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Trait variability differs between leaf and wood tissues across ecological scales in subtropical forests

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Keywords
Chemical traits; Community assembly; Defence syndromes; Functional traits; Habitat filtering; Intra-specific variability; Limiting similarity; Physical traits; Species co-existence; Trait-based approach

Abbreviations
ANOVAs = analysis of variance; DQ = Dongqian Lake Area; EBLFs = evergreen broad-leaved forests; LES = leaf economics spectrum; MLA = Mean leaf area; RY = Ruiyan Forest Park; TM = mesophytic area; TP = peak area; TR = ravine area; SLA = specific leaf area; LDMC = leaf dry matter content; LC = leaf carbon concentration; LN = leaf nitrogen concentration; TWD = twig wood density; SWD = stem wood density; TBT = trunk bark thickness; WC = wood carbon concentration; WN = wood nitrogen concentration

Nomenclature
Flora of China, database as of September 2004. http://frps.eflora.cn/namel/a

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Abstract

Question: Revealing how plant traits vary over disparate spatial scales and how ecological processes mediate such variation is important for understanding plant community assembly. However, to what extent does the distribution of trait variation among ecological scales differ between leaf and wood tissues and between physical and chemical traits? What are the consequences of resource competition and/or habitat filtering on the community assembly with respect to differences between leaf and wood traits, and between physical and chemical traits?

Location: Subtropical evergreen broad-leaved forests in five sites in the Ningbo area (29°41–50′ N, 121°36–52′ E) in eastern China.

Methods: Traits of 96 woody plant species were sampled and variation of ten physical- and chemical-based leaf and wood traits were partitioned across six ecological scales (site, plot, species, individual plant, twigs and leaf age) using a linear mixed model.

Results: From individual plant to site scales, variance partitions were distinct between leaf and wood traits. In leaf tissues, physical and chemical traits showed a consistent pattern, with the majority of variation found among species and individual plants, with little among plots. For wood tissues, the largest variation in physical traits was at the species and individual plant scales, with the largest variation in chemical traits observed at the plot scale. Variance partition was markedly similar within and across species.

Conclusion: Leaf and wood traits vary differently in relation to ecological scale, suggesting that trait variability is tissue-specific. The large variability of wood traits at the plot scale suggests a strong habitat filtering process. The large variation in leaf traits within plots may reflect niche differentiation across species and the importance of intra-specific variation that affects species co-existence. Our study demonstrated that physical and chemical traits may be independent. These decoupled trait axes may increase the dimensionality of niche space and facilitate species co-existence in forest communities.

Introduction

Plant functional traits are defined as any measurable morphological, physiological or phenological features at the individual plant level (Violle et al. 2007). Since these features directly or indirectly affect plant fitness and performance, trait-based approaches are rapidly emerging as a promising way to predict community assembly (Díaz et al. 1998; Lavorel & Garnier 2002; McGill et al. 2006; Shipley et al. 2006). There is a growing body of literature

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concerning the distribution of traits in communities and the underlying ecological processes, such as environmental filtering and niche differentiation, that are thought to generate these distributional patterns (Cavender-Bares et al. 2004; Ackerly & Cornwell 2007; Kraft et al. 2008; Cornwell & Ackerly 2009; Kursar et al. 2009; Jung et al. 2010; Kraft & Ackerly 2010; Paine et al. 2011; Baraloto et al. 2012; Savage & Cavender-Bares 2012; Sedio et al. 2012; Violle et al. 2012). In most of these empirical studies, plant traits have been mainly described by using species mean values, with an emphasis on inter-specific differences between co-occurring species, while the intra-specific variability of plant traits has largely been neglected.

Plant functional traits, however, are variable with plant genetic and developmental factors, and with changing environmental conditions (Reich et al. 1997; de Bello et al. 2011; De Frenne et al. 2011; Violle et al. 2012). For instance, several recent studies have found that the amount of intra-specific variation in plant traits is comparable to inter-specific variation (Albert et al. 2010a,b; Jung et al. 2010; Messier et al. 2010; Bolnick et al. 2011; Fajardo & Piper 2011). In this context, our understanding of trait-based community assembly, species co-existence and distributions could be potentially flawed as a result of ignoring intra-specific variation in plant functional traits (Violle et al. 2012). Moreover, we do not fully understand whether species co-existence and community assembly stand to be changed if intra-specific trait variability is much higher than previously assumed. Hence, it is necessary to know how trait variation is distributed over ecological/spatial scales, since most studies have compared trait (or phylogenetic) variation to that generated by a null model pertaining to a specific spatial scale, rather than decomposed across several spatial scales (e.g. Kraft et al. 2008; Cornwell & Ackerly 2009; Paine et al. 2011).

Variability in plant traits among ecological scales is one of the major issues in functional and community ecology (Albert et al. 2010a, 2011; de Bello et al. 2011; Bolnick et al. 2011; De Frenne et al. 2011; Violle et al. 2012). A recent empirical study reported that variation of two commonly studied leaf traits, i.e. leaf mass area and leaf dry matter content, is fairly evenly distributed across six nested ecological scales (Messier et al. 2010). Along temperature and radiation gradients in an alpine valley, intra-specific variability in three functional traits (height, leaf dry matter and leaf N content) was species- and trait-specific (Albert et al. 2010b). These results suggest that the structure and the extent of functional variability depend not only on the ecological scale, but also on the trait type (e.g. physical vs chemical traits). However, little is understood about how traits vary across different plant tissues or trait types.

