.5. The average similarity indices between plots in a site were as follows: for YJC, 0.42; for NCC, 0.36; for SNZ, 0.31; and for DHC, 0.34. Species richness varied from 5 to 24 species, with an average of 14.37 (±4.37) species per plot. The average density of woody plants for tree individuals with DBH $\geq$1 cm and for shrub and woody vine individuals with BD $\geq$1 cm is 285.16 (±121.44) per plot.

These frequency distribution graphs indicate that the plots have not only similar mean trait values but also

Table 1. Variance Partitioning for the Four Traits Across Four Ecological Scales (Plot, Species, Individual, and Leaf).

	% variance of trait [95% CI]			
Ecological scale	Log SLA	log LA	log LTH	log CHL
Leaf and error	13 [12–15]	9 [5–10]	20 [17–22]	17 [14–19]
Individual	21 [19–22]	21 [18–23]	22 [18–24]	27 [26–29]
Species	64 [62–66]	70 [65–71]	51 [50–57]	56 [54–59]
Plot	2 [0–4]	0 [0–0]	7 [3–8]	0 [0–0]

Note. All data were $\log_{10}$ transformed prior to analysis. Square brackets represent the 95% confidence intervals, which were calculated by bootstrapping (1,000 runs with 16,254 randomly sampled data points with replacements). CI = confidence interval; SLA = specific leaf area; LA = leaf area; LTH = leaf thickness; CHL = leaf chlorophyll content.

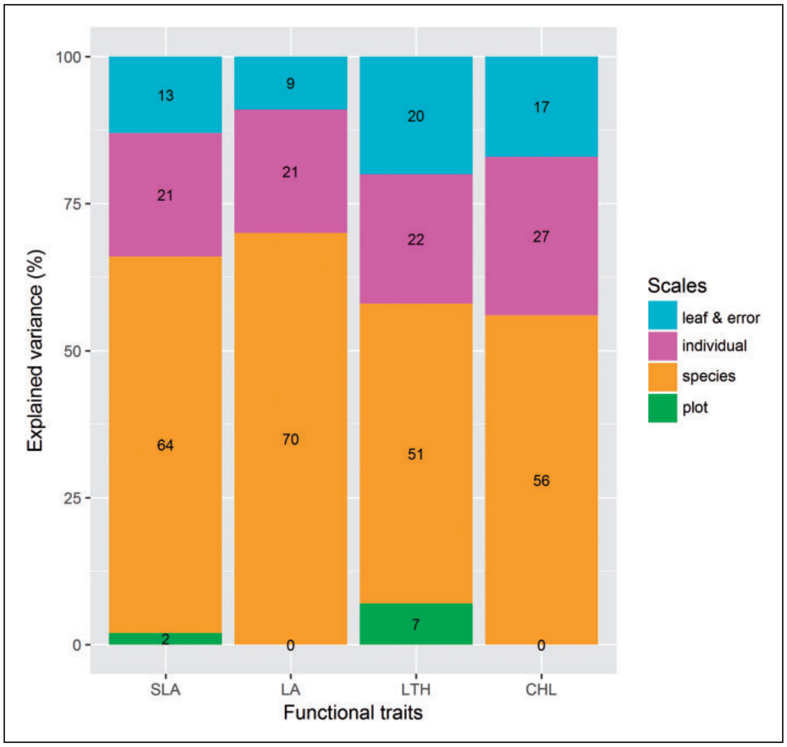

Figure 2. Variance partitioning for the four functional traits across four ecological scales (plot, species, individual, and leaf). SLA = specific leaf area; LA = leaf area; LTH = leaf thickness; CHL = leaf chlorophyll content.

similar trait value frequency distributions, that is, the overall trait distributions are conserved at the plot level.

Discussion

In this study, we assessed how trait variance is distributed and structured across four nested ecological scales in riparian plant communities in Guilin, southwest China. The patterns in the variance components of the four key plant functional traits we studied are rich in information in many respects, and some of the findings from these results are illuminating. Overall, the results indicate three important points that we would like to emphasize: (a) the relative contribution of interspecific variation was much greater than that of intraspecific variation, (b) the importance of including intraspecific variability in trait-based studies, and (c) species turnover at plot level accounts for only a minute percentage of the total variance.

