

Intra- and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest

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- **Background and Aims** How functional traits vary with environmental conditions is of fundamental importance in trait-based community ecology. However, how intraspecific variability in functional traits is connected to species distribution is not well understood. This study investigated inter- and intraspecific variation of a key functional trait, i.e. specific leaf area (leaf area per unit dry mass; SLA), in relation to soil factors and tested if trait variation is more closely associated with specific environmental regimes for low-variability species than for high-variability species.
- **Methods** In a subtropical evergreen forest plot (50 ha, southern China), 106 700 leaves from 5335 individuals of 207 woody species were intensively collected, with 30 individuals sampled for most species to ensure a sufficient sample size representative of intraspecific variability. Soil conditions for each plant were estimated by kriging from more than 1700 observational soil locations across the plot. Intra- and interspecific variation in SLA were separately related to environmental factors. Based on the species-specific variation of SLA, species were categorized into three groups: low-, intermediate- and high-intraspecific variability. Intraspecific habitat ranges and the strength of SLA–habitat relationships were compared among these three groups.
- **Key Results** Interspecific variation in SLA overrides the intraspecific variation (77 % vs. 8 %). Total soil nitrogen (TN, positively) and total organic carbon (TOC, negatively) are the most important explanatory factors for SLA variation at both intra- and interspecific levels. SLA, both within and between species, decreases with decreasing soil nitrogen availability. As predicted, species with low intraspecific variability in SLA have narrower habitat ranges with respect to soil TOC and TN and show a stronger SLA–habitat association than high-variability species.
- **Conclusions** For woody plants low SLA is a phenotypic and probably adaptive response to nitrogen stress, which drives the predominance of species with ever-decreasing SLA towards less fertile habitats. Intraspecific variability in SLA is positively connected to species' niche breadth, suggesting that low-variability species may play a more deterministic role in structuring plant assemblages than high-variability species. This study highlights the importance of quantifying intraspecific trait variation to improve our understanding of species distributions across a vegetated landscape.

Key words: Environmental gradient, intraspecific trait variation, niche, specific leaf area, soil nitrogen limitation.

INTRODUCTION

How functional traits vary across particular environmental gradients is a central question in trait-based community ecology (McGill *et al.*, 2006; Shipley *et al.*, 2016). It is commonly assumed that species-mean trait values represent the niche differentiation among species (Sterck *et al.*, 2011; D'Andrea and Ostling, 2016). However, recent empirical studies have demonstrated that interspecific trait variation does not always override intraspecific variation and the latter may be important in community trait composition at fine scales (Messier *et al.*, 2010; Albert *et al.*, 2011; Auger and Shipley, 2013; Siefert *et al.*, 2015). In addition, studies, empirically and theoretically, have increasingly shown that intraspecific variation contributes substantially to species coexistence and biodiversity maintenance

(Violle *et al.*, 2012; Adler *et al.*, 2013; Siefert, 2014; Laughlin and Joshi, 2015). Thus, quantifying intraspecific trait variation along with the interspecific variation is crucial to understanding niche differentiation and species distribution at local scales.

Specific leaf area (SLA), defined as the ratio of leaf surface area to dry mass, is a key functional trait for plants (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013). SLA reflects the area available for solar irradiance interception per unit of assimilate investment (Milla and Reich, 2007). As a way of resource allocation within leaves, SLA profoundly influences the efficiency of assimilating photosynthetic active radiation and ultimately plant photosynthetic capacity (Green *et al.*, 2003). In addition, SLA is closely associated with other biologically important traits including leaf nitrogen concentration, lifespan and plant relative growth rate

(Lambers and Poorter, 1992; Reich *et al.*, 1997, 2003; Wright *et al.*, 2004). Representing one of the main ecological strategies of plants (Westoby, 1998; Wright *et al.*, 2004), SLA is critical for modulating plant species distribution and community assembly (cf. Niinemets and Kull, 1994; Ackerly *et al.*, 2002; Burns, 2004; Poorter *et al.*, 2009; Hulshof *et al.*, 2013).

Interspecific differences in SLA have been closely linked to niche partitioning among species, with low-SLA species associated with a slow growth strategy and infertile soils (Poorter and De Jong, 1999; Baraloto *et al.*, 2006; Sterck *et al.*, 2006). However, the mean trait value of a species mainly reflects its niche positioning rather than niche breadth. Theoretical studies proposed that niche breadth would be defined by intraspecific trait variability, the latter being due to a combination of genotypic variation and trait plasticity (Violle and Jiang, 2009). Species with low trait variability may display a high level of habitat specialization (Sultan, 2000) and possess a relative fitness advantage within their preferred habitats (Caley and Munday, 2003). However, only sparse empirical evidence exists in support of this argument (Laurans *et al.*, 2012; Sides *et al.*, 2014), which calls for further tests.

Moreover, the link between intraspecific trait variability and niche breadth, if any, could play a significant role in shaping community assembly. Intraspecific trait variability determines the probability that a species will pass through environmental filters (Jung *et al.*, 2010; Violle *et al.*, 2012). In a highly heterogeneous system, low-variability species can only establish in habitats close to their niche optimum (Umaña *et al.*, 2015), but high-variability species could potentially colonize across the entire landscape due to their broad niche width. Thus, we predict that trait variation is more closely associated with specific environmental regimes for low-variability species than for high-variability species (Fig. 1).

In this study, we aimed to quantify the intra- and interspecific variations of SLA and reveal the effects of soil conditions on the SLA variations to understand the plant species assemblage

in a stem-mapped subtropical forest (50 ha) in China. SLA data were intensively sampled and soil properties were fully mapped across the plot. To empirically test the hypothesis, we addressed the following three important questions: (1) How does SLA vary with edaphic factors both within and between species? (2) Do species with low SLA variability show a stronger relationship between SLA and habitats than high-variability species? (3) Do species with low SLA variability have narrower habitat ranges than high-variability species? Answers to these questions would contribute substantially to understanding the functional significance of SLA for species distribution and community assembly.