What are the consequences of environmental filtering and resource competition on the community structure with respect to differences between leaf and wood traits, and between physical and chemical traits? Community assembly theory suggests that two processes affect the distribution of trait values within communities: habitat filtering and resource competition (Ackerly & Cornwell 2007; Cornwell & Ackerly 2009). Within a local community, habitat filtering reduces the spread of trait values, reflecting shared ecological tolerances, while competition leads to ecological differentiation of co-existing species (Kraft et al. 2008; Cornwell & Ackerly 2009; Jung et al. 2010; Kraft & Ackerly 2010). Consequently, habitat filtering selects a set of species with similar functional attributes, leading to the under-dispersion of trait values within communities. On the other hand, resource competition limits the similarity of co-occurring species with respect to functional traits on some spatial scale, resulting in the over-dispersion of trait values within communities.

With respect to plant tissues, it is reasonable to presume that leaf and wood economics are coordinated according to plant life-history theory (Hypothesis 1a, or the null hypothesis). This hypothesis assumes that allocation strategies of cheap or expensive tissues occur at a whole plant level, thus leading to synchronized construction costs of leaf and stem tissues (Grime et al. 1997; Westoby et al. 2002). If this is true, we predict that leaf and stem traits vary over similar spatial scales, or at least are not significantly different in the studied forests (Prediction 1a). However, recent evidence has shown that leaf and wood economics (Reich et al. 1997; Wright et al. 2004; Chave et al. 2009; Freschet et al. 2010) are decoupled (Baraloto et al. 2010; Ordoñez et al. 2010). In this case, we hypothesize alternatively that leaf and wood traits are orthogonal and therefore may vary differently at the same spatial scale, and are independent of one another across spatial scales (Hypothesis 1b), as they mediate plant distribution over distinct habitat gradients (Ordoñez et al. 2010). For example, at the plot scale, environmental filtering appears somewhat more intense on leaf traits than on stem traits in tropical rain forests (Paine et al. 2011). This suggests that the strength of environmental filtering that acts upon each of leaf and wood traits would be dependent on spatial scale. For leaf traits, the 'small/local scale' variability results largely from micro-heterogeneity within plots, associated with variability of individual plants and twigs, that correspond to differences in available light (Messier et al. 2010; Paine et al. 2011). It is at this small scale, co-existing species in local communities usually exhibit spatial or temporal differentiation in microhabitat, resource use or other factors, exhibiting the alpha niche differentiation (Ackerly et al. 2006; Ackerly & Cornwell 2007). For stem wood traits, the 'small/local scale' variability is derived mainly from different macro-habitats or climatic envelopes among plots, such as hydraulic and nutrient properties (Ordoñez et al. 2010; Poorter et al. 2010; Yan et al. 2013). The resulting distribution of stem traits, such as wood density, will be largely allopatric among plots, corresponding to the beta component of trait diversity among habitats (Ackerly et al. 2006; Ackerly & Cornwell 2007). If that is true, it is expected that leaf traits would reflect microhabitat differences while stem traits would reflect tolerances to broad environmental gradients. Therefore, we predict that leaf and stem traits exhibit variation at distinct spatial scales (Prediction 1b). Specifically, leaf traits vary at a spatial scale smaller than the plot, by exhibiting higher variation at fine spatial scales (e.g. within plot, across species and individual plant). In contrast, stem traits exhibit large variation at the intermediate spatial scale (e.g. at the plot scale) as a result of habitat filtering, but exhibit little variation at larger spatial scales.

Trait variability might also be dependent on physical and chemical plant traits. Physical traits reflect structural and morphological characteristics, while chemical traits represent characteristics such as concentrations of elements in plant organs. Investment in physical structure and chemical properties (e.g. N concentration) should result in increased plant growth according to metabolic theory (Niklas et al. 2005; Niklas 2006; Reich et al. 2006; Ishida et al. 2008). Here, we hypothesize that plants might either regulate their physical and chemical properties synchronously (Hypothesis 2a) or they do not (Hypothesis 2b), to cope with environmental changes under a given abiotic stress (Reich et al. 1997; Wright et al. 2004; Ishida et al. 2008; Freschet et al. 2010). If they do, we predict that the structure of the partitioning of a trait's variation among ecological scales should be consistent between physical and chemical traits (Prediction 2a). Alternatively, we predict that variation in physical and chemical traits across spatial scales should be plant tissue-specific (Prediction 2b), because leaf and wood traits may vary differently in relation to spatial scale, as discussed in Prediction 1b. It is well understood that chemical evenness (over-dispersion) of plant traits within plots may represent within-site niche differences in resistance to herbivores (Coley 1983; Carmona et al. 2011), and between-plot chemical evenness may represent coarse differences in investment in defence over environmental gradients (Agrawal & Fishbein 2006; Kursar et al. 2009). Defence syndromes are often associated with particular environmental conditions, and are known for convergent adaptation to resource-poor environments, such as white-sand soils in the case of some Amazonian forests (Fine et al. 2004, 2005). As such, defence syndromes should vary at the plot level, if plots encompass distinct environments. Moreover, since leaf traits are mainly responsible for niche differentiation at the fine scale and wood traits mediate broad, beta-niche differences at the intermediate scale (i.e. Prediction 1b), it is expected that leaf chemical traits should exhibit higher variability within-plots, whereas wood chemical traits should show a large variation across plots.

