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Research paper

The plant economics spectrum is structured by leaf habits and growth forms across subtropical species

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The plant economics spectrum that integrates the combination of leaf and wood syndromes provides a useful framework for the examination of species strategies at the whole-plant level. However, it remains unclear how species that differ in leaf habits and growth forms are integrated within the plant economics spectrum in subtropical forests. We measured five leaf and six wood traits across 58 subtropical plant species, which represented two leaf habits (evergreen vs deciduous) and two growth forms (tree vs shrub) in eastern China. Principal component analysis (PCA) was employed separately to construct the leaf (LES), wood (WES) and whole-plant (WPES) economics spectra. Leaf and wood traits are highly intra- and intercorrelated, thus defining not only the LES and WES, but also a WPES. Multi-trait variations in PCAs revealed that the traits which were representative of the acquisitive strategy, i.e., cheap tissue investment and rapid returns on that investment, were clustered at one end, while traits that represented the conservative strategy, i.e., expensive tissue investment and slower returns, were clustered at other end in each of the axes of the leaf and wood syndromes (PC1-axis) and the plant height strategy (PC2-axis). The local WPES, LES and WES were tightly correlated with each other. Evergreens shaped the conservative side, while deciduous species structured the acquisitive side of the WPES and LES. With respect to plant height strategies, trees formulated the acquisitive side and shrub species made up the conservative side of the WPES, LES and WES. In conclusion, our results suggested that the LES and WES were coordinated to a WPES for subtropical species. The finding of this local spectrum of plant form and function would be beneficial for modeling nutrient fluxes and species compositions in the changing climate, but also for understanding species strategies in an evolutionary context.

Keywords: acquisitive strategy, conservative strategy, functional traits, leaf economics spectrum, plant height, whole-plant economics spectrum, wood economics spectrum.

Introduction

Functional traits, at tissue-to-organismal scales, are increasingly recognized as powerful indicators of plant form and function (Westoby et al. 2002, Violle et al. 2007, Díaz et al. 2016). Over the last few decades, the notion of an economics spectrum has been proposed for elucidating the fundamental trade-offs between functional strategies among vascular plants (Bloom et al. 1985, Givnish 1986, Grime et al. 1997). The economics spectrum is a pattern of correlations among plant functional traits that is strikingly consistent across (Reich et al. 1997, Wright et al. 2004, Craine et al. 2005, Chave et al. 2009, Osnas et al. 2013, Zhang et al. 2015, Díaz et al. 2016) and within species (Niinemets 2015), at both small- and large-scale environmental gradients.

One end of the spectrum represents fast-growing species with cheap tissue investment and rapid returns on that investment (i.e., acquisitive strategy; Wright et al. 2004, Reich 2014). The other end of the spectrum represents slow-growing species

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with expensive tissue investment and slower returns (i.e., conservative strategy; Wright et al. 2004, Reich 2014). Functionally, 'acquisitive vs conservative' strategies should coordinate between leaf and wood tissues (Freschet et al. 2010, Méndez-Alonzo et al. 2012, Reich 2014, Díaz et al. 2016), as allocation strategies of cheap or expensive tissues occur synchronously at the whole-plant level (Grime et al. 1997, Wright et al. 2006, Meinzer et al. 2008, Poorter et al. 2013). However, several recent studies have argued that leaf (LES) and wood economics spectra (WES) are largely decoupled (Baraloto et al. 2010, Ordoñez et al. 2010, Wright and Sutton-Grier 2012, Li et al. 2015). These contrasting findings suggest that the consistency of the plant economics spectrum between leaf and wood tissues remains a matter for discussion.

Theoretically, plant ecological strategies in leaf and wood tissues should be consolidative for building a single whole-plant economics spectrum (WPES), in that variations, not only in leaf traits, but also in wood traits, determine species performance (Grime et al. 1997, Pérez-Ramos et al. 2012, Poorter et al. 2013, Reich 2014). Wide-ranging evidence exists for coordination of LES and WES. For example, stem hydraulic properties and wood density are coupled with leaf photosynthetic capacities or leaf water potentials across species and light environments (Brodribb and Feild 2000, Santiago et al. 2004, Campanello et al. 2008, Ishida et al. 2008, Meinzer et al. 2008, Freschet et al. 2010, Bucci et al. 2012, Méndez-Alonzo et al. 2012). Further evidence for the coupling of LES and WES derives from the coordination between root and leaf traits (Reich et al. 2003, Comas and Eissenstat 2004, Craine et al. 2005, Tjoelker et al. 2005, Freschet et al. 2010, Liu et al. 2010, Prieto et al. 2015, Valverde-Barrantes et al. 2015). Although roots are an integral part of the vascular system, their characteristics are so different as to be considered an independent organ, thus, the coordination between leaf and roots would be a compelling evidence of the WPES, integrated through the WES. We hypothesize that LES and WES should be tightly integrated toward the structuring of a WPES (Hypothesis 1). We thus propose that wood economics traits are correlated with leaf economics traits.

The plant economics spectrum reflects how species with similar strategies converge and/or diverge along the axis of the traits variation (Díaz et al. 2016). Wright et al. (2004) reported that leaf investment strategies array along a global spectrum of leaf economics when species are grouped by leaf habit and growth form. Species grouped in different growth forms and leaf habits are differentiated along the LES. However, it was discovered that leaf longevity and area-based leaf mass are decoupled for deciduous trees and shrubs, due to reduced variation in leaf longevity. Virtually, there are intermediate states between 'true trees' and 'true shrubs' (Scheffer et al. 2014, Castorena et al. 2015, Pei et al. 2015, Qian and Ricklefs 2015). By the same token, the strict classification of evergreen and deciduous obscures much ecological variation, as species vary widely in their leaf shedding rate, thus deciduousness may be considered a semi-continuous trait (Warren and Adams 2004, Méndez-Alonzo et al. 2012). In this context, variations in leaf habits (e.g., evergreen vs deciduous) and growth forms (e.g., trees vs shrubs), two commonly used traits for classifying plants, are expected to integrate within a WPES.

Investigations of the degree of divergence in both LES and WES traits across leaf habits and growth forms would allow us to understand why species arrange in a continuous plant spectrum (Poorter et al. 2013, Díaz et al. 2016). With respect to leaf habits, deciduous plants possess lower leaf mass per unit area (i.e., low LMA), a higher proportion of leaf nutrients in relation to carbon and higher photosynthetic rates than do evergreen plants (Reich et al. 1997, Aerts 1999, Westoby et al. 2002, Wright et al. 2004). Additionally, deciduous species that are capable of rapidly transferring water have low wood density, short leaf life span and high rates of resource acquisition and flux at organ and individual scales, whereas the reverse is true for evergreen species (Monk 1966, Aerts 1999, Kloeke et al. 2012, Méndez-Alonzo et al. 2012). These findings suggest that deciduous species tend to adopt an acquisitive strategy, whereas evergreen species tend to exhibit a conservative strategy (Givnish 2002). We thus hypothesize that deciduous and evergreen species would differentiate along the plant economics spectrum, with deciduous species arraying on the acquisitive side and with evergreen species ranking on the conservative side of the plant economics spectrum (Hypothesis 2).