MATERIALS AND METHODS

Study site

The study site is located in the Heishiding Provincial Natural Reserve (23°27'N, 111°52'E), Guangdong Province, southern China. The region has a humid subtropical monsoon climate with mean annual temperature of 19.6 °C and mean annual precipitation of 1740 mm. Relief is predominantly of low hills, with elevation ranging from 150 to 1000 m above sea level. The vegetation is characterized by evergreen broadleaved forests dominated by Lauraceae, Fagaceae and Theaceae species. Leaf flushing occurs from March to May for most woody species in the region (Li and Wang, 1984).

Following the field protocol of the CTFS-forestGEO network (<http://www.forestgeo.si.edu/>), we established a 50-ha (500 × 1000 m) forest plot in the reserve to monitor long-term forest dynamics. The plot roughly covers a local catchment, with runoffs generally flowing north (Fig. 2). The bedrocks are granitic, on which ferrasol develops as the dominant soil type. Elevation ranges from 430 to 700 m. Slope inclination varies greatly between 10° and 70°.

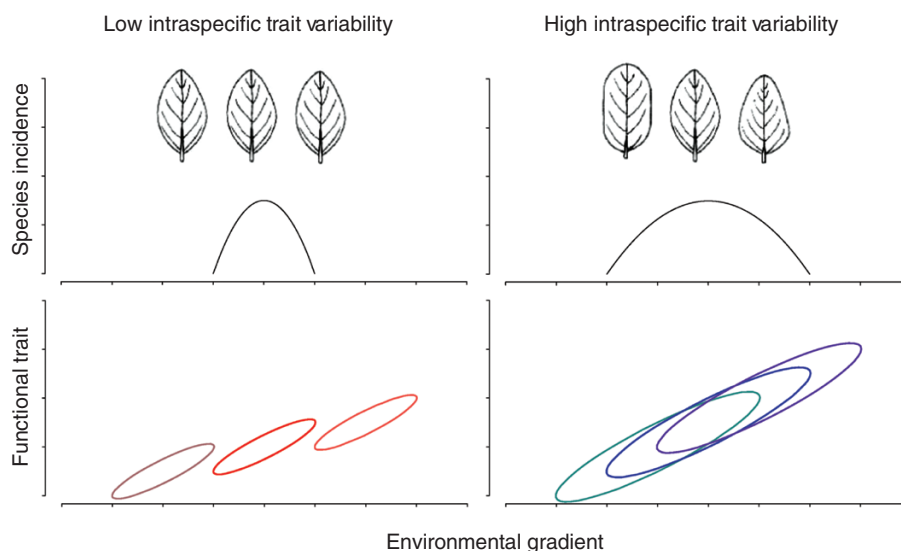


FIG. 1. Conceptual links between intraspecific trait variability and niche occupancy. Species with low intraspecific trait variability are expected to occupy narrow niches and have more predictable positioning along a trait spectrum in terms of their environmental niche (left panels), whereas species with high intraspecific trait variability are expected to display the opposite (right panels).