Functional Trait Variation Is Dominated by Interspecific Variation

Interspecific variation accounted for the largest proportion of the total variance in all traits (for SLA, LA, LTH, and CHL, they were 64%, 70%, 51%, and 56%, respectively). This indicates that variation in these traits was predominantly driven by interspecific variation. Interspecific variation represents the contribution of the total variance attributable to differences between species occupying the same plot. This variation may be due to genetic composition and differences in environmental conditions (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Long et al., 2011). For example, Zhang, Slik, Zhang, and Cao (2010) demonstrated that spatial patterns of wood traits in China are controlled by phylogeny and the environment. Some scholars have also found that LMA, LTH, and CHL often show strong phylogenetic conservatism (Grady et al., 2013; Kraft & Ackerly, 2010; Vasseur, Violle, Enquist, Granier, & Vile, 2012), and significant phylogenetic signals can be detected in many plant functional traits (Mayfield & Levine, 2010). For example, Ackerly and Reich (1999) have reported significant differences between LA, leaf life span, leaf nitrogen content, and leaf photosynthetic capacity per unit area at different phylogenetic stages, through studying the association between the leaf traits of 108 species of angiosperms. Furthermore, in his investigation of the evolution of leaves in California, Ackerly (2004) showed that the SLA had a strong phylogenetic signal. Cao et al. (2013) also reported that the leaf nitrogen content, leaf phosphorus content, LA, wood density, SLA, and seed mass showed a significant phylogenetic signal. These examples suggest that association between species' traits is inseparable from the effects of phylogeny. Indeed, the effects of phylogeny on the association of traits indicate that species trait variation is related to genetics, which is conducive to the survival of plants in a changing environment through functional coordination. Moreover, the interspecies variation of the four functional traits we studied may also be strongly influenced by environmental conditions. This is demonstrated by recent work that has found that soil nutrients has a significant effect on the interspecific trait variability of the tropical cloud forests (Y. Kang et al., 2017).

Riparian vegetation is distributed along rivers and is affected by highly heterogeneous environmental conditions, such as a shallow soil layer, repeated flooding, and high soil humidity. Our study found that the similarity of species composition was relatively low between neighboring plots. Hence, a large proportion of variation in leaf traits was from interspecies activity, which may be explained, in part, to be a result of differing species' composition due to environmental heterogeneity. Generally speaking, these results are consistent with the view of most scholars, which is that variation in plant functional traits is mainly manifested at interspecific levels (Auger & Shipley, 2013; Jung et al., 2010; Y. Kang et al., 2017; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Luo et al., 2016). Interspecific variation in plant functional traits is the basis of species coexistence in natural ecosystems. Therefore, when plant functional traits are used to analyze the adaptation strategies of plants to the environment and species' coexistence mechanisms, the interspecific level should be the focus of the study.

The Importance of Including Intraspecific Variability in Trait-Based Studies

Although the fraction of total intraspecific variation (the sum of all the variation occurring at levels below species level) was lower than interspecific variation for all leaf traits, it nevertheless accounted for a considerable proportion (for SLA, LA, LTH, and CHL, it was 34%, 30%, 44%, and 44%, respectively). This significant contribution of intraspecific variability clearly shows that intraspecific variation is an important, rather than a minor, source of overall functional trait variation. Intraspecific trait variability is the overall variability of trait values and trait syndromes (sets of trait values, including trait trade-offs) expressed by individuals within a species (Albert et al., 2011). This variation can arise from genetic variation between individuals or from phenotypic plasticity in trait values across varying environmental conditions (Violle et al., 2012). Genetic variability is defined as the formation of individuals differing in genotype, or the presence of genotypically different individuals, in contrast to environmentally induced differences which, as a rule, cause only temporary, nonheritable changes of the phenotype (Hughes et al., 2008). It is simultaneously the result of evolutionary processes (genetic drift, mutation, selection, and migration) and the raw material for the future evolution of species (Albert et al., 2011). Phenotypic plasticity is the production of multiple phenotypes from a single genotype under various environmental conditions (Miner, Sultan, Morgan, Padilla, & Relyea, 2005). It shapes trait variability resulting from environmental heterogeneity in space, time, or during an individual's lifetime (Coleman, McConnaughay, & Ackerly, 1994). For example, individuals of a species have been found to enhance their leaf gas exchange in response to submergence so as to cope with oxygen limitation (e.g., Jung et al., 2010; Mommer et al., 2006). As mentioned earlier, the environmental conditions of riparian plant communities change easily, and riparian plants have wide intraspecific variations in functional traits that enable them to adapt to these variable and dynamic environmental conditions. In addition, both genetic and plastic variations determine species' ability to respond to changes in environmental conditions and, thus, are both potentially implied in plant community assembly (Jung et al., 2010). Hence, it is evident that intraspecific trait variability may be important for shaping community assembly and species' coexistence mechanisms in plant communities' responses to submergence stress. Jung et al. (2010) have similarly reported that intraspecific variability in the functional traits of SLA, leaf dry matter content