With respect to growth forms, Falster and Westoby (2005) found that plant potential height was positively correlated with leaf mass per area, leaf nitrogen and wood density in 45 dicot rain forest species along the light gradient in tropical Queensland, Australia. Moreover, Díaz et al. (2016) have reported a global spectrum of plant form and function over 46,000 species worldwide. They found that stem specific density and leaf area (LA) are correlated with the economics spectrum of the size of whole plants and their parts, running from short species with small diaspores to tall species tending to have large diaspores. These results suggested that plant height is coordinated with leaf and wood traits, representing a height-based economics spectrum across species. Relative to short plants, their tall counterparts are adapted to competition for light through rapid volumetric growth, high light capture efficiencies (Givnish 1986, Rowe and Speck 2005) and hydraulic conductance (Ishida et al. 2008). Therefore, along the light gradient, tall plants with rapid vertical growth were associated with resource-acquisition traits, such as high leaf nitrogen, high photosynthetic capacity (Poorter 1999), as well as low wood density, due to the requirement for increased hydraulic conductance (Thomas 1996, Kohyama et al. 2003, Ishida et al. 2008). In contrast, short plants with slow vertical growth rates were associated with shade-tolerant traits and resource conservation strategies

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(Kitajima 1994), such as low specific leaf area (SLA), low leaf nitrogen (Walters and Reich 1999, Reich et al. 2003) and high wood density (Falster and Westoby 2005). Consequently, it is expected that, as a whole-plant trait, plant height coordinates to the plant economics spectrum (Hypothesis 3). Specifically, we predicted that tree and shrub species would be separated along the plant height economics spectrum, with fast-growing trees clustering on the acquisitive side, but with shade-tolerant shrubs distributing on the conservative side of the plant economics spectrum.

For this study, we tested the above three hypotheses by measuring 10 leaf and wood traits and plant maximum heights across 58 subtropical species in Eastern China. Specifically, we were interested in understanding: (i) whether leaf and wood strategies are coordinated toward the integration of a single WPES, (ii) how evergreen and deciduous species differentiated along the plant economics spectrum and (iii) how trees and shrubs were distributed along the plant height economic spectrum.

Materials and methods

Study area, vegetation and plant species

This study was conducted in the lower eastern extension of the Siming Mountains (29°41–50′N, 121°36–52′E), located in the Ningbo coastal area, Zhejiang Province, in Eastern China. The climate of this region is subtropical monsoon. Mean annual temperature was 16.2 °C, with a January minimum of 4.2 °C and a July maximum of 28.1 °C. Mean annual precipitation is 1374.7 mm. Similar to the low subtropical region (Pei et al. 2015), 80% of annual precipitation falls in the wet season (from April to September) and 20% in the dry season (from October to March). The highest peak in this area is at 653 m above sea level, while most other landforms are in the range of 70–300 m. The soils in this region were classified as Ferralsols, according to the FAO soil classification system, with the parent materials consisting mostly of Mesozoic sedimentary rocks, some acidic igneous rocks and residual granite weathering material.

This region supports evergreen broad-leaved forests (EBLFs). Typical EBLFs are distributed primarily in the Tiantong National Forest Park. Mature and secondary EBLFs typically occur in mesophytic habitats. Ravines and mountain bases are dominated by evergreen-deciduous broad-leaved mixed forests. Beyond the forest park, virtually all vegetation is secondary shrubs or young forests, which are comprised of a mixture of deciduous and evergreen species. These secondary shrubs or young forests were, for the most part, formed following the cessation of repeated harvesting, ~30 years ago (Yan et al. 2013).

The selected 58 angiosperms species, belonging to 20 families and 38 genera, were regionally common in either the tree or understory layer across mature and secondary EBLFs, evergreen-deciduous broad-leaved mixed forests and secondary shrubs. These 58 species were representative of the four major life forms with contrasting leaf habits and plant maximum heights (see Table S1 available as Supplementary Data at *Tree Physiology* Online), i.e., evergreen tree and shrub, deciduous tree and shrub.

Across species, shade tolerance varies gradually. Evergreen tree species dominate mostly in the canopy of EBLFs, whereas evergreen shrub species occupy in EBLFs or secondary shrubs. Deciduous tree species occupy evergreen-deciduous broad-leaved mixed forests, and deciduous shrub species occur primarily in shrub-lands. In total, 58 species were recorded, of which 23 were evergreen trees, 21 were evergreen shrubs, 9 were deciduous trees and 5 were deciduous shrubs.

Measurement of plant traits

Plant traits vary considerably across individuals within species (Niinemets 2015). To reduce intraspecific variation in plant traits, we tried to measure individuals of a given species as much as possible. Given the difficulty of finding replicas of individuals for rare and endangered species (Song et al. 2016), three individuals were selected to quantify plant functional traits, whereas in common species up to 58 individuals per species were quantified to minimize intraspecific variation in traits. Individuals were sought out under closed-canopy conditions; however, light-demanding species such as deciduous shrubs were also sampled in gaps and along firebreaks or roads to assure a sufficient number of individuals. Identical species from different habitats were pooled to obtain averages for plant functional traits. For standardization purposes, plant height data for each species included the maximum plant height of that species observed in our study area. Maximum plant height was measured vertically from the forest floor to the apex of the plant by using a clinometer–hypsometer.

Functional traits in leaf and wood tissues were measured from statured adult plants for every species in the growing season (i.e., July and August in 2008). We measured 10 functional traits for each sampled plant, including leaf dry matter content (LDMC), SLA, mean individual LA, leaf nitrogen content (N_{leaf}), leaf carbon content (C_{leaf}), twig wood density (WD_{twig}), stem wood density (WD_{stem}), stem bark thickness (BT), stem nitrogen concentration (N_{stem}) and stem carbon concentration (C_{stem}). We classified most of these traits as associated with plant ecological strategies for leaf and wood tissues (Table 1).

Five branches were collected in the field from five different sites for each sampled plant, i.e., from the four sides and the upper position of the crown. Subsequently, the current year twigs were separated from the collected branches according to the terminal set of internodes. Approximately 20 mature leaves without visible damage were collected per twig, whereafter one current year twig without visible leaf loss was sampled from each branch. Each sample was covered in a moist paper towel and stored in a sealed plastic bag and kept cool until the samples were transported to the laboratory for further analysis. Once in

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Table 1. Functional traits measured on leaf and wood tissues across subtropical plant species, and their assigned strategies.