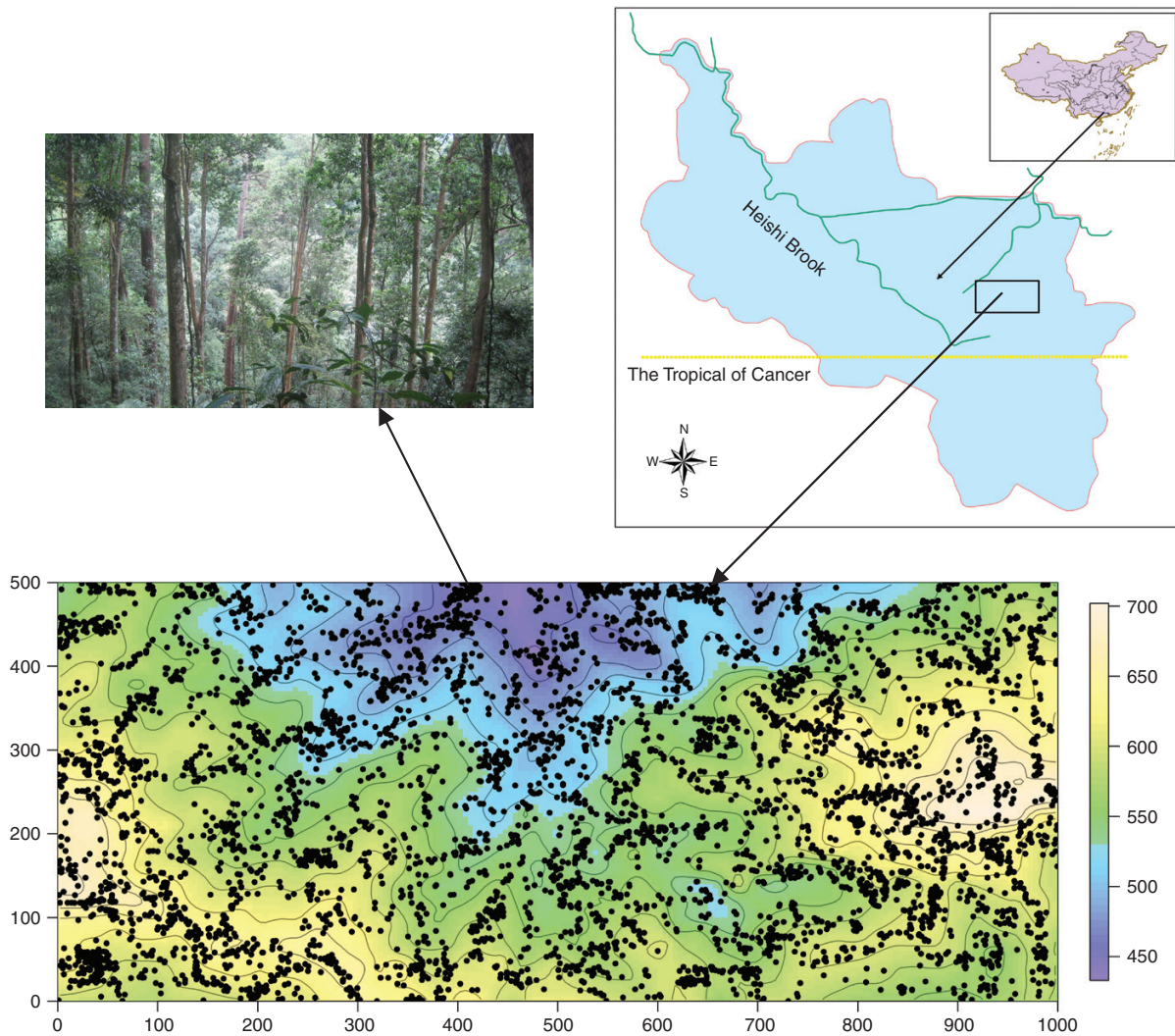


FIG. 2. The geographical location of Heishiding forest plot and the distribution of 5335 sampled plants within the plot. Values are in metres and colours represent altitude above sea level.

All free-standing woody stems with diameter at breast height (dbh) ≥ 1 cm in the plot were tagged, measured, identified to species and mapped within a geographical coordinate frame. A total of 264 394 stems, belonging to 214 woody species, 129 genera and 60 families, were recorded. Most of the 214 woody species were evergreen tree species, along with 32 shrubs and 25 deciduous tree species (Supplementary Data Table S1). The two most abundant species were *Cryptocarya concinna* Hance (Lauraceae) and *Neolitsea phanerophlebia* Merrill (Lauraceae), with abundances of 24 302 and 16 594, respectively.

Leaf sampling and measurement

In 2013 and 2014, leaf sampling was conducted within the 50-ha forest plot during the summer (from June to August) after the leaf flushing season. To capture the community-wide leaf trait variation, we adopted a stratified random sampling strategy with particular reference to species. For species with abundance ≥ 50 individuals across the plot, 30 individuals were randomly

selected for leaf sampling. For species with abundance < 50 individuals, three to 30 individuals were sampled depending on the abundance of those species and the availability of satisfactory leaves. We first sampled leaves along random routes, with nearly 60 % of samples representing common species collected in this step. Subsequently, we sampled rare species according to their locations and in the meantime covered a few common species yet to reach 30 samples. Seven extremely rare species were not sampled due to either tree mortality or the lack of satisfactory leaves (see below).

In total, we sampled 5335 individuals across 207 species. All sampled individuals were well interspersed across the 50-ha plot and a wide variety of microhabitat types was thus encompassed (Fig. 2). The mean dbh of all sampled individuals was very close to that for the whole plot (5.01 ± 0.09 vs. 5.55 ± 0.02 cm, mean \pm s.e.), which indicates the size structure of the forest was representatively sampled.

Twenty healthy-looking, fully developed current-year leaves were detached from each plant, with the assistance of tree pruners where necessary. We removed leaves from one or two twigs

about 1–3 cm in diameter from the outer canopy. Note that the vertical range of leaf sampling was limited to the lowest 6.8 m (height of the person sampling plus pruner length). Our sampling was therefore biased towards collecting leaves from the understorey and may be ontogenetically biased towards early stages for canopy species. On the other hand, it facilitated SLA comparison of understorey plants and saplings of overstorey species in relation to soil parameters at similar (shaded) light regimes. In total, we collected 106 700 leaves from 5335 individuals for subsequent analyses.

All sampled leaves were wrapped in moist filter paper and packed into resealable plastic bags before laboratory processing. Within 24 h of field sampling, leaf area was measured with an LI-3000C leaf area meter (LI-COR) to the nearest 0.01 cm². For some exceptionally large or non-flat leathery leaves, a digital scanner plus with the software ImageJ (v1.48, <http://imagej.nih.gov/ij/>) was used to measure leaf area. Dry mass was measured to the nearest 0.0001 g after 48 h of oven-drying at 80 °C.

Soil survey

Soil cores were extracted to a depth of 10 cm from 1708 sites across the 50-ha plot. The sampling sites were spatially outlined on a regular grid of points every 30 m, with each grid intersection accompanied by additional sample points at 2, 4 or 12 m in a random compass direction (N, E, S, W, NE, NW, SE or SW) from the grid. All soil cores were extracted within 5 h around noon on clear days in autumn 2013. Six soil physical and chemical properties were measured for each core: moisture (MST), total organic carbon (TOC), total nitrogen (TN), available phosphorus (AP), available potassium (AK) and available aluminium (AAI). These factors have been shown to be relevant for shaping species composition in this forest (Zhu, 2015); and AAI was considered because of its toxic effects on plants especially in acid soils (Kochian et al., 2004) that are known to occur in this region (pH = 4.38 ± 0.26, mean ± s.d.).

Soil moisture was gravimetrically determined. A TOC analyser (Shimadzu, TOC-Control V 2.00) was used to determine the TOC concentration using the acid sparging (total carbon minus inorganic carbon) method. TN was determined colorimetrically by using a SmartChem-200 automated discrete analyser (AMS westco, Smartchem 3.1.30) after Kjeldahl digestion. AP, AK and AAI were extracted in Mehlich III solution and measured with an ICP-OES 2100DV atomic emission spectrometer (PerkinElmer, Winlab32 4.0). A summary of these edaphic properties is presented in [Supplementary Data Table S2](#).

