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Correlations between leaf economics, hydraulic, and shade-tolerance traits among co-occurring individual trees

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ABSTRACT

Leaf economics, hydraulic, and shade-tolerance traits involve different resource-use strategies, and are critical for interactive plants, yet it remains unclear whether co-occurring individuals modulate the coupling relationships between these trait dimensions. To address this knowledge gap, we measured four leaf economics, five hydraulic, and two shade-tolerant traits in leaf and wood tissues across 90 individuals from 26 tree species in two subtropical forests in Eastern China. Confirmatory factor analysis (CFA) and Principal Component Analysis (PCA) were employed to explore multi-trait relationships. With respect to leaf economics traits, leaf nitrogen concentrations were positively associated with leaf stomatal density and conductance, leaf-specific hydraulic conductivity, and twig vessel diameter. However, leaf phosphorus concentrations were negatively associated with leaf-specific hydraulic conductivity. The specific leaf area was negatively associated with the light exposure index, light saturation point, and leaf Huber value. Regarding hydraulic traits, twig vessel diameters were positively correlated with the light saturation point and light exposure index. Stomatal conductance was positively associated with the light saturation point, whereas leaf-specific hydraulic conductivity was positively associated with the light exposure index. The first two PCA axes explained 54.23% of the total trait variation. The first axis of the multi-trait variation was mainly explained by leaf habits and represented the trade-offs between acquisitive hydraulic economics and cheap leaf economics. The second axis of the multi-trait variation was mainly explained by plant growth form, and defined the trade-offs between weak shade tolerance and cheap leaf area construction. In conclusion, our results provide evidence for the coupling relationships between leaf economics, hydraulic, and shade-tolerant traits among co-occurring individuals. This study also highlights that bivariate trait relationships based on large-scale interspecific surveys may be the opposite of that within-community scales.

1. Introduction

Functional traits are increasingly recognized as powerful indicators of plant ecological strategies (Westoby et al., 2002), which have important consequences for plant growth and survival (Liu et al., 2016; Poorter et al., 2008). Exploring how plant functional traits and their relationships vary across local, regional, and global scales is one of the major concerns in functional ecology (Diaz et al., 2016; Reich, 2014; Wright et al., 2004). Variations in plant functional traits are often trait-specific that depend on leaf habits (deciduous vs. evergreen) and growth forms (e.g., trees and shrubs) (Kang et al., 2014; Messier et al., 2010). Leaf economics, hydraulic, and shade-tolerant traits are involved

in different key resources (Li et al., 2015) and are critical for plant competition between co-occurring individuals (Kunstler et al., 2016). Yet, it remains unclear whether co-occurring individuals with contrasting leaf habits and growth forms can modulate the within-community scale multivariate relationships between leaf economics, hydraulic, and light-demanding traits.

Leaf economic trait variations characterize how plants make tradeoffs between investments and returns for nutrients and carbon in leaves (Wright et al., 2004). Similarly, variations in hydraulic traits reflect how plants balance water demands and supplies under environmental stress (Blonder et al., 2011; Brodribb et al., 2007). For physiological and hydraulic reasons, leaf economics and hydraulic traits were

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found to be coupled across ecological scales (Brodribb et al., 2005, 2007; John et al., 2017; Nardini et al., 2012; Scoffoni et al., 2016; Villagra et al., 2013; Yin et al., 2018). However, some recent studies have reported a decoupled relationship between these two key trait dimensions (Baraloto et al., 2010; Li et al., 2015). The main reason proposed for the independent variations between leaf economics and hydraulic traits may account for the additional mechanical functions of hydraulic traits (Reich, 2014). Another rationale for this independent relationship might be the internal segregation of leaf structures, in that economic traits associate with xylem veins, while hydraulic traits have a functionally independent correlation with structural traits at the interfaces between minor veins and extra-xylary tissues (Li et al., 2015). However, the relationships between leaf economics and hydraulic traits might be coupled by variations within species, or likely due to variations in light-demanding traits across locally co-occurring individuals within a community (He and Yan, 2018; Niinemets, 2015).

Fine-scale multi-trait relationships are proposed to be mediated by co-occurring species with contrasting leaf habits and growth forms, due to distinct trait combinations between component species (Nardini and Lugilo, 2014). Species with distinct leaf habits (i.e., evergreen and deciduous) possess different functional traits (Wright et al., 2004). As a consequence of environmental filtering, species with similar trait combinations can be restricted to a given site (Messier et al., 2010). Similarly, species with dissimilar trait combinations may be distinguished by different functional groups and growth forms along the axes of plant ecological strategies (Cingolani et al., 2007; Kleyer et al., 2012).