Trait (abbreviation)	Unit	Strategy	A priori group
Leaf dry matter content (LDMC)	%	Leaf resource capture and defense	Leaf
Mean leaf area (LA)	mm^2	Leaf resource capture	Leaf
Specific leaf area (SLA)	$m^2\ kg^{-1}$	Leaf resource capture and defense	Leaf
Leaf carbon concentration (C_{leaf})	%	Leaf resource capture	Leaf
Leaf nitrogen concentration (N_{leaf})	$mg\ g^{-1}$	Leaf resource capture	Leaf
Twig wood density (WD_{twig})	$g\ cm^{-3}$	Stem transport, structure and defense	Wood
Stem bark thickness (BT)	mm	Stem structure and defense	Wood
Stem wood density (WD_{stem})	$g\ cm^{-3}$	Stem transport, structure and defense	Wood
Stem carbon concentration (C_{stem})	%	Stem structure and defense	Wood
Stem nitrogen concentration (N_{stem})	$mg\ g^{-1}$	Stem structure and defense	Wood
Maximum tree height (H)	m	Stem structure	Wood

the laboratory, the leaves were separated from the twigs, after which the twig lengths and twig diameters (at midpoint) were measured using an electronic vernier caliper (accurate to 0.1 mm). The cross-sectional areas of the twigs were calculated via the diameter, while the twig volume was calculated assuming that the twigs had a cylindrical shape. Simultaneously, 20 mature leaves from each branch were collected to form separate samples. The leaves were then scanned using an LA meter (LI-3100C, Li-Cor, Lincoln, Nebraska, USA) to determine the LA. Twig and leaf samples were then dried at 75 °C for 48 h in an oven to determine dry twig and leaf mass, toward calculations of LDMC, SLA and WD_{twig}. Finally, the leaf samples were ground to determine the N_{leaf} using a flow-injection auto-analyzer (Skalar-1000, Breda, North Brabant, The Netherlands) and C_{leaf} was determined using an oil bath-K_2CrO_7 titration method.

We measured the BT directly at a height of 1.3 m for trees, and at a height of 50 cm for shrubs, using an electronic vernier caliper (accurate to 0.1 mm) once the bark was cut with a knife. We used stem segments to determine WD_{stem}, and to obtain sufficient sample mass, stem segments were collected by cutting branches as large as possible from each plant, which were employed for the collection of twig and leaf samples. In the laboratory, pith and bark were removed, and fresh volume was measured by the water displacement method. Following the measurement of fresh volumes, the samples were dried at 75 °C in an oven for 72 h to determine the dry mass and to calculate WD_{stem}. The reported values were oven dry mass per fresh volume ($g\ cm^{-3}$). Finally, the stem samples were ground and digested to determine the N_{stem} and C_{stem}. The list of species, growth forms, leaf habits and summary of functional traits, are shown in Table S1 available as Supplementary Data at *Tree Physiology* Online. This work was conducted based on Forestry Standards for 'Observation Methodology for Long-term Forest Ecosystem Research' of the People's Republic of China (LY/T 1952–2011).

Data analysis

For each species, the mean value for each trait was employed. Initially, standardized major axis (SMA) regression with 95% confidence intervals were fitted to bivariate leaf and wood trait relationships across species. In this case, all species were combined, regardless of leaf habits and growth forms. The relationships between the leaf and wood traits were described by a mathematical equation of the type $y = bx^a$, linearized under the form $\log(y) = \log(b) + a \log(x)$.

Secondly, principal component analyses (PCAs) were performed separately for each of the WPES traits (11 traits), LES traits only (five traits) and WES traits only (six traits). Given the generally high proportions of variance explained by PC1 and PC2, these scores were used in all subsequent analyses as a proxy for the WPES, LES and WES. To understand the patterns of variation between individual traits and resource economics, the scores of the first and second PC were correlated again to each trait. In this way, the relative contribution of each trait to the PC1 and the PC2 was estimated.

To test for the significant differences between each of leaf habits and growth forms, an independent-samples *T*-test was carried out on the species scores, with respect to each of PC1 and PC2, based on the trait sets of the whole-plant, leaf and wood scale. In this case, leaf habits and growth forms were considered as the discrete variable. An independent-samples *T*-test and PCA were conducted using SPSS (version 19), and all statistical tests were considered significant at the $P < 0.05$ level.

Finally, to test for the levels of associations among the WPES, LES and WES, and between LES and WES, SMA regression was again employed to determine the slope and intercept for these 'scaling' relationships. Bivariate spectrum relationships were fitted by species scores on the whole-plant PCA (PC1 and PC2), and each pair of PC1 and PC2 derived from the PCAs for the leaf and wood traits. In order to investigate how plant species differing in leaf habit and/or growth form structure the 'scaling' relationships among the whole-plant, leaf and wood economics spectra, cross-species regressions were fitted separately for each of evergreen and deciduous species and/or tree and shrub species.

Since species differing in leaf habit were grouped primarily by the PC1 axis at the whole-plant and leaf economics scales

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($T = -3.58$, $P < 0.001$; independent-samples T-test), three pairs of bivariate spectrum relationships, including whole-plant PC1 vs leaf PC1, whole-plant PC1 vs wood PC1 and leaf PC1 vs wood PC1, were fitted separately for each of evergreen and deciduous species. Similarly, species differing in growth form were grouped mainly by the PC2 axis across the whole-plant, leaf and wood economics scales (detailed in Results). Bivariate spectrum regressions were run for each of whole-plant PC2 vs leaf PC2, whole-plant PC2 vs wood PC2 and leaf PC2 vs wood PC2.

Regression procedures were carried out using (S)MATR (Version 2.0, Falster et al. 2006). Confidence intervals for scaling slopes, the heterogeneity of regression slopes, common slopes among groups and differences in the y-intercept and shifts against the common slope were tested by the post hoc Tukey test in ANOVA, in this software.

Results

Relationships between leaf and wood traits

In most cases, leaf traits significantly correlated with wood traits (Table 2). The scaling relationship between LDMC and each of WD_{twig}, WD_{stem}, BT, N_{stem} and H was positive. The LA was positively correlated to BT and H, but negatively correlated to WD_{stem}. There was a negative scaling relationship between SLA and each of WD_{twig} and WD_{stem}. The C_{leaf} correlated to H only. The N_{leaf} was negatively correlated to WD_{twig}, WD_{stem} and C_{stem}, but positively correlated to H.

For trait relationships within leaf tissues, LDMC was negatively correlated to SLA, but positively correlated to C_{leaf}. The LA was positively correlated to SLA and N_{leaf}, and the scaling relationship between SLA and N_{leaf} was positive (Table 2). With respect to wood traits, WD_{twig} was positively correlated to WD_{stem}, and BT was positively correlated to N_{stem} and H. The WD_{stem} was also positively correlated to N_{stem}, which was positively correlated to H (Table 2).

Multi-traits variability at leaf, wood and whole-plant scales

The selected 11 traits varied considerably across species, thus showing the trade-offs between the acquisition and conservation of resources. Plant species with small SLA exhibited low N_{leaf} but large LDMC (Figure 1a, Table 3). In addition, plant species with high H showed low wood density and C_{stem} (Figure 2a, Table 3). Moreover, plants had high wood density but low SLA, LA and N_{leaf}, while plant species with low C_{stem} showed high N_{leaf} (Figure 3a, Tables 2 and 3). Therefore, a LES, a WES and a WPES were defined, respectively, across 58 subtropical plant species.

Trade-offs in resource strategies for leaf and wood tissues were graphically expressed by multi-trait variations in the PCA axis (Figures 1a, 2a and 3a). PC1 allowed us to test whether species differing in leaf habits were ordered from acquisitive to conservative, and PC2 allowed us to test whether shrubs differed from trees along the LES, WES and WPES. The percentages of variations in leaf traits explained by PC1 and PC2 were 44.6% and 26.7% (Figure 1a), respectively. All other traits, except for C_{leaf}, contributed substantially to the PC1 axis (Figure 1a, Table 3). Along the PC1 axis, the traits representative of the acquisitive strategy were decreased (SLA, LA and N_{leaf}), while the trait (LDMC) representing the conservative strategy was increased (Figure 1a), defining a leaf economics spectrum. Consistent with the PC1 axis, most of the evergreen species were spread at the conservative side, while most of the deciduous species were clustered on the acquisitive side of the leaf economics spectrum (Figure 1b). On the basis of the species scores on the leaf PC1 axis, the evergreen species differed significantly from the deciduous species ($P < 0.001$; Table 4).