We tested the above mutually exclusive predictions in subtropical forests in eastern China. Specifically, we were interested in understanding: (1) whether variability in plant traits across ecological scales of the individual plant, species, plot and site differs between leaf and wood tissues; (2) whether the distribution of trait variation differs between physical and chemical traits; and (3) whether intra-specific trait variation is large relative to inter-specific variation.

Methods

Study sites

This study was conducted in the lower eastern extension of the Siming Mountain (29°41–50′ N, 121°36–52′ E), in the Ningbo coastal area of eastern China (Fig. 1). The area has one peak at 653 m a.s.l., with most other relief in the range of 70–300 m (Yan et al. 2009). The region has a typical monsoon climate, with a hot, humid summer and a drier, cold winter.

The pre-disturbance vegetation in this region is subtropical, evergreen broad-leaved forests (EBLFs), which were severely disturbed in recent history, with only small tracts of intact or semi-intact EBLFs left around the Buddhist temple in the Tiantong Forest Park (TT), Ruiyan Forest Park (RY) and Dongqian Lake Area (DQ). These three sites, spaced ca. 15 km from each other, were subjected to different intensities of human disturbance (usually logging) throughout history. Depending on their distance to Ningbo city and local villages (TT is the farthest, RY is intermediate and DQ is the nearest to Ningbo and local villages), these three sites represent a gradient of anthropogenic disturbance in the area (Fig. 1). In addition, among the three sites, TT has the largest area of EBLFs with a relatively wider range of topographic features, including a mesophytic area (TM), a peak area (TP) and a ravine area (TR). In general, there was relatively low similarity of species composition among the three sites (Appendix S1). Given that local micro-environmental conditions may change with the variable terrain, the EBLFs in TM, TP, TR, RY and DQ also represent a topography-mediated soil moisture gradient in the region (Fig. 1). In this study, we selected intact or semi-intact EBLFs among these five sites to characterize trait variation along anthropogenic disturbance and soil moisture gradients.

Fig. 1. Map of the lower eastern extension of the Siming Mountain (29°41–50′ N, 121°36–52′ E), Ningbo coastal area, eastern China. Study site locations appear as small black circles (DQ: Dongqian Lake Area; RY: Ruiyan Forest Park; TM: mesophytic area in Tiantong Forest Park; TP: peak area in Tiantong Forest Park; TR: ravine area in Tiantong Forest Park) within three study sites, represented in dark grey color.

Sampling design

We sampled 96 woody plant species among the five sites (TM, TP, TR, RY and DQ) based on the following principles: (1) plant species were sampled from different life (evergreen and deciduous) and growth forms (shrub and tree) to test the robustness and generality of patterns; (2) the species were sufficiently dominant in either the tree or shrub layer in a given community; and (3) the species were truly site- or habitat-specific, i.e. to be found only in a given community.

We assessed the variation of plant traits across six ecological scales: (1) between leaves pertaining to an individual leaf from the current year to the last year for evergreen species, and between young and mature leaves for deciduous species; (2) among twigs within an individual plant; (3) among individual plants within a species; (4) among species within a plot; (5) among plots within a site; and (6) among sites (see Fig. 2 for the sampling protocol).

These scales contained a mixture of taxonomic (species) and spatial factors, with explicit environment alone (twig) or combined with disturbance history (site), or with no immediately obvious environmental gradients (leaf, individual plant and plot). The EBLFs in each of TM, TP, TR, RY and DQ were selected to represent effects of environmental conditions and to serve as a proxy for putative differences in disturbance history between sites on plant trait variation at the site level. Plots within each of five sites were established systematically 100–500 m apart, located on similar slope positions and had similar vegetation history and soils. In total, we established nine plots in TM, four plots in TP, six plots in TR, four plots in RY and eight plots in DQ, with each plot (20 × 20 m) located at least 100 m from the stand edge. Because 20 × 20 m is the smallest reasonable area to be considered as a community for subtropical forests (Song & Wang 1995), we used a plot of this size to represent a forest community in the sense of a set of species co-existing together and interacting in a locality. We realize and caution the reader that co-existence is a phenomenon that occurs over much larger areas than a 20 × 20 m plot. On average, stem density of woody species with DBH (diameter at breast height) ≥ 1 cm was 36 per plot.