(LDMC), and the tree height of grassland communities in a flood meadow play an important role in community assembly. Also, Bolnick et al. (2011) and M. Kang et al. (2014) found that intraspecific trait variability influences population dynamics and community structure by enabling plants to pass through both biotic and abiotic filters. Consequently, it is necessary to understand to what degree intraspecific variability promotes species coexistence and plant associations. However, most previous studies on plant trait variability have focused only on the interspecific level, while intraspecific variability has largely been ignored. We therefore argue that trait variability should focus on the individual level so as to understand the processes of species coexistence and community dynamics. Having made these recommendations, we stress that the relative importance of intraspecific variation is not the only factor determining whether, and to what extent, intraspecific variation will influence ecological processes. Even when intraspecific variation is relatively low, it can have significant effects at the community level (e.g., Jung et al., 2010). Nevertheless, this is an important step in designing trait-based plant ecology studies, and our findings may also provide data for simulations testing the importance of intraspecific variation for specific ecological questions (Albert et al., 2011). As many of these traits have been strongly implicated in community assembly and ecosystem functioning, integrating intraspecific variation in future studies should significantly improve our mechanistic understanding about the effects of environmental change on both biodiversity and ecosystem functioning.

Low, or Even Lack of Variance at Plot Level

The plot level is responsible for only a minute, or even nil, percentage of total variance in all traits (for SLA, LA, LTH, and CHL, it was 2%, 0%, 7%, and 0%, respectively). Figure 3 shows that most of the plots not only have a similar mean trait value but also have similar trait value frequency distributions, that is, the overall functional trait value frequency distributions is conserved at plot level. This suggests that much variation in plant traits may exist at local/small ecological scales (i.e., species, individual plants, twigs, and leaf age), rather than at broad ecological scales (e.g., plot). Most strikingly, the low, or even lack of, variance at plot level indicates that environmental filtering may play a central role in the species assemblage of a local community. This is evidenced by the lack of significant variation in leaf functional traits at plot level in studies by Messier et al. (2010) and Albert, Thuiller, Yoccoz, Douzet, et al. (2010). Trait-based plant community assembly theory reveals that two opposing nonrandom processes affect the distribution of functional trait values within communities: niche differentiation and habitat filtering. Although both may operate simultaneously in nature, these two distinct assembly processes have different effects on ecological strategies (Cornwell, Schwilk, & Ackerly, 2006). Habitat filtering selects a series of species with similar functional trait attributes, resulting in the underdispersion of trait values within communities (Jung et al., 2010). Niche differentiation, however, prevents coexisting species from being ecologically too similar and causing the overdispersion of trait values within communities. Thus, the negligible amount of variation in these individual leaf traits between neighboring plots, despite higher species turnover among plots, indicates that the habitat filter operates on the overall frequency distribution of functional trait values, regardless of species composition. If true, then the presence of an individual within a local community is controlled by the environment as a series of filters occurring on leaf functional traits, rather than on species identity *per se*, and this is of great importance in driving community assembly (Messier et al., 2010). These filters on leaf functional trait values also act as a coarse sieve or filter on species assembling in communities, because each species has a substantial, but finite, extent of variability in its expression of leaf functional trait values. This finding has important implications for understanding how environmental filters influence the structure of ecological communities.

Riparian zones are an important buffer zone between aquatic and terrestrial ecosystems for exchanging material, energy, and information. They have unique biotic, biophysical and landscape characteristics (Qin et al., 2017). As an important part of riparian ecosystems, riparian vegetation has crucial ecological functions, providing food and habitats for terrestrial organisms, maintaining ecosystem stability, providing a buffer zone that filters sediments and controls nutrients, and stabilizing riverbanks (Alahuhta et al., 2011; Richardson et al., 2007). They are greatly affected by fluvial processes, such as flooding and the deposition of alluvial soil, and form a distinctive flora in structure and function from adjacent terrestrial vegetation (Richardson et al., 2007).