In plant communities, functionally diverse species typically adapt to fine-scale changes in resource availability to normalize their physiological functionality (Kimball et al., 2016; Kunstler et al., 2016). The core resources associated with niche partitioning between coexisting individuals primarily include light, nutrients, and water resources. The resource use strategies of plant are often closely linked with their vertical stature (Craine and Dybzinski, 2013), as a result of physiological and structural limitations, which are the outcomes of their mechanical and conductive demands (Enquist, 2002). For example, the canopy layer of trees might have an advantage in so far as the capturing of light and water resources in an acquisitive manner, while those in the understory layers (e.g., shrubs and small trees) are generally shade-tolerant and

conservative in terms of resource use (Kume et al., 2003).

There is increasing evidence that distinct trait dimensions can be coupled at the fine-scale (Messier et al., 2017), and trade-offs or coordination inherently operate at the whole-plant level (Reich, 2014). This means that multiple traits with different dimensions simultaneously impact plant form and function due to the combined effects of biophysical and hydraulic constraints. Importantly, employing the multivariate trait approach might be a better choice for exploring the coupling relationships between trait dimensions, in contrast to traditional bivariate relationships (Messier et al., 2017; Poorter et al., 2008).

To this end, we developed a conceptual model based on the interrelations between leaf economics, hydraulic, and shade-tolerant traits across 90 tree individuals within two subtropical forest communities in Eastern China (Fig. 1). We used confirmatory factor analyses (CFA) in addition to principal component analysis (PCA) to address the following two questions: 1) Are leaf economics, hydraulic, and shade-tolerant traits associated with each other at the community scale? 2) How do leaf habits and growth forms construct multi-trait relationships between co-occurring plants? We hypothesized that leaf economics, hydraulic, and shade-tolerant traits are coupled among co-occurring individuals. Further, we predicted that leaf habits (evergreen and deciduous) and growth forms (trees, small trees, and shrubs) will be the main variation sources for formulating such multi-trait relationships between co-occurring individuals.

2. Material and methods

2.1. Study sites and forest plots

The current study was conducted in Tiantong National Forest Park (29°52′ N, 121°39′ E) and Putuo Island (29°58′ N, 122°23′ E), in Zhejiang Province, of Eastern China. These two sites are located at the transition zone between the mainland and the East China Sea, and share a similar subtropical monsoon climate. The mean annual temperature and precipitation are 16.2 °C and 1374.7 mm in Tiantong, and 16.9 °C and 1358.14 mm in Putuo, respectively. The soils were classified as Ferralsols with pH ranging from 4.7 in Tiantong to 5.9 in Putuo (Yan et al., 2013b, 2018).
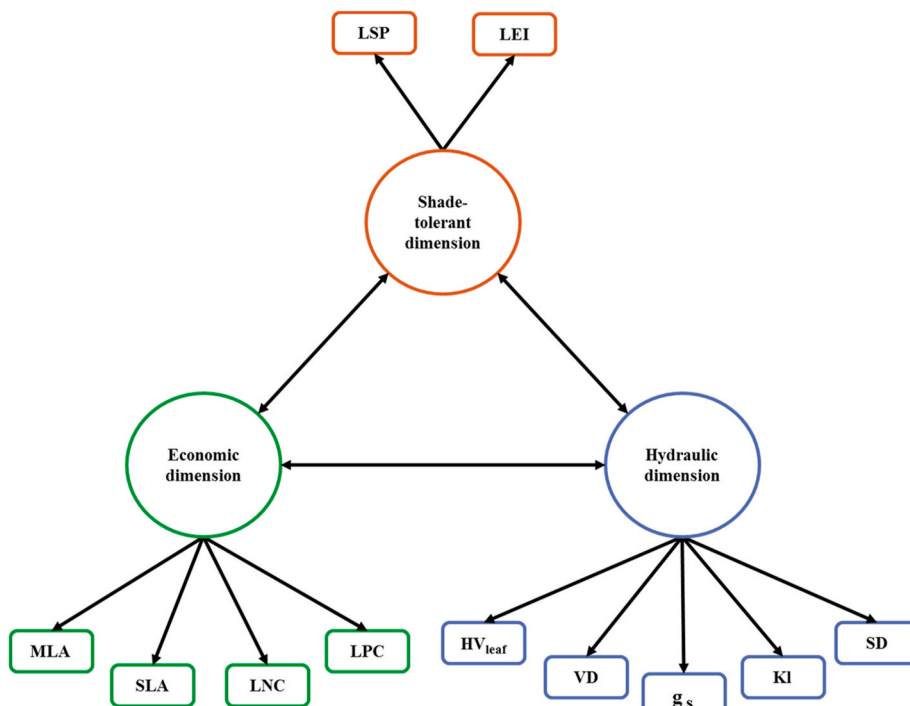
Fig. 1. Conceptual model for coupling relationship between leaf economics, hydraulic, and shade-tolerant trait dimensions. Green: leaf economic traits. Blue: hydraulic traits. Orange: shade-tolerant traits. Traits include SLA (specific leaf area), MLA (mean leaf area), LNC (leaf nitrogen concentration), LPC (leaf phosphorus concentration), VD (vessel diameter), Kl (leaf-specific hydraulic conductivity), HV_{leaf} (leaf Huber value) SD (stomatal density), g_s (stomatal conductance), LSP (light saturation point), and LEI (light exposure index). Three latent variables are linked with double headed arrows, and 11 apparent parameters are delineated as single arrows, which describe how the three latent variables are correlated overall. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Vegetation in the region is characterized by evergreen broadleaf forests (EBLFs), which have been well protected from anthropogenic disturbances, as they surround Buddhist temples. Apart from these small patches of EBLFs, virtually all vegetation is secondary, and semi-intact EBLFs and broadleaved deciduous forests occur widely following the cessation of human disturbances over the last 40 years (Yan et al., 2009). In Tiantong, forests are dominated mainly by *Schima superba* communities, which are secondary EBLFs that are widespread across subtropical China. In Putuo, a large portion of the vegetation is represented by broadleaved deciduous forests, where the *Liquidambar formosana* community is one of the dominant species.