We followed the protocol recommended by Cornelissen et al. (2003) to select plant species and individual plants in a specific plant community. In each plot, the most abundant woody species were selected to assess trait variation among species within a plot. For each species, three individual plants per plot were randomly selected to estimate trait variation among individual plants within a species. For each individual plant, traits may differ between sun and shade leaves, as sunlight intensity varies with plant crown position. To evaluate effects of this micro-environment on plant traits within a tree, five branches from the four sides (east, south, west and north) and the upper position of the plant crown were chosen to study the variation at twig level. Since leaf longevity is strongly correlated with major trade-offs in plant functional traits (Aerts & Chapin 2000; Cornelissen et al. 2003), here we focus on leaf traits in both mature (leaves formed in the previous year and older) and current year leaves, attempting to screen the variation between ages of leaves within a

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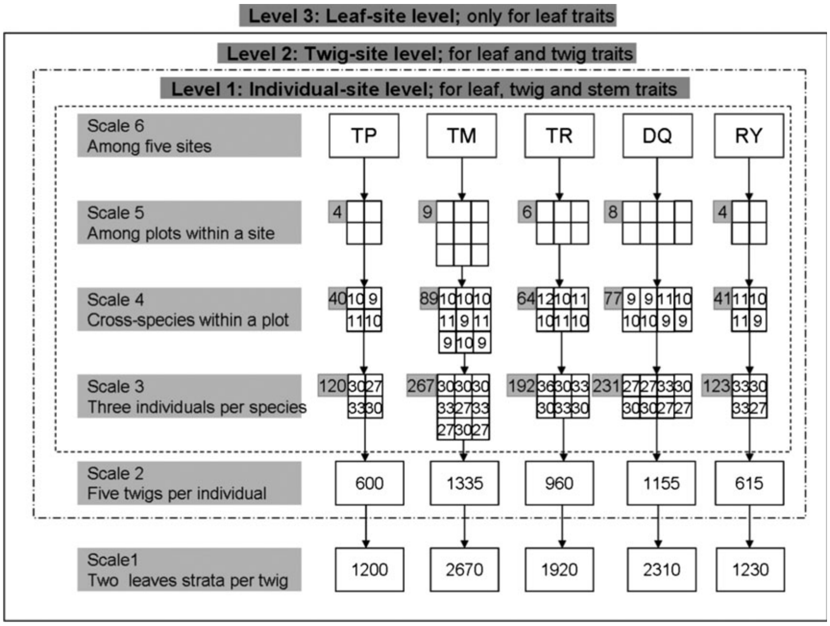

Fig. 2. Sampling scheme for the six ecological scales of leaf, twig, individual plant, species, plot and site. In order to decompose all traits at the same levels, the structure of ecological scales was classified into three levels, with each level presented at the top of the panel in dark grey, and the corresponding scale system is indicated (by line weight). The scale classes are given at the left of the panel in light grey. The sampling scheme is detailed on the right side.

branch. Hence, at the branch level, the leaves attached on each of current and last year's twigs were separated, treating them as mature and current leaves for evergreen species, and mature and young leaves for deciduous species. In total, we sampled 96 species (72 evergreen and 24 deciduous), 933 trees, 4665 twigs and 9330 leaves (see Fig. 2 for the sampling scheme).

Plant traits data collection

We studied ten traits that represent different ecological strategies and functional types pertaining to both leaf and wood tissues (Table 1). Leaf traits measured include specific leaf area (SLA), leaf dry matter content (LDMC) and leaf carbon (LC) and nitrogen (LN) concentrations. Wood traits measured were both at twig and stem (at the base of the trunk) levels, including twig wood density (TWD), stem wood density (SWD), trunk bark thickness (TBT), wood C (WC) and N (WN) concentrations.

To control for temporal variation in traits, all data were collected during the summer season (from June to August) in 2008. In each plot, three plants per species were randomly selected to collect twig and leaf samples. For each plant, five branches were cut from five different positions of the plant as described earlier, and the current year twigs were immediately separated from the branch based on the location of the terminal set of internodes. For each branch, ca. 20 mature leaves attached on the last year's shoot were chosen and sampled to represent mature leaves, and then one current year shoot without apparent leaf loss was sampled. The current year shoot is defined here as the twig, and leaves supported on it are defined as current or young leaves. The samples were wrapped in a moist paper towel, stored in sealed plastic bags and kept cool until brought back to the laboratory for measurement, which was usually performed within 12 h of sample collection.

In the laboratory, leaves and twigs were separated for each shoot type and the number of leaves per twig counted. Then twig length and twig diameter at the midpoint along the length were measured. Twig diameter was measured at two angles perpendicular to each other using an electronic vernier caliper, accurate to 0.1 mm. Twig cross-sectional area was calculated from diameter. Twig volume was calculated assuming the twig to be approximately cylindrical, with mid-point stem diameter as the cylinder diameter and stem length as the cylinder height. At the same time, 20 mature leaves and all fresh leaves attached on the current year shoot were each combined to form separate samples. The leaves in those samples were then scanned using a leaf area meter (LI-3100C, Li-Cor, Lincoln, NB, USA) to determine the mean leaf area. For compound leaves, we considered a leaflet as the laminar unit. Then twig and leaf samples were dried at 75 °C in an oven for 48 h to determine twig and leaf dry mass, which

Table 1. Functional traits measured in the study, and their assignment to leaf, twig and stem groups.