Implications for Conservation

Riparian zones (the fringes of rivers or streams) are diverse, dynamic and complex habitats of critical concern for conservation worldwide, as they filter agricultural contaminants, buffer landscapes against erosion, and provide habitats for a great diversity of species (Sabo et al., 2005). As an important part of riparian zones ecosystems, riparian plant communities is crucial for future management plans dealing with the vegetation and biodiversity of these highly vulnerable ecosystems. The results of our study indicate three important points

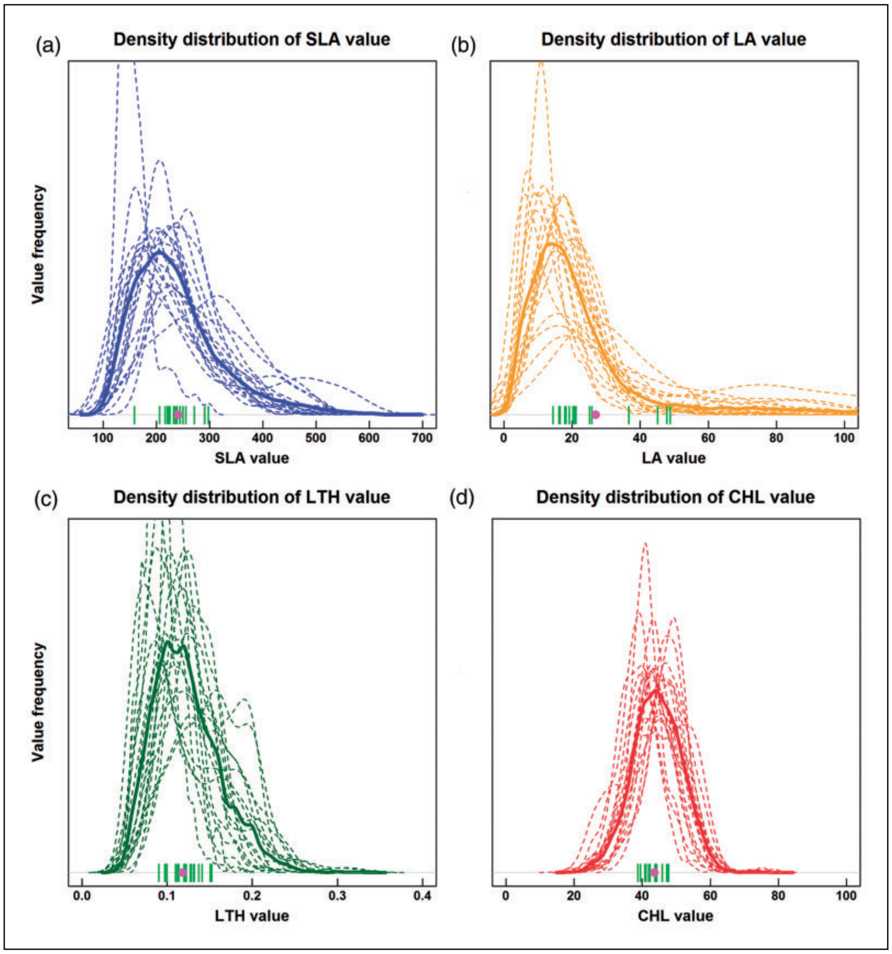

Figure 3. Frequency distributions of SLA, LA, LTH, and CHL values for individual leaves for all plots. The solid lines represent the four sites. Dashed lines represent the individual plots in the four sites. The four sites mean values are shown by a bullet point (•) on the abscissa and the plot mean values by a tick mark (|). These graphs show that the plots within the four sites have not only similar mean trait values but also similar trait value frequency distributions, that is, the overall trait distribution is conserved at the plot level. SLA = specific leaf area; LA = leaf area; LTH = leaf thickness; CHL = leaf chlorophyll content.

that we would like to emphasize in order to further the conservation of the regional biodiversity and the integrity of the forest landscape. First, that most of the total variance in all traits was observed at interspecific level indicates that variation in these traits was predominantly driven by interspecific variation. Second, intraspecific variability in all traits was considerable and demonstrated that intraspecific trait variation data should not be neglected. Thus, in order to further the understanding of species coexistence in communities, we urge future trait-based studies to measure traits at multiple levels of biological organization, including at the population or individual level. Third, the plot level accounted for only a minute percentage of the total variance, and this shows that the presence of an individual within a local community is controlled by environment filters occurring on leaf traits rather than on species identity *per se*. Trait-based habitat filtering could therefore play a central role in plant community assembly. A better understanding of these three points is critical for developing conservation areas and informing the design of effective conservation strategies for these unique riparian zones and their related ecosystems.

Author Contributions

Yong Jiang, Shichu Liang, and Wenxing Long conceived and designed the study. Runhong Liu collected the field data and did the morphological identifications. Shichu Liang, Yong Jiang, and Runhong Liu performed the statistical analyses. Runhong Liu and Yong Jiang wrote the first draft of the paper. All authors read and approved the final manuscript. Runhong Liu and Shichu Liang contributed equally to this article.

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Supplemental Material

Supplemental material for this article is available online.

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