Since these two communities characterize the general forest features in the region, one plot with an area of 20 m × 40 m was specifically established for both the *Schima superba* and *Liquidambar formosana* communities in Tiantong and Putuo, respectively. The *Schima superba* community is comprised purely of evergreen broadleaf species, with the vertical structure being apparent with two distinct layers. In Putuo, the *Liquidambar formosana* community includes a combination of evergreen broadleaf and deciduous species, with the community structure also having two vertical layers (see Table A.1 for details on characteristics of species and individuals).

2.2. Trait measurement

The selected plant traits primarily involved those that are generally measured for leaf economics, hydraulic properties, and shade tolerance (Table A.2 for trait variation across coexisting individuals). We measured four leaf economic traits that included the specific leaf area (SLA), mean leaf area (MLA), leaf nitrogen concentration (LNC), and leaf phosphorus concentration (LPC). Five hydraulic traits of leaf and wood tissues included leaf-specific hydraulic conductivity (Kl), leaf stomatal conductance (g_s), leaf stomatal density (SD), xylem vessel diameter (VD), and leaf Huber value (HV_{leaf}), which is a proxy for the hydraulic capacity of leaves, and was calculated as the ratio of the base cross-sectional area of the petiole to leaf area (Huber, 1928). Shade-tolerant traits were measured for the light saturation point (LSP) and light exposure index (LEI). The latter reflects how much light the plant crown receives, and indirectly correlates with plant shade tolerance (Poorter et al., 2005).

In each plot, woody individuals with heights greater than 1.5 m were identified by species. Overall, the *Schima superba* community consisted of 56 individuals, belonging to 19 evergreen species, 11 genera, and six families. There were 34 individuals from six evergreens and two deciduous species that belonged to seven genera and five families in the *Liquidambar formosana* community. The woody plants were categorized into trees, small trees, and shrubs, based on their form factors. We defined small trees as woody plants with actual heights lower than the maximum heights of shrub species in the plot. The heights of 90 individual plants were measured using a telescopic pole, whereas the diameters at breast height were quantified using a measuring tape.

Simultaneously, the LEI was estimated for each individual by two independent observers. We followed the standard of LEI classification proposed by Poorter et al. (2005), which graded LEI on a five-point scale. In this system:

Scale-1: No direct light reaches the crown.
Scale-2: The crown receives only lateral light.
Scale-3: Partial overhead light.
Scale-4: More than 90% of the crown receives light.
Scale-5: The crown receives direct light from all directions.

In July and August of 2015, three sun-facing canopy rim branches per plant were collected using tree pruners. The end cut of the sampled branches were immediately immersed in a water bucket, whereafter three to five healthy leaves were selected for measurements. We directly measured the LSP and g_s in the field using a portable photosynthetic gas exchange system (LI-6400XT Portable Photosynthesis System, LI-COR, Nebraska, USA) between 0800 and 1300 h. The carbon dioxide concentration was maintained at 400 ppm and photosynthetic active radiations (PAR) at 1500 µmol m^{-2} s^{-1}, respectively. Prior to measurements, the selected leaves were exposed to sunlight or artificial LED light sources during cloudy days.