The leaf PC2 axis was primarily contributed by C_{leaf}, LDMC, LA and N_{leaf} (Figure 1a, Table 3). A common pattern of leaf economy also emerged along the PC2 axis. Leaf traits representing the acquisitive strategy were distributed at the upper side of the PC2 axis, whereas traits representing the conservative strategy were distributed at the low side (Figure 1a). Most of the tree species were grouped on the acquisitive side, while most of the shrub species grouped on the conservative side of the PC2 axis, regardless of leaf habits (Figure 1b). The tree and shrub species differed significantly from each other on the basis of the PC2 scores ($P < 0.001$; Table 4).

With respect to the total variation in wood traits, PC1 and PC2 explained 31.3% and 26.2%, respectively (Figure 2a, Table 3). Along the PC1 axis, wood traits did not define a WES (Figure 2a). Evergreen and deciduous species spanned almost the entire range (Figure 2b), and did not depart from each other on the wood PC1 axis ($P = 0.34$; Table 4).

Along the scores on the wood PC2 axis, traits (wood density and C_{stem}) representing the conservative strategy were decreased, while traits (H and BT) representing the acquisitive strategy were increased (Figure 2a, Table 3). Along this plant height economics spectrum, most of the tree species exhibited the acquisitive strategy, while most of the shrub species displayed the conservative strategy (Figure 2b). Tree and shrub species departed significantly from each other in this plant height spectrum ($P < 0.001$; Table 4).

With respect to the whole-plant scale, PC1 and PC2 accounted for 28.1% and 20.7% of overall variations, respectively, in leaf and wood traits (Figure 3a, Table 3). On one hand, with increasing scores on the PC1 axis, traits representing the acquisitive strategy were decreased, i.e., SLA, LA and N_{leaf}, while traits representing the conservative strategy were increased, i.e., LDMC, C_{stem}, N_{stem} and wood density (Figure 3a). Consistent with this plant strategy axis (PC1 axis), most evergreen species were clustered on the conservative side of the spectrum. In contrast, most deciduous species were grouped on the acquisitive side of the spectrum (Figure 3b). Evergreen and deciduous species departed significantly from each other on this WPES ($P < 0.001$; Table 4).

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Table 2. Bivariate relationships between leaf and wood traits across subtropical plant species in Eastern China.

		Leaf traits					Wood traits					
		Log LDMC	Log LA	Log SLA	Log C_{leaf}	Log N_{leaf}	Log WD_{twig}	Log BT	Log WD_{stem}	Log C_{stem}	Log N_{stem}	Log H
Leaf traits	Log LDMC		−4.8 (−6.3 to −3.7)	**−2.1 (−2.7 to −1.7)**	**0.6 (0.4 to 0.7)**	−1.8 (−2.3 to −1.4)	**1.7 (1.3 to 2.1)**	**2.5 (1.9 to 3.1)**	**0.99 (0.8 to 1.3)**	0.9 (0.7 to 1.1)	**4.7 (3.7 to 5.9)**	**5.1 (4.0 to 6.5)**
	Log LA	0.04		**0.4 (0.3 to 0.6)**	0.1 (0.1 to 0.2)	**0.4 (0.3 to 0.5)**	−0.4 (−0.5 to −0.3)	**0.5 (0.4 to 0.7)**	**−0.2 (−0.3 to −0.2)**	−0.2 (−0.2 to −0.1)	−0.9 (−1.3 to −0.8)	**1.1 (0.8 to 1.4)**
	Log SLA	**0.25*** **	**0.07***		−0.3 (−0.3 to −0.2)	**0.8 (0.7 to 1.0)**	**−0.8 (−1.0 to −0.6)**	−1.1 (−1.5 to −0.9)	**−0.5 (−0.6 to −0.4)**	−0.4 (−0.5 to −0.3)	−2.2 (−2.9 to −1.7)	−2.4 (−3.0 to −1.8)
	Log C_{leaf}	**0.19** **	0.01	0.01		3.2 (2.5 to 4.2)	−3.0 (−3.9 to −2.3)	−4.4 (−5.7 to −3.4)	−1.8 (−2.3 to −1.4)	−1.6 (−2.0 to −1.2)	−8.4 (−10.9 to −6.4)	**9.1 (7.1 to 11.7)**
	Log N_{leaf}	0.04	**0.21*** **	**0.40*** **	0.02		**−0.9 (−1.2 to −0.7)**	1.4 (1.1 to 1.8)	**−0.6 (−0.7 to −0.4)**	**−0.5 (−0.6 to −0.4)**	2.6 (2.0 to 3.4)	**2.9 (2.2 to 3.7)**
Wood traits	Log WD_{twig}	**0.23*** **	0.06	**0.10***	0.02	**0.07***		1.5 (1.1 to 1.9)	**0.6 (0.5 to 0.7)**	0.5 (0.4 to 0.7)	2.8 (2.2 to 0.7)	−3.1 (−3.9 to −2.3)
	Log BT	**0.11** **	**0.12** **	0.03	0.01	0.01	0.02		0.4 (0.3 to 0.5)	0.4 (0.3 to 0.5)	**1.9 (1.5 to 2.5)**	**2.1 (1.7 to 2.6)**
	Log WD_{stem}	**0.23*** **	**0.12** **	**0.13** **	0.03	**0.13** **	**0.33*** **	0.06		0.9 (0.7 to 1.1)	**4.7 (3.7 to 6.1)**	−5.2 (−6.7 to −3.9)
	Log C_{stem}	0.04	0.02	0.07	0.00	**0.20*** **	0.03	0.00	0.03		5.4 (4.2 to 7.0)	−5.9 (−7.6 to −4.5)
	Log N_{stem}	**0.14** **	0.05	0.03	0.00	0.00	0.03	**0.14** **	**0.15** **	0.03		**1.1 (0.8 to 1 .4)**
	Log H	**0.18** **	**0.15** **	0.01	**0.12** **	**0.08***	0.00	**0.26*** **	0.01	0.03	**0.07***	

Standardized major axis slopes with 95% confidence intervals are given in the upper right section of the matrix (*y* variable is column 1, *x* variable is row 1). Coefficients of determination (R^2) and significant correlations are given in the lower left section of the matrix. Significant correlations are represented in bold with asterisks; *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$. Abbreviations of functional traits are defined in Table 1.