Kriging interpolation

Kriging maps were created for each of the soil properties for the 50-ha plot so that the soil data can be obtained at any location in the plot, including the locations of the 5335 sampled trees. First, observed soil properties were Box–Cox transformed and detrended by quadratic trend-surface regressions. Empirical variograms were computed based on the residuals after detrending and fitting against spherical or exponential models. Models with the lowest residual sums of squares were selected for ordinary kriging. The removed trend was then added back to the kriged values, and the values were

back-transformed to the original scale. Leave-one-out cross-validations showed that the coefficient of variation (CV) of the root-mean-square deviation was <16 % in most cases except that AP had a root-mean-square deviation of = 25 % (see details in [Table S2](#)). Geostatistical modelling was performed using the R package ‘geoR’ (Ribeiro and Diggle, 2001).

Data analysis

Pairwise Pearson’s correlations for the six edaphic variables were performed to examine collinearity between variables. The strongest correlation was found between TOC and TN with a coefficient of 0.46, followed by that between MST and TN with a coefficient of 0.34. The highest variance inflation factor (VIF) in the dataset was 1.38, much less than the commonly recommended VIF = threshold of 10, and therefore no factor was considered redundant and all were retained. All pairwise correlation coefficients for the six variables are shown in [Supplementary Data Table S3](#).

We used a linear random effect model (LRE) to decompose the hierarchical variance (Messier et al., 2010; Auger and Shipley, 2013), with leaves nested within individuals and with individuals nested within species. Sampling dates were also incorporated as a random factor in the model. The nested LRE was fit using restricted maximum likelihood (REML). Intra- and interspecific variation in SLA were separately modelled in relation to environmental factors. The following linear mixed effects model (LME) was applied at the intraspecific level:

$$y_{ij} = \beta_0 + \sum_{k=1}^6 \beta_k e_{ijk} + u_i + \varepsilon_{ij} \quad (1)$$

where y_{ij} is the SLA (averaged across 20 leaves and then log-transformed) of the j th individual plant of the i th species, e_{ijk} is the k th environmental variable (centred and scaled by the standard deviation), β_k is the fixed effect of each of the $k = 1, 2, \dots, 6$ environmental variables, β_0 is the fixed intercept, u_i is the random variance term to account for the species-level SLA variation, and ε_{ij} is the error. This model evaluated how SLA of individual plants varies with proximate environmental variables. Marginal and conditional R^2 values (for the variance explained by the fixed and random effects, respectively) were obtained following the method proposed by Nakagawa and Schielzeth (2013). We also incorporated a random slope term (i.e. interspecific differences in response to soil variables) into this model but found the coefficient estimates were minimally influenced. In addition, we also considered a spherical spatial correlation structure into this model but found that the results were well preserved ([Supplementary Data Table S4](#)). Here we only presented the results from models without considering random slope or spatial autocorrelation.

At the interspecific level, SLA was modelled using a simple linear regression:

$$u_i = \alpha_0 + \sum_{k=1}^6 \alpha_k \frac{\sum_{j=1}^n e_{ijk}}{n} + \varepsilon_i \quad (2)$$

where u_i is the random effect (i.e. averaged SLA) of the i th species in Model (1), α_0 is the intercept, $\alpha_1, \alpha_2, \alpha_3$ and up to α_k are the effects of species-averaged environmental variables

(centred and scaled by the standard deviation) and n is the number of sampled plants of the i th species. This model evaluates how species with different SLA are distributed along environmental gradients.

The most parsimonious model was selected using backward selection based on the Akaike (1974) information criterion (AIC) (Burnham and Anderson, 2003). The R packages ‘stats’ and ‘lmerTest’ (Kuznetsova et al., 2014) were used in model fitting and model selection.

The CV of SLA across conspecific individuals was assumed to represent a species’ capacity to adjust its traits according to the local environment. No evident association was detected between species-specific CV and sample size ($r = 0.12$, $P = 0.08$, $n = 207$). The hypervolume of edaphic factors within a species was assumed to reflect the species’ niche breadth. We used the algorithm proposed by Blonder et al. (2014) to quantify each species’ niche space. This algorithm integrated multivariate kernel density estimation and importance-sampling Monte Carlo methods to define a hypervolume. Bandwidth was specified with a Silverman estimator across 264 394 individuals and then uniformly used for each species. In addition to high-dimensional hypervolumes defined by all six edaphic factors, we considered low-dimensional ones defined by edaphic factors showing significant relationships with SLA. We tested the correlations between species-specific CV in SLA and edaphic hypervolumes, with sample size (species abundance for niche hypervolumes) as the controlling factor. We also quantified edaphic hypervolume based on a reduced dataset (i.e. the 5335 plants with SLA measured) and checked its correlation with intraspecific SLA variability (i.e. CV).

The 33th and 66th percentiles of species-specific CV were taken as the cut-points to categorize 207 species into three equal-size subsets, referring to low-, intermediate- and high-variability species, respectively. Equation (2) was applied separately to each subset of species so that we could examine the differences in environmental constraints on the three subsets. Specifically, we were concerned with whether the coefficient of determination (R^2) was lower for high- than for low-variability species. Equation (1) was also applied separately to three subsets with different degree of SLA variability but at the individual level. For this, determined whether intraspecific SLA variation originating from environmental forces (marginal R^2) differed between the contrasting subsets.