For leaf economic trait measurements, we have selected a minimum of ten fully developed healthy leaves from each branch as described above. These samples were wrapped in moist paper and stored in sealed plastic bags to keep them cool until transported to the laboratory for subsequent measurements, which were performed within 12 h of sample collection. Twenty mature leaves from three branches of each plant were selected and scanned with a leaf area meter (LI-3100C, Li-Cor, USA) to determine the MLA. In addition, the diameters at the base points of the petioles per leaf were measured using an electronic vernier caliper (0.1 mm accuracy). The petiole cross-sectional area was calculated from the diameter, which assumed the leaf petiole to be approximately round. The HV_{leaf} was calculated as the ratio of the base cross-sectional area of a petiole to the leaf area. The leaf samples were oven-dried at 75 °C for 72 h to determine the leaf dry mass, and to calculate the SLA (leaf area divided by leaf weight). Finally, to determine the LNC and LPC of the leaf samples were ground using a discrete auto-analyzer (Smartchem 200, Alliance, France).

To measure the hydraulic traits, three sun-exposed terminal branches of each individual were excised from the upper canopy in the early morning. The branch samples were kept with end cut under water and were covered with black plastic bags to reduce transpiration, and to prevent embolism formation. The samples were transported directly to the laboratory within half an hour, and terminal twigs from each branch were re-cut in water into about 15 cm lengths. Any leaves attached to the twigs were separated for measuring the total leaf area with a leaf area meter (LI-3100C, Li-Cor, USA). Subsequently, the twig hydraulic conductivity was determined using a high-pressure flow meter (HPFM-Gen3, Dynamax, Houston, USA). The twig ends were connected to a pressure coupler and pressure was gradually inserted up to 500 kPa. During this process, the real-time hydraulic conductivity data, i.e., velocity versus pressure, was automatically recorded on a computer using dedicated software. Later, the sample twig lengths and cross-sectional areas were measured using a vernier calliper following the removal of 2–5 mm bark at the twig ends. The Kh was calculated according to equation (1), and the Kl was calculated according to equation (2).

$$Kh = LF / \Delta P \tag{1}$$

where, L (m) is the length of the segment, F (kg min^{-1}) is the flow rate of water through the twig segment, and ΔP (MPa) is the pressure difference in MPa (Fu et al., 2012)

$$Kl = Kh / LA \tag{2}$$

were LA (cm^2) is total leaf area of the terminal twig (Fu et al., 2012).

Using the same branch samples, three healthy leaves per branch were selected for the measurement of stomatal density through the nail-polish imprint method (Franks et al., 2009). Transparent nail polish was applied to the undersides of the leaf samples after any water droplets were cleared with a bibulous paper. After 5–10 min, the applied portion of nail polish was peeled off with forceps or scotch tape after which the impression was mounted on a slide with a coverslip. The stomatal density was subsequently measured for each prepared slide using an electronic microscope (OLYMPUS BX53, Japan).

Furthermore, terminal twigs (3 cm long) from each branch as described above were also excised for measuring the vessel traits and immerse in a Formalin acetic alcohol (FAA) fixation solution. The twig samples were cut into thin (30–60 µm) slices using a manual slicing machine (Leica, SM 2010 Germany) in the laboratory. The sliced samples were rinsed using distilled water in a petri dish and dipped in safranine solution (colouring pigment) for 15 min. Later, the samples

were dipped in alcohol with concentrations of 35%, 55%, 75%, and 95% accordingly. Appropriate slice samples were then mounted onto slides with a coverslip for the measurement of vessel diameter using an Olympus Microscope Imaging System (OLYMPUS, BX53, Japan) at 5x - 20x magnification, respectively. The imagery was photographed using Image-pro Plus (IPP, Canada) software, for measuring the vessel size, area, and density.

2.3. Statistical analyses

Trait data was log-arithmetically transformed to increase the homogeneity of variance and normality prior to analysis (Grace et al., 2016). To test the multivariate relationships between leaf economics, hydraulics, and shade-tolerance trait dimensions, confirmatory factor analysis was conducted by following a hypothesized concept model (Fig. 1). We selected three trait dimensions as our latent variables. Apparent variables underlying the leaf economics trait dimensions were MLA, SLA, LNC, and LPC, and those under the hydraulic trait dimensions were HV_{leaf}, VD, g_s, Kl, and SD, whereas variables relevant to the shade-tolerance trait dimension were LSP and LEI.

Several tests were taken under consideration for determining the goodness of fit for the CFA model, including chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR), and Akaike information index (AIC). The best-fit model was selected according to insignificant chi-square (χ^2) test statistics (P > 0.05), SRMR < 0.08, and both GFI and CFI > 0.95. To assess the fitness of the CFA model, we critically considered a χ^2 test statistics, for maximum likelihood estimation. The CFA model was performed using the *lavaan* package in R software (Rosseel, 2002).