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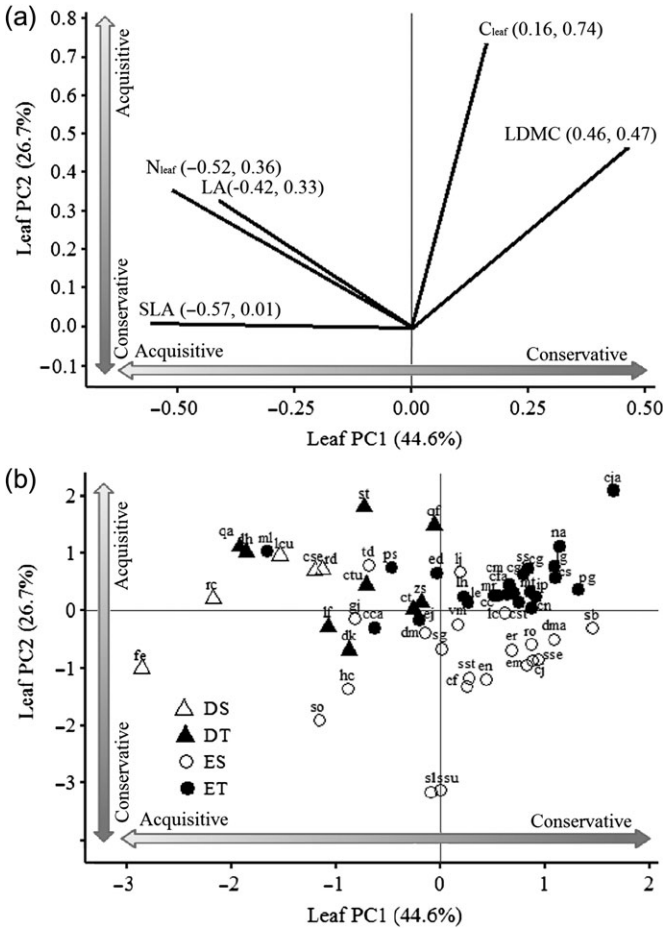

Figure 1. The leaf economics spectra range from acquisitive (left) to conservative (right) species along the trait axis of leaf PC1 with respect to leaf habit, and range from acquisitive (upstream) to conservative (downstream) species along the trait axis of leaf PC2 with respect to growth forms. (a) Leaf traits used for the PCA are displayed with their vector for the leaf economics spectrum (the first half for PC1 and latter half for PC2 within bracket). (b) Location of species with different leaf habits and growth forms in the leaf economic spectra. Abbreviations of species names are provided nearing to their position on the graph. See Table S1 for the abbreviations of the species names. Symbols represent leaf habits of species, i.e., circle for evergreen and triangle for deciduous; while colors represent growth forms of species, i.e., black for trees and white for shrubs. DS, deciduous shrubs; DT, deciduous trees; ES, evergreen shrubs; ET, evergreen trees.

On the other hand, except for wood density and SLA, all other traits (H in particular), contributed greatly to the PC2 axis (Figure 3a, Table 3). Along this height-related axis, traits representing the acquisitive strategy, i.e., LA, N_{leaf}, C_{leaf}, LDMC, H, BT and N_{stem}, were increased; however, traits representing the conservative strategy, i.e., C_{stem}, were decreased (Figure 3a). Most tree species were clustered on the acquisitive side, while most shrub species were grouped on the conservative side of this axis (Figure 3b). Tree and shrub species were significantly different from each other on the PC2 axis ($P < 0.001$; Table 4).

Scaling relationships among LES, WES and WPES

Leaf and wood PC1 positively correlated with whole-plant PC1 for evergreen and deciduous species (Figure 4a and b). There was no difference in the regression slope between evergreen and deciduous species for both relationships. The common regression slope did not statistically differ from 1 (Figure 4a and b), indicating an isometric relationship between the WPES and each of the leaf and wood economics spectra. However, significant shifts of the intercept were found between evergreen and deciduous species ($P < 0.001$). The intercept was greater in deciduous than in evergreen species for the scaling relationship between the whole-plant PC1 and the leaf PC1 (Figure 4a, see Table S2 available as Supplementary Data at *Tree Physiology* Online), but was greater in the evergreen than in the deciduous species for the scaling relationship between the whole-plant PC1 and the wood PC1 (Figure 4a, see Table S2 available as Supplementary Data at *Tree Physiology* Online). Leaf PC1 was positively correlated with wood PC1 for evergreen species only (Figure 4c), and for deciduous species the relationship between leaf PC1 and wood PC1 was weak ($R^2 = 0.01$, $P = 0.3$).

Leaf PC2 and wood PC2 positively correlated with whole-plant PC2 for both tree and shrub species (Figure 5a and b). The regression slope in the relationship between whole-plant PC2 and leaf PC2 was heterogeneous for tree and shrub species (Figure 5a, see Table S2 available as Supplementary Data at *Tree Physiology* Online). In contrast, in the relationship between

Table 3. Bivariate relationships between individual traits and the scores of the first and second PC in each of the whole-plant, leaf and wood economic spectra across subtropical plant species in Eastern China.

		Leaf traits					Wood traits					
		Log LDMC	Log LA	Log SLA	Log C_{leaf}	Log N_{leaf}	Log WD_{twig}	Log BT	Log WD_{stem}	Log C_{stem}	Log N_{stem}	Log H
LES	PC1	**0.69*** **	**−0.57*** **	**−0.84*** **	0.24	**−0.76*** **						
	PC2	**0.54*** **	**0.39** **	0.04	**0.85*** **	**0.44*** **						
WES	PC1						**0.67*** **	**0.66*** **	**0.72*** **	0.20	**0.62*** **	**0.37** **
	PC2						**−0.45*** **	**0.47*** **	**−0.40** **	**−0.57*** **	0.12	**0.76*** **
WPES	PC1	**0.72*** **	**−0.52*** **	**−0.73*** **	0.03	**−0.68*** **	**0.68*** **	0.20	**0.72*** **	**0.48*** **	**0.40** **	−0.01
	PC2	**0.52*** **	**0.47*** **	−0.01	**0.43** **	**0.44** **	0.04	**0.67*** **	0.06	**−0.27* **	**0.38** **	**0.85*** **

Significant correlations are represented in bold with asterisks; *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$. Abbreviations of functional traits are defined in Table 1.

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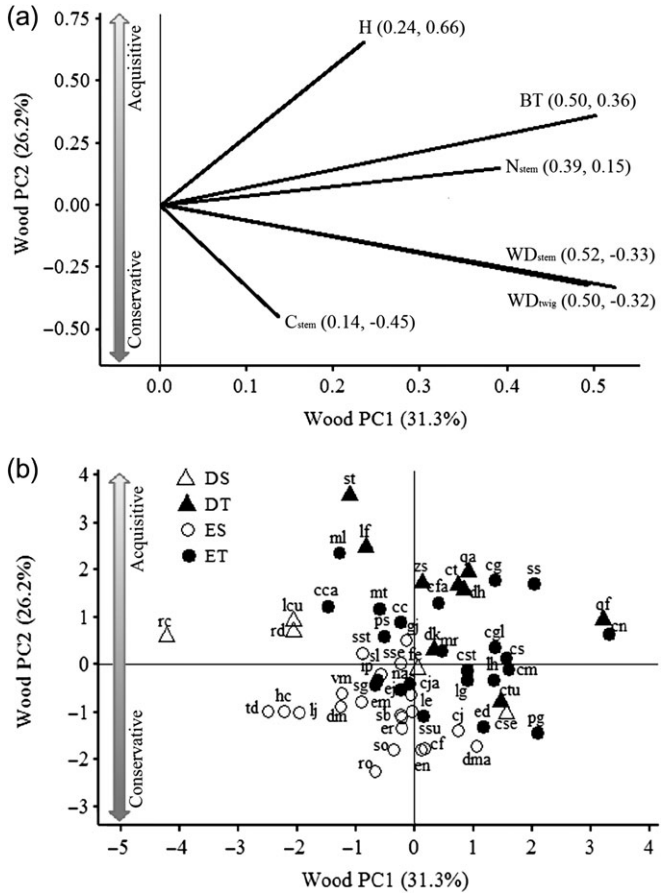