RESULTS

SLA ranges from 55.4 to 652.4 cm² g⁻¹ across all sampled individuals with a mean of 146.8 cm² g⁻¹. The two most abundant species have similar SLA, both of which are close to the average value (*Cryptocarya concinna* with 143.9 cm² g⁻¹ and *Neolitsea phanerophlebia* with 135.7 cm² g⁻¹). The species with the lowest and highest mean SLA are *Camellia semiserata* C.W. Chi (76.9 cm² g⁻¹) and *Alangium chinense* (Lour.) Harms (461.8 cm² g⁻¹), respectively. Variance partitioning demonstrates that 77.1, 8.3 and 14.6 % of the total variation in SLA are attributable to species, individual and unexplained origins, respectively (Fig. 3). The contribution of leaves-within-individual and sampling dates to total variation is negligible (<<0.001 and 0.019 %, respectively) when these two factors were incorporated into the nested model structure.

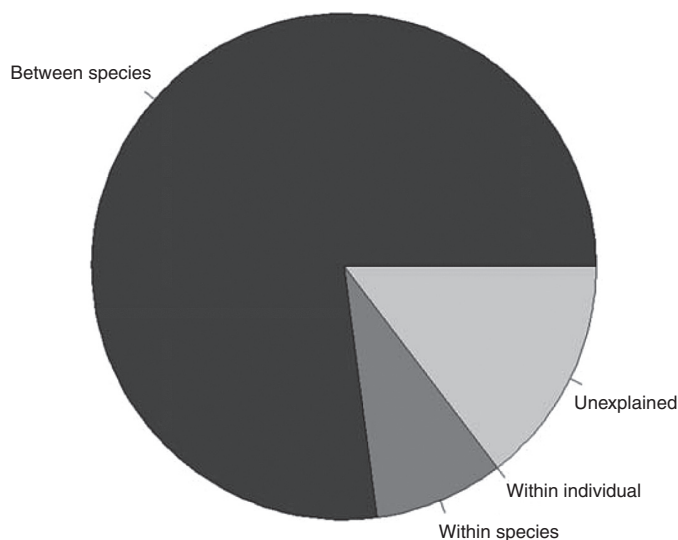


FIG. 3. Hierarchical variance partitioning in specific leaf area as revealed by the linear random effects model.

SLA varies positively with soil TN but negatively with soil TOC, and these trends are consistent at both intraspecific and interspecific levels (Fig. 4). Environmental factors account for 1.2 % of intraspecific SLA variation (marginal $R^2 = 0.001$ divided by intraspecifically originating variance 0.083) and 8.5 % of interspecific SLA variation, respectively. Intraspecific variability in SLA is positively correlated with the soil niche hypervolume defined by TOC and TN but not with that defined by all six factors (Fig. 5). When the soil niche hypervolume was quantified for the 5335 plants with SLA measured, these relationships were qualitatively similar (results not shown).

SLA is not related to any environmental factor for low-variability species (Fig. 6A). For high-variability species, only soil TN was strongly positively associated with SLA (Fig. 6E). However, for intermediate-variability species, three environmental factors, i.e. soil TN, TOC and AAI, significantly influenced SLA (Fig. 6C). Intraspecific SLA variation originating from environmental factors for each of the three groups (low-, intermediate- and high-variability species) is consistently low (marginal $R^2 \leq 0.004$, Fig. 6A, C, E).

Low-variability species with high SLA tend to be distributed at locations with high soil nitrogen but low organic carbon (Fig. 6B). This pattern holds for the intermediate- and high-variability species with high SLA (Fig. 6). The proportion of interspecific SLA variation explained by environmental factors declines from the low- to high-variability species (21.0, 14.4 and 7.2 %; Fig. 6B, D, F).

DISCUSSION

SLA variation and edaphic factors

Experimental evidence has demonstrated that nitrogen fertilization can increase SLA (Knops and Reinhart, 2000; Meziene and Shipley, 2001; Al Haj Khaled et al., 2005) and high nitrogen availability favours the dominance of high-SLA species (Craine et al., 2001). Likewise, our analysis showed that SLA is positively related to soil nitrogen concentration (TN) both within and across species (Fig. 4). In contrast, the relationship between