Further, Principal Component Analysis (PCA) was employed to investigate how the multivariate trait relationships between the three key trait dimensions were constructed by leaf habits and growth forms (i.e., hypothesis 1). PCAs were carried out using *factoextra* and *devtools*

packages in R software. All statistical analyses were conducted in R. 3.5.1 version (R Core team 2015).

3. Results

3.1. Multivariate correlations between leaf economics, hydraulic, and shade-tolerance trait dimensions

The CFA model was accepted with the maximum livelihood estimation ($\chi^2 = 14.54$, $P = 0.558$, Table A.3). According to the χ^2 test, the leaf economics and hydraulic trait dimensions had the strongest feedback ($\beta = 0.88$, $P < 0.05$), followed by leaf economics vs. shade-tolerance trait dimensions ($\beta = 0.69$, $P < 0.01$), and hydraulic vs. shade-tolerance dimensions ($\beta = 0.41$, $P < 0.05$; Fig. 2). Apart from the LNC and Kl, which were not statistically significant ($P > 0.05$), all remaining traits revealed significant correlations with respective apparent variables (Fig. 2, Table A.4).

The CFA model exhibited significant multivariate trait relationships across distinct trait dimensions (Figs. A.1, A.2, A.5; Table A.5), with either coordination or trade-offs between the trait dimensions. As relates to the hydraulic traits, the vessel diameter was significantly positively correlated with the light saturation point ($\beta = 0.86$, $P < 0.05$), light exposure index ($\beta = 0.51$, $P < 0.05$), and leaf nitrogen concentration ($\beta = 0.28$, $P < 0.05$). The stomatal conductance was positively associated with the light saturation point ($\beta = 0.28$, $P < 0.05$) and leaf nitrogen concentration ($\beta = 0.23$, $P < 0.05$). Leaf-specific hydraulic conductivity was also positively correlated with the light exposure index ($\beta = 0.31$, $P < 0.05$) and leaf nitrogen concentration ($\beta = 0.22$, $P < 0.05$), but negatively correlated with the leaf phosphorus concentration ($\beta = -0.29$, $P < 0.05$) and mean leaf area ($\beta = -0.22$, $P < 0.05$). The stomatal density was significantly positively associated with leaf nitrogen concentration ($\beta = 0.88$, $P < 0.05$). The leaf Huber value was negatively correlated with both the specific leaf area ($\beta = -0.53$, $P < 0.05$) and
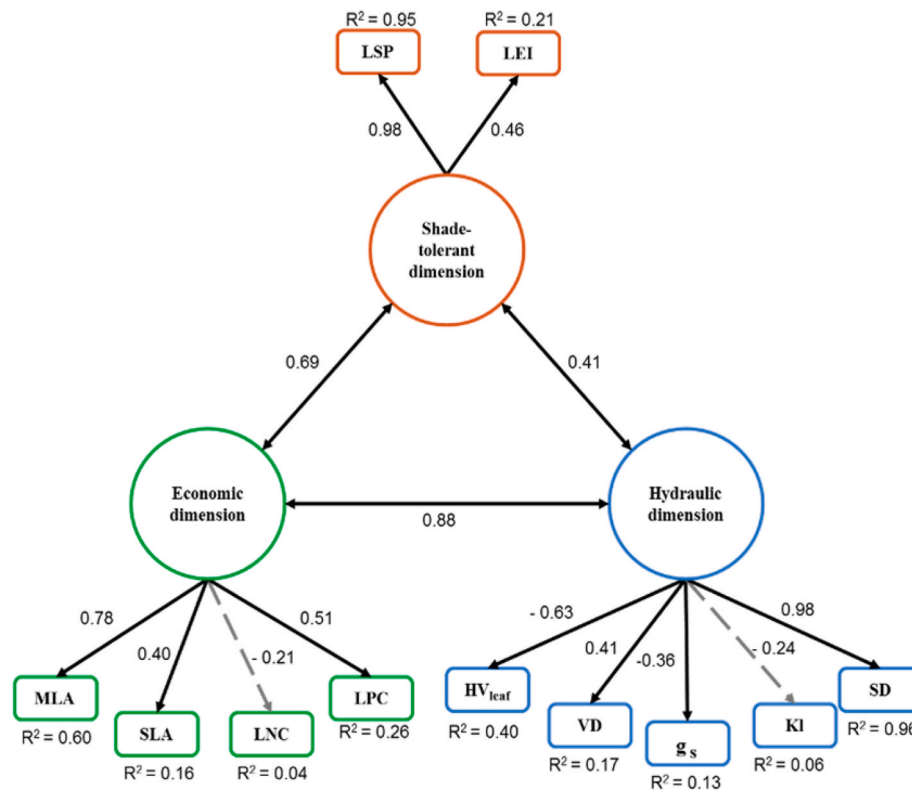

Fig. 2. The accepted integrated model between leaf economics, hydraulic, and shade-tolerance trait dimensions according to confirmatory factor analyses (CFA). Solid black lines represent significant relationships, while dotted grey lines represent non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mean leaf area ($\beta = -0.52$, $P < 0.05$). With respect to the relationships between leaf economics and shade-tolerance traits, the specific leaf area was negatively correlated with the light exposure index ($\beta = -0.38$, $P < 0.05$) (Fig. A.2; Table A.5).