Figure 2. The wood or plant height-related economics spectra range from acquisitive (upstream) to conservative (downstream) species along the trait axis of wood PC2 with respect to growth forms. (a) Wood traits used for the PCA are displayed with their vector for the wood economics spectrum (the first half for PC1 and latter half for PC2 within bracket). (b) Location of species with different leaf habits and growth forms in the wood or plant height-related economics spectra. Abbreviations of species names are provided nearing to their position on the graph. See Table S1 for the abbreviations of the species names. Symbols represent leaf habits of species, i.e., circle for evergreen and triangle for deciduous; while colors represent growth forms of species, i.e., black for trees and white for shrubs. DS, deciduous shrubs; DT, deciduous trees; ES, evergreen shrubs; ET, evergreen trees.

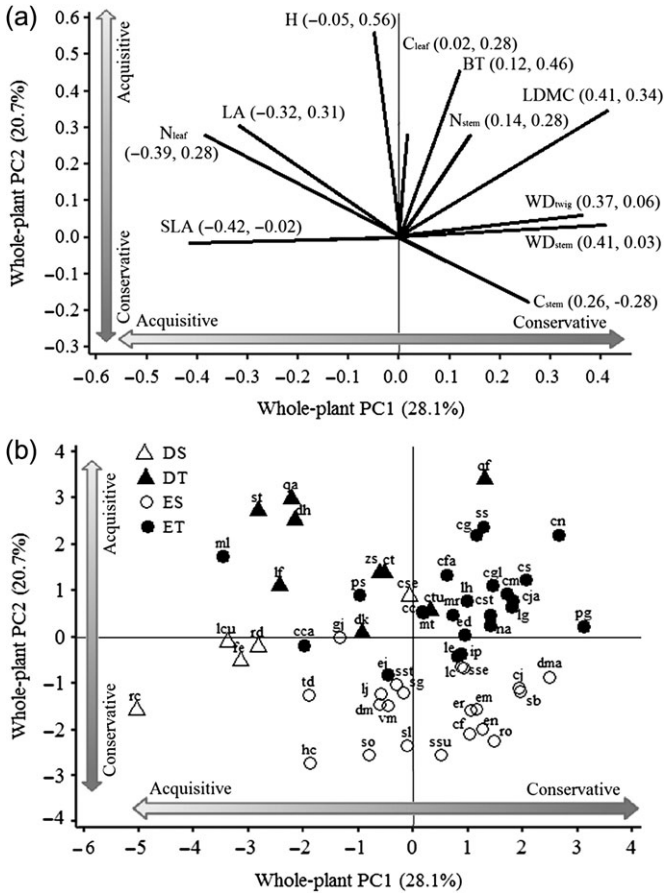

Figure 3. The whole-plant economics spectra range from acquisitive (left) to conservative (right) species along the trait axis of whole-plant PC1 with respect to leaf habit; and the plant height-related economics spectra range from acquisitive (upstream) to conservative (downstream) species along the trait axis of whole-plant PC2 with respect to growth forms. (a) Leaf and wood traits used for the PCA are displayed with their vector for the whole-plant economics spectrum (the first half for PC1 and latter half for PC2 within bracket). (b) Location of species with different leaf habits and growth forms in the whole-plant economics spectra. Abbreviations of species names are provided nearing to their position on the graph. See Table S1 for the abbreviations of the species names. Symbols represent leaf habits of species, i.e., circle for evergreen and triangle for deciduous; while colors represent growth forms of species, i.e., black for trees and white for shrubs. DS, deciduous shrubs; DT, deciduous trees; ES, evergreen shrubs; ET, evergreen trees.

whole-plant PC2 and wood PC2, the regression slope was not different between tree and shrub species, and a common regression slope could be calculated (Figure 5b). The intercept was greater in tree than in shrub species in the relationship between whole-plant PC2 and wood PC2 (see Table S2 available as Supplementary Data at *Tree Physiology* Online). There was not a significant relationship between leaf PC2 and wood PC2 for each of the tree and shrub species (Figure 5c).

When evergreen and deciduous species were combined, leaf PC1, wood PC1 and whole-plant PC1 were positively correlated (Figure 4). Similarly, when tree and shrub species were combined, leaf PC2, wood PC2 and whole-plant PC2 were positively correlated (Figure 5).

Discussion

Intracorrelation between leaf and wood traits and multi-trait variations in the leaf and wood PCA axes together defined trade-offs in resource allocation, thus suggesting an LES and WES for the 58 subtropical species studied. The significant relationships between leaf and wood traits and between trait axes highlighted the coupling between LES and WES (Poorter et al. 2013, Reich 2014, Díaz et al. 2016). Therefore, our Hypothesis 1, wherein the plant economics spectrum operates at the whole-plant scale in the studied site, was confirmed.

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Table 4. Results of independent-samples *T*-test for elucidating the differences between deciduous and evergreen species along PC1, and the differences between tree and shrub species along PC2, in terms of acquisitive vs conservative strategies.

		Leaf habit		Growth form		Significance test	
		Deciduous	Evergreen	Shrub	Tree	*T*	*P*
Whole-plant PCA	PC1	−0.76 ± 0.24a	0.24 ± 0.14b			−3.58	<0.001
	PC2			−0.80 ± 0.12a	0.65 ± 0.13b	−8.03	<0.001
Leaf PCA	PC1	−1.03 ± 0.22a	0.33 ± 0.12b			−5.44	<0.001
	PC2			−0.61 ± 0.21a	0.49 ± 0.11b	−4.98	<0.001
Wood PCA	PC1	0.22 ± 0.28a	−0.07 ± 0.15a			0.96	0.34
	PC2			−0.66 ± 0.13a	0.53 ± 0.16b	−5.55	<0.001
Whole-plant PCA	PC1	−0.76 ± 0.24a	0.24 ± 0.14b			−3.58	<0.001
	PC2			−0.80 ± 0.12a	0.65 ± 0.13b	−8.03	<0.001

Data are mean ± standard deviation for PC1 and PC2 scores. Different letters between leaf habits and/or growth forms indicate significant differences ($P < 0.05$). *T*- and *P*-values are provided.

Plant economics strategy, in fact, works on the entire plant rather than just isolated tissue traits (Grime et al. 1997). Díaz et al. (2016) have recently revealed that three-quarters of variation in six major traits critical to growth, survival and reproduction is captured in a 2D global spectrum of plant form and function across 46,085 vascular plant species worldwide. One major dimension, which represents the LES, runs from species with cheaply constructed, 'acquisitive' leaves to species with 'conservative' leaves. The other runs from short species tending to have small diaspores to tall species tending to have large diaspores, reflecting the size of whole plants and their parts (Díaz et al. 2016). Interestingly, our results obtained in a subtropical forest provided local evidence for such a global survey, suggesting that there are conspicuous patterns of integration for leaf and stem economics at both global and local scales.