Trait (Abbreviation)	Unit	Ecological strategies	N	Range	Plant tissue type	Trait type
Mean individual leaf area (MLA)	mm^2	Light harvesting, energy and water balance	9330	22.98–16846.8	Leaf	Physical
Specific Leaf Area (SLA)	mm^2·mg^{-1}	Light harvesting, potential relative growth rate, defence	9330	1.17–77.81	Leaf	Physical
Leaf Dry Matter Content (LDMC)	%	Leaf physical strength, defence, leaf life span	9330	5.18–65.96	Leaf	Physical
Leaf C Concentration (LC)	%	Carbon status, resource capture	933	23.80–66.25	Leaf	Chemical
Leaf N Concentration (LN)	mg·g^{-1}	Nitrogen status, N and water capture	933	4.76–41.59	Leaf	Chemical
Twig Wood Density (TWD)	g·cm^{-3}	Twig water and nutrient transport, structure and defence	4665	0.02–0.84	Twig (wood)	Physical
Stem Wood Density (SWD)	g·cm^{-3}	Stem transport, structure and defence	933	0.12–1.26	Stem (wood)	Physical
Trunk Bark Thickness (TBT)	mm	Stem water and nutrient transport, structure and defence	933	0.11–4.57	Stem (wood)	Physical
Stem Wood C Concentration (WC)	%	Carbon status, biomass allocation	933	16.78–73.95	Stem (wood)	Chemical
Stem Wood N Concentration (WN)	mg·g^{-1}	Nitrogen status, N investment	933	0.10–16.31	Stem (wood)	Chemical

were then used to calculate leaf dry matter content, specific leaf area and twig wood density (TWD, dry mass divided by twig volume). Finally, the leaf samples were ground to determine C and N concentrations. Leaf N concentration was later measured using a flow-injection autoanalyser (Skalar, NL), and leaf C concentration was determined using an oil bath-K_2CrO_7 titration method (Nelson & Sommers 1975).

Stem traits, such as bark thickness at breast height (1.3 m) for trees and at 50-cm height for shrubs, were measured directly using an electronic vernier caliper (accurate to 0.1 mm) after trunk bark was cut with a knife. At the same time, we collected a tree core with a 5-mm diameter increment corer at the same position to determine stem wood density. In the laboratory, the length of the tree core was measured using an electronic vernier caliper, and then volume of the tree core was calculated. Next, core samples were dried at 75 °C in an oven for 72 h to determine dry mass used to calculate stem wood density. Then the samples were ground and digested for determining stem wood N and C concentrations (see the method for leaf N and C concentrations determination).

Data analysis

We used a linear mixed model to decompose trait variation across ecological scales, to test our hypotheses that the distribution of trait variation would differ between leaf and wood traits, and would be similar between physical and chemical traits. The linear mixed model used the six ecological scales in increasing order of leaf, twig, individual plant, species, plot and site. First, due to the unavailability of stem traits at the leaf and twig levels, variations in the ten traits were decomposed across individual plant, species, plot and site levels individually (individual–site levels). In this case, variation in leaf and twig traits was grouped at the individual plant level, with the variance partition patterns compared among leaf, twig and stem. Second, an analysis was conducted separately across twig, individual plant, species, plot and site scales for leaf and twig traits only to detect variability between these latter two specific tissues (twig–site levels).

In this procedure, the proportion of variation in the lowest level of the scale (twig or leaf) also includes measurement error. Given that the mixed model assumes that the observations within each subgroup are normally distributed and have equal variations, we $\log_{10}$-transformed the data for each of the ten plant traits to achieve normality of both residuals and random effects in the calibrated linear model. This analysis was conducted using a restricted maximum likelihood (REML) method in the 'lme' function of R (v. 2.11.1; R Foundation for Statistical Computing, Vienna, AT). In this procedure, we extracted variance components with the 'varcomp' function in R package 'ape'.

Finally, to confirm whether chemical traits coordinate with physical traits in different plant tissues at different spatial scales, we conducted regression analysis among and within plot levels to calculate the regression coefficients between chemical and physical traits for both leaf and wood tissues. Regression analysis was performed within as well as across plots to assess the strength of chemical–physical relationships. For within plot analysis, we selected one plot to represent a typical community in the region.

Results

Variance decomposition

The variance decomposition of physical and chemical traits differed between leaf and wood tissues. At the individual plant to site levels (across four scales), variation in five leaf traits and five wood traits showed distinct patterns (Table 2). For leaf tissue, physical and chemical traits showed a consistent pattern in variance decomposition

Table 2. Variance partitioning of the full nested linear models on ten plant functional traits in leaf and wood tissues across four ecological scales. All data were log10 transformed prior to analysis. Values in brackets represent 95% confidence interval, which was calculated by bootstrapping with 500 runs with randomly sampled data points with replacement.

Scale	Variance of plant functional traits (%)									
	Leaf tissues					Wood tissues				
	Leaf					Twig	Stem			
	Physical traits			Chemical traits		Physical traits			Chemical traits	
	MLA*	SLA	LDMC	LC	LN	TWD	SWD	TBT	WC	WN
Individual & Error	17 (16–18)	33 (18–46)	52 (41–57)	60 (41–53)	41 (33–41)	62 (64–69)	44 (23–57)	43 (28–47)	25 (6–21)	37 (10–31)
Species	74 (73–76)	57 (34–78)	41 (37–51)	39 (44–56)	47 (53–61)	17 (16–23)	37 (33–67)	40 (44–67)	2 (4–17)	14 (18–44)
Plot	6 (4–7)	1 (0–2)	0 (0–0)	0 (0–1)	2 (0–4)	18 (12–25)	15 (10–22)	15 (7–21)	71 (66–87)	41 (31–56)
Site	3 (2–3)	9 (0–11)	7 (5–9)	1 (1–5)	10 (4–8)	4 (4–6)	4 (1–10)	2 (0–8)	2 (0–4)	8 (0–15)

*See Table 1 for abbreviations of traits.

among the four ecological scales. The majority of variation was among species and individual plants, with very little at the plot level. Variation at the site level was comparatively smaller (Table 2). For wood tissue, variance partitioning between physical and chemical traits showed different patterns: TWD, SWD and TBT had most of the total variance at the species and individual plant levels, and WC and WN exhibiting the largest variation at the plot level (Table 2). In contrast to leaf traits, there was a large percentage of the total variance for wood traits at the plot level. At the site level, wood traits had the smallest amount of variation (Table 2).