3.2. Position of leaf habits and growth forms along the major trait axes

Traits from the three dimensions were loaded primarily along the first two major component axes, which together explained 54.23% of the total trait variation across co-occurring individuals (Fig. 3a). The stomatal density and mean leaf area loaded in the positive end, while the leaf Huber value loaded in the negative end at the first component axis, which indicated a functional trade-off between plant hydraulic efficiency and leaf economics properties. The positive side of the second axis was mostly defined by the light exposure index, light saturation point, and xylem vessel diameter, while the negative side was defined by the specific leaf area, which suggested a trade-off between shade tolerance and leaf area construction across co-occurring individuals.

Leaf habits constructed the first trait axis, with deciduous species displaying great leaf size and low hydraulic efficiency, but with evergreens covering a large range of the plant economics spectrum (Fig. 3b). Moreover, plant growth form constructed the second trait axis. Trees were positioned on the weak shade tolerance side, while shrubs and small trees with cheap leaf area construction were positioned on the shade-tolerant side (Fig. 3c).

4. Discussion

As hypothesized, leaf economics, hydraulic, and shade-tolerance traits were functionally associated across co-occurring individuals within two subtropical forest communities. Previous empirical studies have reported that leaf economics and hydraulic trait dimensions were either coupled (Brodribb et al., 2005; Nardini et al., 2012; Scoffoni et al., 2016; Yin et al., 2018) or decoupled (Li et al., 2015) at large spatial scales. Our results suggested that the coupling relationships between two leading trait dimensions held at the within-community-scale, as the consequence of functional integration with the shade-tolerance trait dimension. Moreover, our results demonstrated that leaf habits and growth forms were critical for formulating these multi-trait relationships across co-occurring individuals. Therefore, this study strongly reconciled the debate regarding coupled/decoupled relationships between leaf economics and hydraulic traits.

The coupling relationships between leaf economics, hydraulic, and shade-tolerance traits across co-occurring individuals at within-community-scales might be attributable to several factors. First, conspecific and heterospecific individuals with different plant heights within a community can mediate multi-trait variations, particularly for intraspecific trait variations, which is often neglected based on the trait-
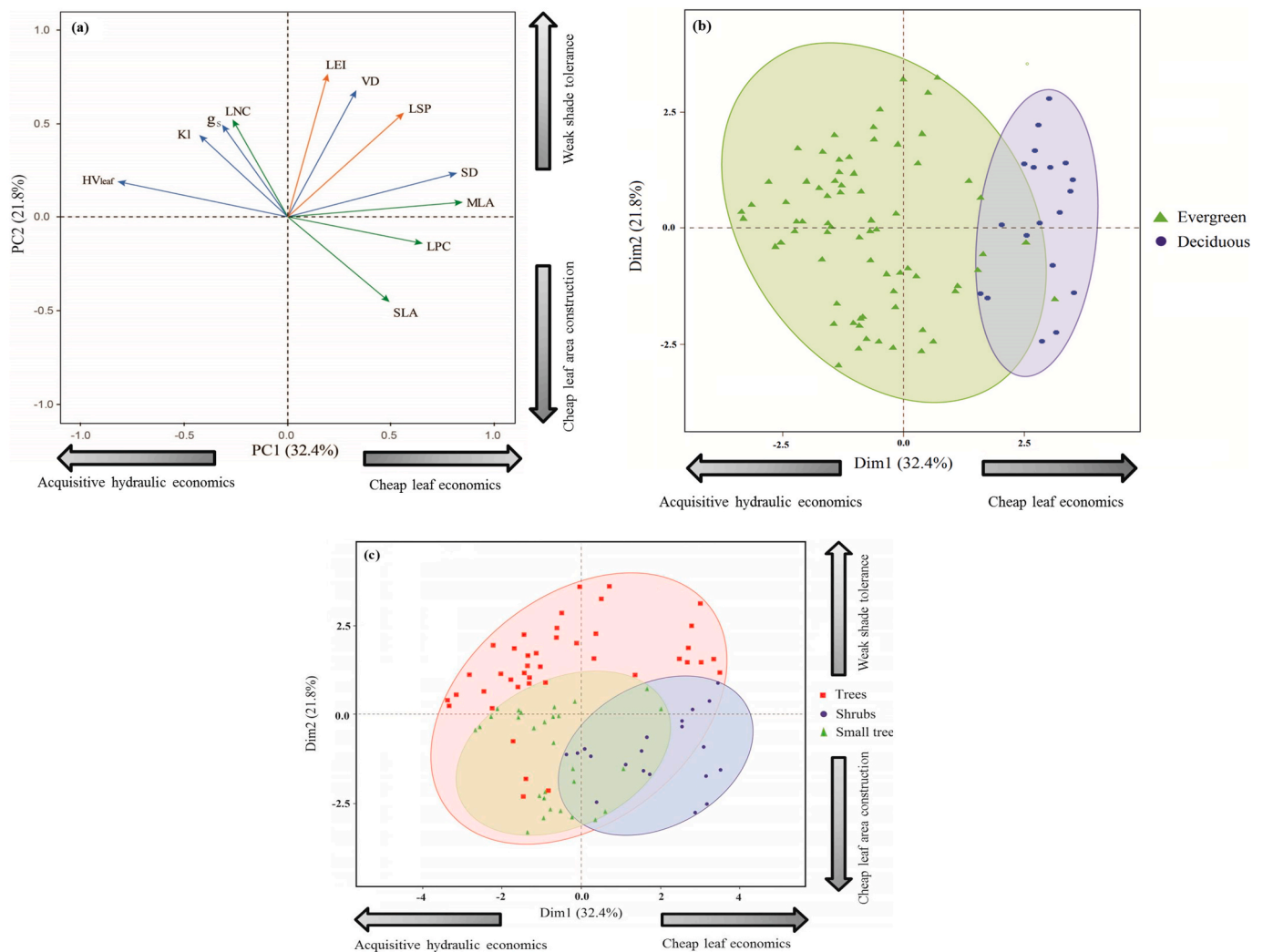