The notion of traits coordination between leaf and wood organs was also supported by other individual ecosystems. For example, stem traits related to hydraulic properties coupled tightly with leaf traits in relation to water transport and photosynthesis (Brodribb and Feild 2000, Meinzer et al. 2008, Bucci et al. 2012, Méndez-Alonzo et al. 2012). Moreover, wood traits in roots correlated with stem and leaf traits (Craine et al. 2005, Tjoelker et al. 2005, Withington et al. 2006, Freschet et al. 2010, Liu et al. 2010, de la Riva et al. 2016). However, results from tropical forests have shown trade-offs in LES and WES to be independent (Baraloto et al. 2010), and LES traits and leaf hydraulics are uncoupled (Li et al. 2015). The LES and WES defined and the sets of traits examined in Baraloto et al. (2010) were quite limited to trees, i.e., without considering shrubs, and leaf traits were measured on every individuals, rather, wood and chemical traits were measured at the species level. Whatever, these contrasting results suggest that trait integration may be contingent to the set of traits selected (Reich 2014) and the abiotic characteristics of the environment. Probably, as the environment is more restricted by seasonality, the covariation between leaf and stem traits is more tightened and in less seasonal environments there is more opportunity for different types of economics strategy to coexist (Méndez-Alonzo et al. 2012).

The strong integration of traits in different organs suggested that parallel 'acquisitive vs conservative' strategies were advantageous at the whole-plant scale, as the evolution of leaf and of stem features are intimately linked (Reich 2014, Díaz et al. 2016). The negative relationships of SLA and N_{leaf} with wood density in this study indicated that strategy trade-offs of resource investment were defined at the whole-plant level, on one hand by species using nutrients exploitatively and economically with large leaves (i.e., high SLA and N_{leaf}), and on the other hand by species with high leaf and wood tissue expenditures (i.e., high WD_{twig} and WD_{stem}). In addition, it has been found that it is expensive for species with low SLA and N_{leaf} to build tissue with thick laminas or high tissue densities (i.e., high LDMC in this study), or both (Niinemets 1999, Wright et al. 2006), for withstanding physical damage (Wright and Cannon 2001). Similarly, high wood densities also conferred great resistance against mechanical damage (King et al. 2006). Consequently, species with high wood density corresponded to expensive leaf strategies (Westoby et al. 2002) and slow growth (Reich 2014).

In contrast, the positive relationships between LDMC and each of wood density, BT and plant height indicated that dry mass invested to leaf and wood tissues were coordinated with increasing tree height (Díaz et al. 2016). For example, wood density scaled isometrically with leaf mass (Table 2). Correspondingly, the positive relationships between plant height and each of LDMC, LA, C_{leaf} and N_{leaf} might be explained by the metabolic and stoichiometry theories. Annual plant growth rates (indirectly related to plant height) scaled linearly with respect to standing leaf mass and total leaf mass scaled isometrically with respect to nitrogen (Cornelissen et al. 1996, Niklas 2006).

The results in this study also supported our Hypotheses 2 and 3, that deciduous and tree species were grouped on the acquisitive side, while evergreen and shrub species were grouped on the conservative side across LES (Figure 1b), WES (Figure 2b) and WPES (Figure 3b). Additional evidence for differentiated

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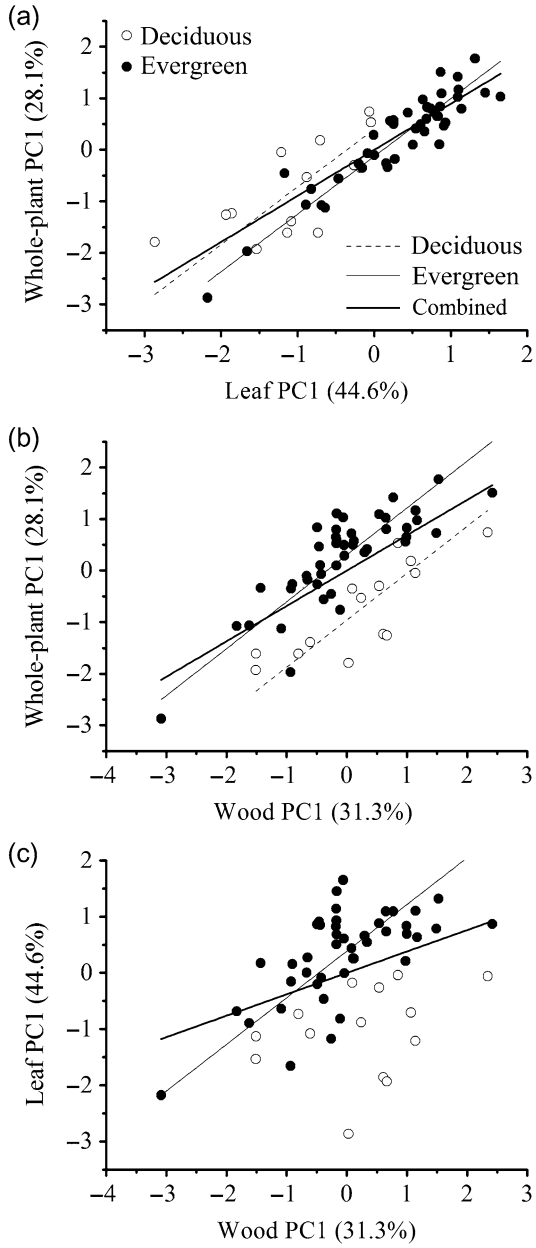

Figure 4. Regression relationships among leaf PC1, wood PC1 and whole-plant PC1 with respect to evergreen (E) and deciduous (D) species. (a) The relationship between leaf PC1 and whole-plant PC1. The regression coefficient of determination (R^2) is 0.52 ($P < 0.01$), 0.86 ($P < 0.001$) and 0.80 ($P < 0.001$), respectively, for each of deciduous and evergreen species alone and combined. Since the slopes were homogeneous (not statistically different, $P = 0.94$), the common regression slope was calculated to be 1.12 (95% CIs were between 1.00 and 1.25). (b) The relationship between wood PC1 and whole-plant PC1. The regression coefficient of determination (R^2) is 0.69 ($P < 0.01$), 0.68 ($P < 0.001$) and 0.46 ($P < 0.001$), respectively, for each of deciduous and evergreen species alone and combined. Since the slopes were homogeneous (not statistically different, P = 0.61), the com¬mon regression slope was calculated to be 0.91 (95% CIs were between 0.78 and 1.06). (c) The relationship between leaf PC1 and wood PC1. For deciduous species, there was not a significant relationship (R^2 = 0.01, P = 0.30), and the regression coefficient of determination (R^2) is 0.43 ($P < 0.01$) and 0.13 ($P < 0.001$), respectively, for evergreen species alone and evergreen and deciduous combined.