When the twig level was added to the ecological scales (i.e. considering five scales from twig to site levels), the percentage of the total variation in five leaf and one twig traits decreased at the individual plant level, but increased at the twig level (Table 3), indicating that the twig level was responsible for a significant amount of within-individual variation. Similar to results at the individual plant to site levels, the amount of variation in five leaf traits was significantly larger at the species level than those at the site and plot levels. For twig traits, the variation was fairly evenly distributed between species and plot levels, with little partitioned at the site level (Table 3). When leaf age was added into the ecological scales (as a sixth scale), variation at the twig level became zero, while variation at the leaf level increased (Appendix S2). This indicated that, once leaf age was incorporated into the ecological scale as another level, variation at the twig level was transferred to the leaf level. For instance, two-way ANOVAs demonstrated that leaf age accounted for nearly 100% of the variation in each of SLA and LDMC, while variation at the twig level was negligible.

Among the four ecological scales, a large portion of the total variation was within species level for the leaf and wood traits studied. The intra-specific variation was almost equal to the inter-specific variation for leaf and wood traits, except for MLA and TWD. For MLA, intra-specific

Table 3. Variance partitioning of the full nested linear models on six plant functional traits in leaf and twig tissues across five ecological scales. All data were log10 transformed prior to analysis. Values in brackets represent 95% confidence interval, which was calculated by bootstrapping with 500 runs with randomly sampled data points with replacement.

Scale	Variance of plant functional traits (%)					
	Leaf tissues					Wood tissues
						Twig
	Physical traits			Chemical traits		Physical traits
	MLA*	SLA	LDMC	LC	LN	TWD
Twig & Error	13 (12–14)	27 (19–32)	49 (40–58)	60 (24–70)	41 (16–48)	49 (34–40)
Individual	7 (6–9)	12 (8–16)	5 (2–9)	0 (0–13)	0 (0–8)	19 (14–21)
Species	71 (70–73)	51 (44–61)	39 (31–45)	39 (29–50)	47 (39–54)	10 (10–17)
Plot	5 (4–6)	1 (0–3)	0 (0–0)	0 (0–1)	2 (0–5)	18 (26–31)
Site	3 (2–4)	10 (8–11)	7 (6–9)	1 (1–3)	10 (7–13)	3 (2–4)

*See Table 1 for abbreviations of traits.

variation was smaller than inter-specific variation, whereas for TWD, the intra-specific variation was much higher than inter-specific.

Correlation between physical and chemical traits

Among plots, there were significant relationships between chemical and physical traits for leaf tissue (Table 4). For example, LC was positively correlated with LDMC, while LN was positively correlated with SLA and MLA (Table 4), indicating that variation among leaf traits was synchronous. In contrast, no relationship between chemical and physical traits was found for wood tissue (Table 4). Within plots, regression analysis showed that LC was correlated with MLA and LDMC, while LN was correlated with SLA for leaf tissue. For stem tissue, the only correlation was between WC and SWD (Table 4).

Discussion

Variation partitioning of tissue-specific traits among ecological scales

We showed that the variation among ecological scales was not consistent between leaf and wood tissues, providing evidence for the tissue-specific trait variability in subtropical woody plants. This suggests that trait variability across ecological scales would be more similar within leaf traits or wood traits than between the two sets of traits. It is understandable that variation partitioning of plant traits among ecological scales was not coordinated between leaf and wood tissues, because leaf and wood tissues play different roles in plant ecological strategies. For a plant, leaves are mainly responsible for the process of photosynthesis and transpiration, associated with light interception and CO_2 assimilation. In contrast, woody tissues, such as twigs and stems, transport water and nutrients (Cornelissen et al. 2003) as well as providing mechanical support, thus generating height and improving a plant's competitive fitness for light. Such tissue-specific functions indicate that trade-offs in plant ecological strategies operate independently at the leaf and wood tissue levels. For example, Baraloto et al. (2010) demonstrated that the axis of leaf trait variation is orthogonal to the axis of wood trait variation. Leaf habit and woodiness were reported to regulate different leaf economies for 105 species in the Netherlands (Ordoñez et al. 2010). Environmental filtering more strongly acts upon leaf than stem traits, but leaf and stem traits together exhibited strong evidence of environmental filtering (Paine et al. 2011). However, our results suggest that the opposite is true in the studied region: plots varied more with respect to stem traits than with respect to leaf traits. This is consistent with the observation that stem traits such as wood density are better predictors of plant performance than leaf traits such as specific leaf area (Poorter et al. 2008).