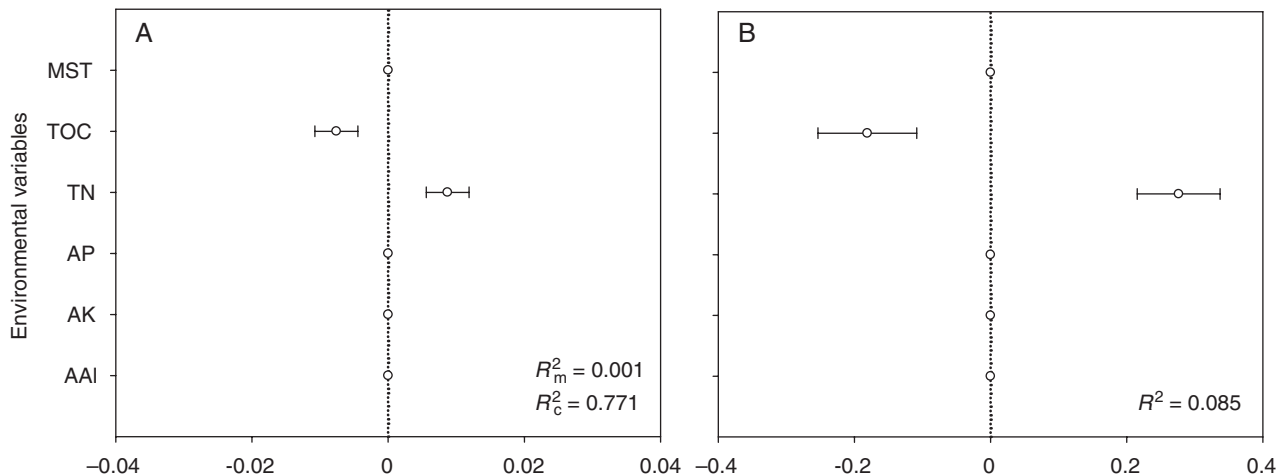


FIG. 4. Effect sizes of environmental variables on specific leaf area at the intraspecific (A) and interspecific (B) levels. Only the most parsimonious models based on the Akaike information criterion are shown (i.e. predictors with zero effect size were excluded). The magnitude (\pm s.e.) and direction of the effects are shown by slope estimates determined from the linear models. The overall strength of the effects is shown by the coefficient of determination (R^2). The variations explained by environmental variables (R_m^2) and by species (R_c^2) are also shown. Abbreviations on the y-axis: MST = soil moisture, TOC = soil total organic carbon, TN = total nitrogen, AP = available phosphorus, AK = available potassium, AAI = available aluminium.

SLA and soil organic carbon (TOC) displays an opposite pattern (Fig. 4). This is probably because more nitrogen was locked up in relatively recalcitrant soil organic matter and therefore less available for uptake by plants, and also because of stoichiometric constraints (Janssen, 1996; Ordoñez *et al.*, 2009). In fact, a negative relationship between SLA and soil C/N ratio has been reported on a global scale (Ordoñez *et al.*, 2009). In the present study, we found a similar negative association between these two variables (Supplementary Data Fig. S1a,f). This lends further support for a ubiquitous role of soil nitrogen limitation in driving SLA variability, especially at a given (understorey) light regime (Hodgson *et al.*, 2011).

For species with intermediate variability in SLA, a negative relationship between SLA and available aluminium content in soil (AAI) was detected (Fig. 6C). It is widely accepted that a high concentration of aluminium in soil would limit water and mineral nutrient uptake, comprising a stress for plants (Kochian *et al.*, 2004). In fact, acid soils rich in soluble aluminium in cerrado vegetation were found to favour leaf scleromorphy (Delgado *et al.*, 2013), a feature characterized by low SLA. After analysing species with intermediate intraspecific variability, we found that many of them were acid-sensitive, such as *Michelia* spp., *Eurya* spp., *Manglietia moto*, *Rhodomyrtus tomentosa* and *Camellia sinensis* (Hou, 1954). This is partly

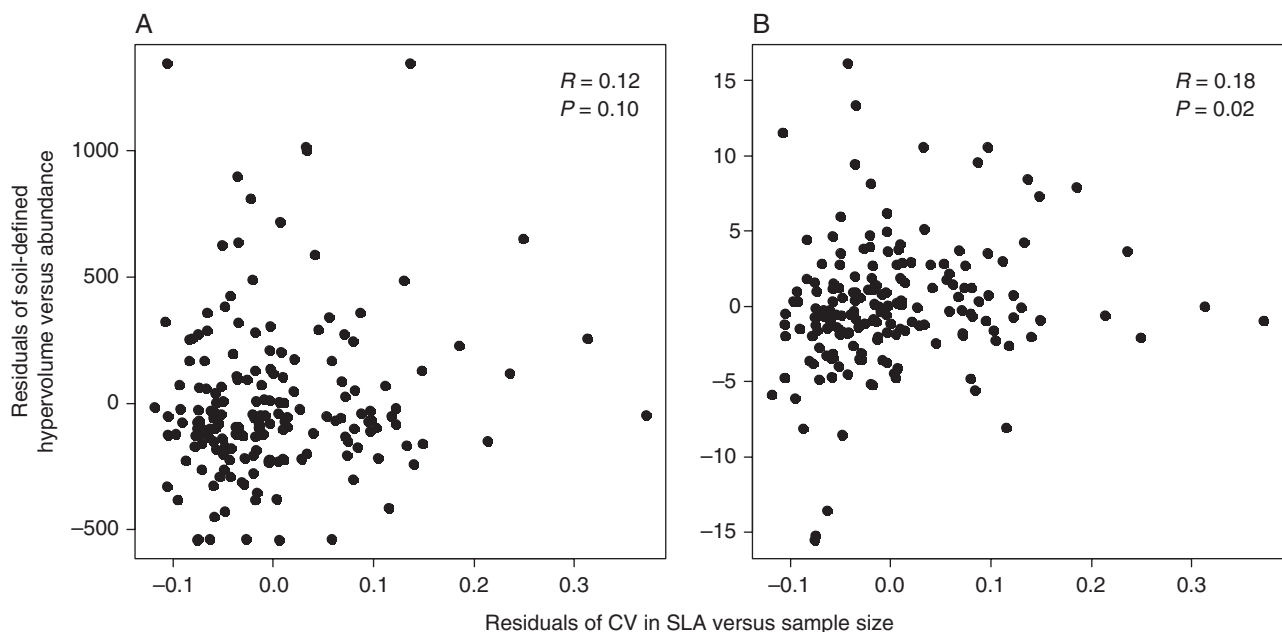


FIG. 5. Correlations between intraspecific variability (i.e. CV) in SLA and soil-defined hypervolume with sample size as the controlling variable. (A) Six-dimensional hypervolume defined by all soil factors. (B) Two-dimensional hypervolume defined by TOC and TN (i.e. two significant factors).