Fig. 3. Principal component analyses of leaf economics, hydraulic and shade-tolerant trait dimensions (a) positions of leaf habits (b) and growth forms (c). See Fig. 1 for trait abbreviations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mean approach (Albert et al., 2010). Plant size modified trait variations can potentially structure an 'intraspecific plant economic spectrum' (He and Yan, 2018; Niinemets, 2015), consequently strengthening the coupling relationships between distinct trait dimensions. Additionally, as our results showed that plant growth forms (i.e., trees, small trees, and shrubs) were largely involved in the formulation of the coupled relationships between the multi-trait dimensions. Collectively, our study suggested that plant height modulated the coupling relationships between functionally distinct trait dimensions across co-occurring individuals.

Second, the strong coordination between functional strategies across co-occurring individuals reinforced the degree of trait integration at the within-community scale. We found that vessel diameter, as one of the key hydraulic traits, was significantly coordinated with leaf nitrogen content (one of key leaf economics traits) and shade-tolerance traits (light saturation point and light exposure index). This suggested a remarkable integration and functional relevance between hydraulic, physiological, and leaf economics properties (Onoda et al., 2004). Mechanically, an increase in vessel diameter translated to high hydraulic efficiency in the xylem; thus, greater rates of nutrient assimilation and photosynthesis in leaves (Brodribb et al., 2007; Kotowska et al., 2015; Sack and Scoffoni, 2013; Xiong et al., 2014). Integration between hydraulic, leaf economics, and shade-tolerance traits were also evident via several other trait-trait coordinations: i) leaf stomatal conductance vs. leaf nitrogen concentration and light saturation point; ii) leaf-specific hydraulic conductivity vs. leaf nitrogen concentration and light exposure index, and iii) leaf stomatal density vs. leaf nitrogen concentration. It is understandable that the stomatal in leaves controlled carbon-water exchange under variable light availability in the humid subtropical environment, where an increase in stomatal conductance enhanced leaf nutrient concentrations (Hepworth et al., 2015).

Third, ecological trade-offs between co-occurring individuals with contrasting leaf habits might have accounted for the integration of functionally distinct trait dimensions. In this study, leaf-specific hydraulic conductivity was negatively associated with leaf phosphorus concentrations; thus, informing a unique trade-off between leaf economics and hydraulic strategies across evergreen and deciduous plants. This pattern indicated that evergreen plants with great hydraulic efficiency were particularly conservative in leaf phosphorus concentrations, while deciduous plants were the opposite. Such special hydraulic vs. leaf economics trade-offs might have been associated with specific ecosystem properties in this study. The region under investigation was characterized by a subtropical climate with excessive water availability, albeit with limited soil phosphorus for plant growth (Yan et al., 2009). Therefore, plants with great leaf hydraulic efficiencies were advantageous in terms of transporting and evaporating water to reduce hydraulic failures, but disadvantageous as relates to conserving more limited nutrients in leaves (Aerts and Chapin III, 1999). Economically, evergreen plants tend to have high leaf hydraulic conductivity, as a consequence of high carbon-water exchange rates during photosynthesis (Carter and White, 2009), which in turn deprives more limiting-nutrients; thus, decreasing phosphorus concentrations in leaves. Similar hydraulic and leaf economics trade-offs were also present between leaf-specific hydraulic conductivity and mean leaf area, as well as between leaf Huber value and leaf area (Fig. A.5). These results further demonstrated that co-occurring individuals followed special acquisitive hydraulic economics vs. cheap leaf economics trade-offs in the forest communities under study.