The ecological scale at which particular ecological processes play out is thought to be reflected by the higher magnitude of trait variation detected at that scale. However, what are the consequences of environmental filtering and resource competition on the community structure with respect to differences between leaf and wood traits? The results in this study did not support our null hypothesis (Hypothesis 1a) that leaf and stem traits are developmentally or genetically linked or functionally correlated, and so do not vary independently. Therefore, Prediction 1a, i.e. the scale at which variation is exhibited will not differ significantly between leaf and wood traits, is not confirmed. Rather, consistent with our competing hypothesis and prediction (1b), our results showed that stem traits varied more across plots than within plots, whereas leaf traits exhibited higher variation within plots, suggesting a relatively strong habitat filtering process on stem traits, but not leaf traits, at a spatial scale commensurate with the forest plots in our analysis. Relative to wood traits, variations in leaf traits were higher at individuals and species levels, indicating that resource competition limits the similarity of

Table 4. Coefficients (r^2 and significance level) from linear regression between physical and chemical traits in each of leaf and stem tissues for woody plants among plots and within plots that represent a typical forested community of subtropical forests in the lower eastern extension of the Siming Mountain, the Ningbo coastal area, eastern China.

Chemical traits	Physical traits in leaf tissues			Chemical traits	Physical traits in wood tissues	
	MLA†	SLA	LDMC		SWD	TBT
Among plots						
LC	0.001 ns	0.01 ns	0.16***	WC	−0.01 ns	0.02 ns
LN	0.20***	0.21***	0.001 ns	WN	0.02 ns	0.004 ns
Within plot						
LC	0.12**	0.02 ns	0.15***	WC	0.76***	0.12 ns
LN	0.001 ns	0.09*	0.01 ns	WN	0.23 ns	0.10 ns

†See Table 1 for trait abbreviations. Significance levels are indicated as *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. The sample size (n) for among plots was 933, and for within plots was 40.

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co-occurring species with respect to leaf traits within communities (Kraft et al. 2008). It is thought that habitat filtering tends to reduce trait variation relative to a regional species pool (Kraft et al. 2008; Cornwell & Ackerly 2009). The elevated standard deviations of nearest-neighbor trait distances are likewise interpreted as evidence of a more even distribution of traits (e.g. Kraft et al. 2008; Cornwell & Ackerly 2009; Jung et al. 2010; Paine et al. 2011; Baraloto et al. 2012; Sedio et al. 2012). In this study, stem traits exhibited much higher variation across plots, suggesting that habitat filtering may be operating at this scale. This might be due to differences in underlying environmental conditions between plots (Yan et al. 2013). In this case, stem traits might be more plastic and permit species from the same clade to adapt to very different habitat properties, by exhibiting the beta component of trait diversity among plots (Ackerly et al. 2006). Leaf traits, on the other hand, exhibited higher variation among individual plants or among species within a plot, with little variation between plots. This variation pattern in leaf traits might be related to competitive exclusion of similar individual plants/species or by local niche differentiation. The role of such leaf traits in defining fine-scale niche differentiation (Ackerly et al. 2006) – and the importance of intra-specific variation for species co-existence (Violle et al. 2012), suggest that the leaf traits measured in this study reflect niche differentiation (i.e. alpha niche) that affect species co-existence.

At the plot level, variation between leaf and wood traits might also be associated with the strength of the environmental filtering that acts differently on leaf and wood tissues. For wood traits, such as stem traits, the 'local/small scale' is the plot level. At this level, stems are considered to exist in a micro-niche with variable conditions such as of the amount of light received by individual plants and the amount of water and nutrients available (Yan et al. 2013). In contrast, the 'local/small scale' for leaves is the individual plant or the twig level that correspond to differences in available light (position of twigs within a tree) and to leaf age (differently aged leaves within a twig). This can be demonstrated by the lack of significant variation in leaf traits at the equivalent 'plot' level in Messier et al. (2010) and Albert et al. (2010a). In this study, variation in leaf traits at the local/small scale (within plot) was probably due to micro-heterogeneity, such as variation in twig positions and leaf ages. Effectively, physiological processes in plant leaves differ significantly between leaves of different ages. For evergreen species, given the difference in leaf longevity, photosynthesis and resource use, strategies should differ between current year and older leaves (Chabot & Hicks 1982; Aerts & Chapin 2000). For deciduous plants, young leaves are more metabolically active than mature leaves, and appear to be functionally different (Aerts & Chapin 2000; Ryser & Urbas 2000).

Site level differences may also be associated with dissimilar plant functional types, as a result of filtering processes. In this study, the site level was responsible for a relatively small part of variation for both leaf and wood traits, indicating that environmental shifts and disturbance regimes among the five sites were not strong enough to engender variation in plant traits. It also suggests that much variation in plant traits may exist at small/local ecological scales (i.e. species, individual plants, twigs and leaf age), rather than at broad ecological scales (e.g. site).

Variability between physical and chemical traits

Variance partitioning of physical and chemical traits among the four ecological scales was consistent for leaf tissue but not for wood tissue. This partly confirmed our Hypothesis 2a and Prediction 2a that variation partitioning across ecological scales should be consistent between physical and chemical traits in leaf tissues. This is supported by the existence of the significant relationships between physical and chemical traits either among plots or within plots for leaf traits, but not for wood traits (Table 4). Although metabolic theory predicts that allocation strategies of leaf and stem tissues are synchronous (Niklas et al. 2005; Niklas 2006), the lack of co-variation between leaf and stem traits indicated that plant physical and chemical properties did not vary simultaneously at the whole plant level, but were plant tissue-specific. In this context, Hypothesis 2a and the related prediction were partly rejected, and therefore the alternative hypothesis and prediction (i.e. 2b) were accepted.