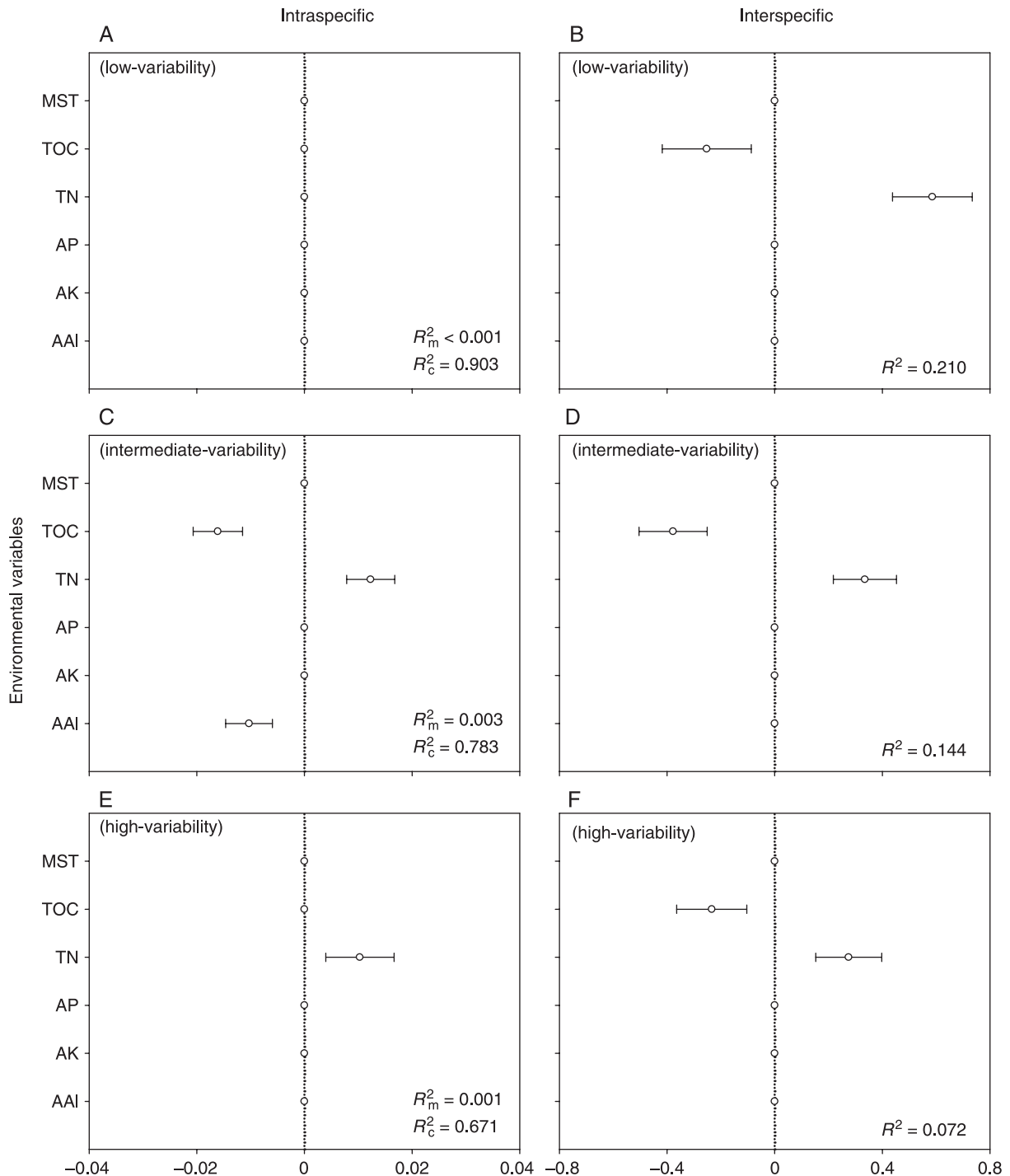


FIG. 6. Effect sizes of environmental variables on specific leaf area (SLA) for low-, intermediate- and high-SLA-variability species. Only the most parsimonious models based on the Akaike information criterion are shown (i.e. excluded predictors with zero effect size). The effects for the low-, intermediate- and high-SLA-variability species are successively shown from top to bottom. Left (A, C and E) and right (B, D and F) panels represent the intraspecific and interspecific level, respectively. See Fig. 4 for the interpretation of R^2 and abbreviation notation on the y-axis.

responsible for the significant SLA–AAI relationship found in this group.

Although phosphorus is a limiting nutrient for plant development and growth throughout the world (Vance *et al.*, 2003), SLA and soil AP were not related in the present study. Interestingly, at the global scale no effect of soil phosphorus on SLA was

detected either (Ordoñez *et al.*, 2009). This may intricately involve the interaction between soil phosphorus and radiation. Generally, for plant growth phosphorus deficiency discourages the interception of photosynthetically active radiation (PAR) rather than the efficiency of conversion of PAR into biomass (Colomb *et al.*, 2000). The function of SLA is, however, largely

linked to PAR conversion efficiency (Green *et al.*, 2003), and this function seems more important in less well-exposed environments (Mitchell and Woodward, 1988) just as for the situation in the present study.

Nitrogen limitation appeared to have prevalent impacts on SLA, as demonstrated at both the intra- and interspecific levels (Fig. 4), suggesting this factor represents a relevant environmental gradient in this subtropical forest plot. For the intermediate-variability species, besides nitrogen availability, available aluminum (AAl) strongly influenced SLA as well, but negatively (Fig. 6C). These results are in line with patterns observed in the leaf economic spectrum (Reich *et al.*, 2003; Wright *et al.*, 2004), which shows that more stressed habitats (particularly low nitrogen availability here) select against resource-acquisitive, weak and disposable leaves (with high SLA) but favour resource-retentive, sturdy and enduring leaves (with low SLA).

Inter- vs. intraspecific SLA variation

A meta-analysis of recent studies reported that intraspecific variation in SLA accounts for on average 30 % of the total variation within plant communities (Siefert *et al.*, 2015). We found that interspecific SLA variation in a subtropical forest in South China quantitatively overrides its intraspecific counterpart (77 % vs. 8 %, Fig. 5). This result is not necessarily at odds with the expectation of more pronounced intraspecific trait variation at local scales from previous work (Albert *et al.*, 2011; Auger and Shipley, 2013). In our study the rather low intraspecific SLA variability may to some extent be attributed to sampling leaves from the understorey. If we had collected overstorey leaves as well, the overall variability would probably have been greater (Keenan and Niinemets, 2016).