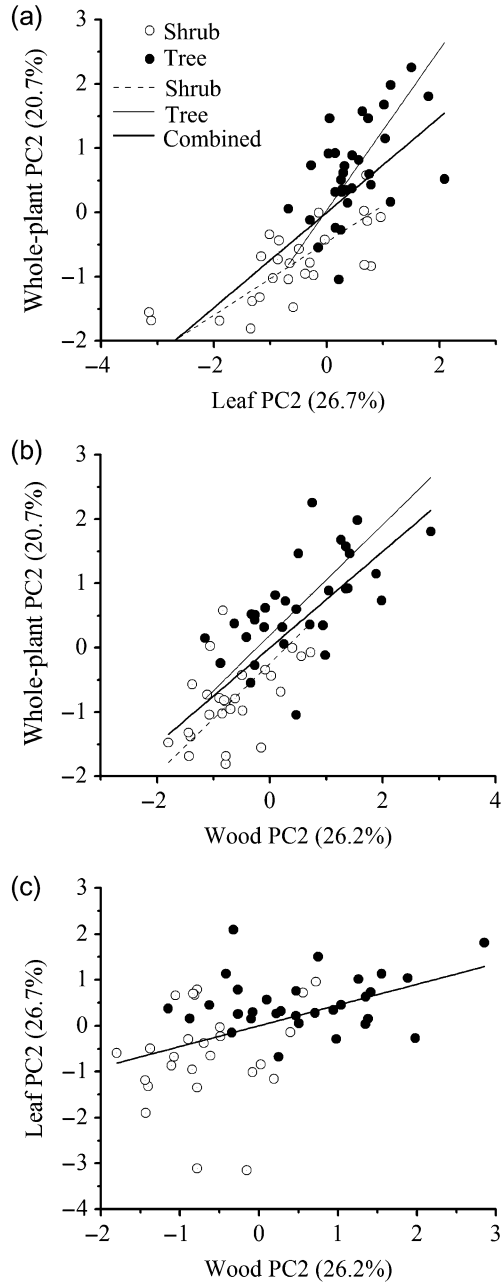

Figure 5. Regression relationships among leaf PC2, wood PC2 and whole-plant PC2 with respect to trees (T) and shrubs (S). (a) The relationship between leaf PC2 and whole-plant PC2. The regression coefficient of determination (R^2) is 0.28 ($P < 0.01$), 0.53 ($P < 0.001$) and 0.54 ($P < 0.001$), respectively, for each of trees and shrubs alone and combined. The regression slope in the relationship between leaf PC2 and whole-plant PC2 was heterogeneous ($P = 0.001$). (b) The relationship between wood PC2 and whole-plant PC2. The regression coefficient of determination (R^2) is 0.37 ($P < 0.001$), 0.24 ($P < 0.01$) and 0.55 ($P < 0.001$), respectively, for each of trees and shrubs species alone and combined. Since the slopes were homogeneous (not statistically different, P = 0.61), the common regression slope was calculated to be 0.86 (95% CIs were between 0.69 and 1.07). (c) The relationship between leaf PC2 and wood PC2. For both trees ($P = 0.28$) and shrubs ($P = 0.31$), there were not significant relationships. In contrast, there was a significant relationship between leaf PC2 and wood PC2 when tree and shrubs were combined (R^2 =0.19, $P < 0.001$).

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leaf habits and growth forms along plant economics spectra derives from the allometric relationships among the LES, WES and WPES (Figures 4 and 5). Plants respond to differences in leaf habits by changing the *y*-intercepts of the relationships between the WPES and each of the LES and WES, while keeping the exponent value of the relationship as an invariant constant (Figure 4a and b). On one hand, the invariant isometric relationship suggested that conservative and/or acquisitive strategies associated with the organ levels remain parallel to the whole-plant level (Freschet et al. 2010, Reich 2014, Díaz et al. 2016).

The shifts of *y*-intercepts in the scaling relationships, on the other hand, indicated that evergreen and deciduous species structured the WPES differently. It is understandable that evergreen and deciduous species differ in many aspects of their strategies, such as phenology (Monk 1966, Lusk et al. 2008), leaf life span (Westoby et al. 2002, Kloeke et al. 2012) and nutrient-use efficiencies (Aerts 1999, Warren and Adams 2004). Evergreenness is an adaptive response to low resource availability, and deciduousness is an adaptation to reduce water loss during dry periods (Monk 1966, Givnish 2002, Warren and Adams 2004, Lusk et al. 2008, Méndez-Alonzo et al. 2012). Therefore, species grouped as evergreen and deciduous were differentiated along the LES and WPES in tropical and subtropical environments. It was noteworthy that evergreen and deciduous species did not depart from each other on the wood PC1 axis (Figure 2b). This might have resulted from our experiment limitation that we did not differentiate early vs late deciduous species. Late deciduous species are more drought tolerant and have higher mechanical resistance in wood and lower SLA in comparison with early deciduous species (Méndez-Alonzo et al. 2012). In this case, the economics strategies of late deciduous species might be similar to evergreen species growing in drought sites. Correspondingly, wood economics strategies of early deciduous species would be more similar to evergreen species in the wet sites (Méndez-Alonzo et al. 2013).

With respect to growth forms in the scaling relationships of the economics spectra, tree species showed an isometric relationship, but shrub species exhibited a negative allometric relationship (regression slope being significant lower than 1) between WPES and LES (Figure 5a, see Table S2 available as Supplementary Data at *Tree Physiology* Online). This suggested that plant height strategies impacted both whole-plant and leaf levels synchronously for tree species, but disproportionally for shrub species. For scaling the relationship between the WPES and WES, tree and shrub species shared a common isometric regression slope, while shifting the *y*-intercept (Figure 5b). The invariant isometric scaling slope in this relationship suggested that plant height strategies act simultaneously on the whole-plant and wood levels (Scheffer et al. 2014, Castorena et al. 2015, Qian and Ricklefs 2015). The greater *y*-intercept (great value of whole-plant PC2 score) for trees than for shrubs in the scaling relationship implied that trees were acquisitive and shrubs were conservative in the plant height strategy (Figure 5b).

Patterns of tree and shrub species along the plant height axis may be discussed in terms of their shade tolerance and hydraulic conductance. Trees are sun-adapted and shrubs are shade-adapted in forests, thus being significantly different insofar as their light-use strategies (Falster and Westoby 2005, Rowe and Speck 2005). In order to grow rapidly within a given timeline, tree species should possess greater photosynthetic productivity and hydraulic efficiency than shrub species (Kitajima 1994, Thomas 1996, Westoby et al. 2002, Kohyama et al. 2003, Reich et al. 2003). Therefore, tree species that have the capacity to rapidly transport water and mineral nutrients have low wood density and high rates of resource acquisition and flux, at both organ and whole-plant levels. The reverse is true for shrub species that operate under slow-growth strategies (Reich 2014).

In conclusion, this study focused on plants with contrasting leaf habits and growth forms to identify how leaf phenology and tree height shape the plant economics spectrum in subtropical forests. High correlations between and within leaf and wood traits, and two major directionalities of multi-traits variability, provided strong local evidence for an integrated WPES across 58 subtropical species in the context of the global spectrum of plant structure and function. This finding would enrich our understanding of how plant species with contrasting leaf habits and growth forms are integrated within the economics trait spectra, thus assisting with the elucidation of individual ecological strategies, community assembly processes, and the functionality of ecosystems in species-rich and function-divergent forests.

Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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