In this study, synchronization of physical and chemical properties is more evident with the leaf economics spectrum (LES) than with the wood economics spectrum at both across- and within-community scales (Table 4). For leaf tissues, the strength of correlation between SLA and LN was stronger among plots than within plots. This suggests that LES is operating at scales larger than plots (larger than direct interaction among plants), and is weakly contributing to plot-level species co-existence. Across plots, the relatively strong relationship between physical and chemical traits suggests that plants might regulate their physical and chemical properties synchronously to cope with environmental changes (Niklas et al. 2005; Niklas 2006; Reich et al. 2006). This is the case in terms of the LES. For example, in nutrient-rich soils, plants with inexpensive short-lived leaves provide rapid returns on C and nutrient investments; conversely, with costly long-lived leaves, plants in nutrient-poor soils, provide slow returns on investments (Wright et al. 2004). In contrast, the weak support for the LES within the plot might be associated with the hypothesis that co-existing species should exhibit limited similarity in their functional traits (Kraft et al. 2008; Cornwell & Ackerly 2009). Recent work has shown that within habitats, co-existing species can show significant trait dispersion (Cavender-Bares et al. 2004; Jung et al. 2010). It may be that local competition serves to select for species with more divergent multivariate strategies, reducing the power of the LES within the community (Wright & Sutton-Grier 2012).

For wood tissue, the contrasting variation partition between physical and chemical traits suggests asynchronous variation between cost of physical structure and chemical investment. In particular, much of the variation in physical traits existed at the species and individual plant levels, but most of the variation in chemical traits existed at the plot level. This suggests that there were environmental differences between plots, which may account for why woody chemical traits differed between plots as well, independent of species or individual plants. The underlying mechanisms might be related to the idea that within-plot chemical evenness may represent within-site niche differences, while chemical evenness (over dispersion) of plant traits among plots represents coarse differences in investment in defence over environmental gradients (Agrawal & Fishbein 2006; Kursar et al. 2009). This can be evidenced by recent work that defence syndromes are often associated with particular environmental conditions (i.e. white-sand soils) in some Amazonian forests (Fine et al. 2004, 2005). It is interesting to note that there was little variation in leaf C and N at the plot level, but much variation in stem C and N at the plot level. It is possible that stem chemical traits might also be related to alternative plant defence 'syndromes' at a given spatial scale (Agrawal & Fishbein 2006; Kursar et al. 2009).

In addition to the defence syndromes, other mechanisms may also be responsible for the asynchronous variation between physical and chemical traits. For example, habitat filtering and interactions among plants are thought to mediate variation in physical and chemical allocation of plants over environmental gradients (Kraft et al. 2008; Cornwell & Ackerly 2009). In general, physical traits are more strongly determined by the evolutionary history of a species (Poorter et al. 2008; Chave et al. 2009; Baraloto et al. 2010), but chemical traits exhibit a strong environmental signal. In this study, the similarity of species composition was relatively low across sites and between neighbouring plots. Hence, a large proportion of variation in physical traits in wood tissue was allocated to within-plot, which might have been a result of the differing species composition. Whereas, the dominant variation partitioning at the plot level for chemical traits might be due to the differences in soil nutrient availability between plots.

The importance of intra-specific variability of plant traits

The fraction of the total within-species variation (the sum of all the variation occurring at levels below species) was equal or even greater than the inter-specific variation for most leaf and wood traits. Our results hence provide clear evidence for strong intra-specific variation in physical and chemical traits in both leaf and wood tissues. It also suggests that within-species variation in leaf and wood traits may be important for shaping community assembly and species co-existence across spatial scales. However, in most empirical studies, plant traits have been assessed mainly at the inter-specific level, while the intra-specific variability has been largely ignored (de Bello et al. 2011; Bolnick et al. 2011). We argue that trait variability should be evaluated at the individual plant level or at least at the population level to understand patterns of species co-existence and community dynamics. A poor understanding of intra-specific trait variation could be one reason why models predicting plant performance or abundance have low predictability (Albert et al. 2010a, 2011; Bolnick et al. 2011). In such situations, part of the residuals of these models may be explained by intra-specific variation (Cianciaruso et al. 2009; Messier et al. 2010; Paine et al. 2011; Violle et al. 2012).

Conclusions

Leaf and wood traits vary differently in relation to ecological scale, providing strong evidence for tissue-specific trait variability in subtropical woody plants. The above conclusion is consistent with recent evidence that leaf and stem economics might be controlled by orthogonal axes (Baraloto et al. 2010). Our study demonstrated that physical and chemical traits might also be independent. These orthogonal trait axes might have important implications for community assembly because they allow plants to respond to habitat gradients over distinct spatial scales. More importantly, these orthogonal trait axes decouple the leaf-mediated niche from the stem-mediated niche, thus increasing the dimensionality of trait, and hence niche space facilitates the co-existence of higher species richness in forest communities.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Sørensen (L) index values between sites.

Appendix S2. Variance partitioning of functional traits in leaf tissues across six ecological scales.