Further, we provided evidence for these ecological trade-offs between leaf economics and shade-tolerance traits. The negative relationships of specific leaf area with both light saturation point and light exposure index revealed a strong trade-off between leaf construction strategies and light capture abilities. Locally co-occurring plants with a great capacity for light interception and/or carbon gain tended to construct leaves with expensive investments per biomass produced (e.g., low specific leaf area), and vice versa. Notably, such trade-offs were

contrary to our common understanding regarding the leaf economics spectrum, apparent at global or regional scales, where plants with an acquisitive strategy develop cheap leaves per biomass investment, i.e., large specific leaf area (Reich, 2014; Westoby et al., 2002; Wright et al., 2004).

The within-community scale may be relevant to the deviation of the trade-offs between leaf construction strategies and light capturing abilities from the global leaf economics spectrum (Messier et al., 2017). Light is the most dominant environmental stress for plant growth within a community, which in general is not the critical limiting resource at regional and global scales (Onoda et al., 2011), where factors such as temperature, water, and soil nutrients are the main drivers of the leaf economics spectrum (Diaz et al., 2016). At within-community scales, the global leaf economics spectrum might be weakened by decreased variations in these climatic and soil drivers, and even reversed through strong light stress. Further, the intraspecific trait plasticity can even obscure or reverse the broad-scale patterns of the plant economics spectrum (Anderegg et al., 2018).

Effectively, the mechanism discussed above operated in the communities under study, where active photosynthetic radiation decreased significantly, from the canopy to understory layers (unpublished data, Figs. A.3 and A.4). The remarkable shift of active photosynthetic radiation across vertical layers indicated that light availability played a key role in shaping plant functional strategies between co-occurring individuals that occupied different vertical positions. Compared to shade-tolerant species in the understory, plants in overstory received more light, but maintained a conservative resource investment strategy.

The decline in mean leaf area and specific leaf area for plants with a high capacity for light interception may be associated with an optimization strategy in resource allocation to construct expensive leaves (Prentice et al., 2014). The overall high irradiation and wind-exposed conditions in the overstory favors small leaves, which typically do not require additional structural support (Milla and Reich, 2007; Niinemets et al., 2007) and have lower hydraulic costs (Kenzo et al., 2015; Niinemets, 2002; Thomas and Winner, 2002). This is beneficial for balancing the cost of carbon gain and water loss through the construction of expensive leaves. In the studied late successional forest (i.e., canopy closure), air moisture is higher and light availability is lower in the understory than in the overstory. Thus, with low evaporative demand in the understory, plants produce large leaves that intercept more solar radiation (Kenzo et al., 2015; Yan et al., 2013a).

In conclusion, this study generalizes the coupling relationship among distinct trait dimensions from the global and regional to within-community scales. Partly different from the ecological trade-offs underlying the global plant economics spectrum, this study provides evidence that the trade-offs between leaf-specific hydraulic conductivity and leaf phosphorus concentration, and the trade-offs between specific leaf area and light saturation point play a strong role for coupling functionally distinct trait dimensions. These two ecological trade-offs have not been demonstrated at a broad spatial scale and found to be coordinated between trait dimensions in general. The presence of these special functional strategies trade-offs among woody individuals may explain why coordination apparent at a broad scale does not hold up at a fine-scale. This study, therefore, calls for the attention that trait-trait relationships based on the large-scale interspecific surveys may opposite to that apparent at the fine-scale, in which distinct ecological trade-offs maintain community assembly. Its worth noting that, despite the small sampling effort with only 90 individuals within two forest communities, this study is very perceptible to justify the coupling relationship among leaf economics, hydraulic and shade-tolerant traits across co-occurring individuals. We argue that functional ecology would benefit more by focusing on the trait-trait relationships at within-community scale.

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Author contributions

UAA and ERY conducted the research; UAA compiled and analyzed the data; UAA, WHY, and ERY designed the study and wrote the paper via multiple rounds of revision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2020.103673.

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