Furthermore, the relative weight of interspecific/intraspecific trait variation could be context-dependent. Critically, defining how fine a local scale is should consider the dimensions of the community (e.g. forest vs. herbaceous vegetation) and the level of environmental heterogeneity. In a speciose and heterogeneous assemblage such as that in the present study, it is not surprising that interspecific trait variation would dominate the variability of the trait of interest (Siefert *et al.*, 2015). It is notable that environmental heterogeneity in this forest is more salient in soil nutrient concentration, but gentle in moisture (Table S2). The locally narrow gradient of moisture may partly explain the lack of its relationship with SLA (Figs 4 and 6).

Interspecific SLA variation, based at least partly on the evolutionary adaptation of the species involved, apparently has profound implications for species distribution across communities. Species with low SLA are associated with soils poor in total nitrogen but rich in total organic carbon (Fig. 4B), suggesting that low SLA or the underlying traits (e.g. leaf tissue density; Witkowski and Lamont, 1991) is beneficial in N-limited habitats. This highlights the functional significance of SLA in shaping species distribution along environmental gradients (Burns, 2004; Pollock *et al.*, 2012) and again substantiates that SLA plays a crucial part in plant overall adaptive strategies (Westoby, 1998). For example, evergreen species on average have lower SLA than deciduous species (158 vs. 257 cm² g⁻¹, Table S1), and thus tend to specialize their niche on poor soils.

At the intraspecific level, SLA also tends to decrease with stronger nitrogen limitation (Fig. 4A). This corroborated that there is a fundamental underlying association between SLA and nitrogen availability. Moreover, this finding indicates that a species could decrease its SLA in response to reduced nitrogen availability, and will be replaced by species with lower SLA if nitrogen supply is below some threshold.

Low- vs. high-variability species

Intraspecific variability in SLA is positively correlated with its habitat variability with respect to soil TOC and TN (Fig. 5). Similarly, Laurans *et al.* (2012) noted that SLA plasticity was lower in more specialized species along a light gradient in a tropical forest, while others documented that higher variability in SLA was related to broader species distribution across plant communities (Burns, 2004; Sides *et al.*, 2014), which implies that intraspecific trait variability has a role in determining a species' niche breadth (Laughlin and Joshi, 2015).

Environmental variables explained more interspecific SLA variation where low-variability species were exclusively considered (Fig. 6B). Indeed, there was a more stringent SLA shift with environmental variations for low-variability species. This is in agreement with the result from Nordic lake islands, where species with lower intraspecific trait variability were more responsive to a composite environmental gradient linked to island size, soil fertility and spatial heterogeneity (Kumordzi *et al.*, 2014).

SLA of individual plants, from within either high- or low-variability species, showed similarly weak relationships with proximate habitats (Fig. 6A, C, E), which indicated that other abiotic and/or biotic constraints (e.g. light competition) not measured in this work could have operated on individual plants. Also, a plant's SLA itself can influence the competitive effect it has on its neighbours (Kunstler *et al.*, 2016), thereby indirectly affecting these neighbours' SLA as well irrespective of any influence of soil regime. While individual plants were grouped into species, SLA of high-variability species were less associated with the species' average habitats (Fig. 6F). This suggests that the SLA variation within each high-variability species can more flexibly adjust the species' traits to improve overall fitness in given environmental conditions. Umaña *et al.* (2015) noted that species in homogeneous habitats were subject to stabilizing selection and consequently showed low intraspecific trait variability. According to Umaña *et al.* (2015), how intraspecific trait variability shapes fitness should be dependent on the magnitude of habitat heterogeneity. Our result clearly demonstrates that species with low intraspecific trait variability are associated with limited habitat ranges covering relatively homogeneous environmental conditions.

Intraspecific variability in SLA is positively associated with species' niche breadth, which implies that low-variability species operate as a more deterministic force in structuring communities compared with high-variability species. As a result, given a particular combination of habitat and trait, we are able to predict more reliably the occurrence of species with lower trait variability across the landscape, which helps us to forecast species distributions in a changing world and offer more

reliable information for next-generation dynamic global vegetation models (Scheiter *et al.*, 2013).

CONCLUSIONS

This study, to our knowledge, represents the most extensive mapping of SLA variation and its environmental determinants in forests, based on over 100 000 leaves across plants in a large forest plot (50 ha). In particular, we have explicitly demonstrated how intraspecific variability in SLA is connected to species distribution across the plot. We found that species with high SLA preferentially colonize relatively N-rich habitats and this pattern is more predominant in low-variability species. In addition, species with low variability in SLA show narrow habitat ranges with respect to soil TN and TOC. These findings have important implications for linking trait patterns to niche occupancy, and in turn to species distribution. A caveat should be made explicitly that soil conditions could also be modified by plants, which in turn involves how to define niche itself. We generally follow the Grinnellian definition of niche (i.e. species' positions along particular environmental gradients) in the present work. Thus, how to link SLA and other important functional traits to the Eltonian niche (i.e. species' role in an interactive system) remains poorly resolved (D'Andrea and Ostling, 2016; Rosado *et al.*, 2016).

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: Summary of species information. Table S2: Summary of observed environmental variables and Kriging modelling parameters. Table S3: Pairwise correlations between environmental variables. Table S4: Summary of linear mixed effect models with and without spatial autocorrelation. Fig. S1: Model diagnostics for assumptions of normality, homoscedasticity and linearity.

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