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Scaling relationships among functional traits are similar across individuals, species, and communities

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Abstract

Question: Bivariate relationships among functional traits reflect how plants adjust to environments through the allocation of limiting resources. Bivariate relationships are well studied across species, but whether the nature of these trait relationships changes across organizational levels (individual, species, community), and whether processes driving these relationships vary across these levels, is seldom explored.

Location: The tropical cloud forests of the Bawangling Nature Reserve, Jianfengling Nature Reserve and Limushan Nature Reserve on Hainan Island, Southern China.

Methods: We measured leaf mass per area (LMA), plant height (H) and wood density (WD) for 4,748 individual trees, 174 species and 48 communities in three tropical cloud forests, and recorded five soil characteristics that are important for plant growth. We evaluated bivariate relationships between these traits across the three organizational levels, and assessed the effects of soil conditions on these trait relationships.

Results: LMA versus H, WD versus H, and LMA versus WD were all positively and disproportionately related, suggesting differential carbon investment between leaves and stem, as well as between stem height and stem density. The slopes of these relationships did not differ significantly across the three levels, suggesting a similar allocation strategy operating at different hierarchical levels. Soil phosphorus had a significant effect on the scaling exponents across all three organizational levels, indicating that phosphorus limitation in cloud forests is a principal driver of resource allocation patterns in trees.

Conclusions: We conclude that tropical cloud forest trees have relatively consistent scaling relationships between three primary functional traits across the individual, species, and community levels. The coordinated resource allocation strategies in plants are most likely driven by the prevailing environmental constraints.

KEYWORDS

bivariate trait relationships, environmental stress, leaf mass per area, plant height, plant strategy, soil phosphorus, tropical forest, wood density

1 | INTRODUCTION

In environments with limited resources, plants generally employ strategies to optimize the allocation of resources to different functional traits (Price and Weitz, 2012) and increase growth, survival, and reproduction in a given environment (Reich *et al.*, 1997; Westoby, 1998; Fonseca *et al.*, 2000; Wright *et al.*, 2004; Chave *et al.*, 2009; Onoda *et al.*, 2011; Díaz *et al.*, 2016). Such allocation strategies can be explored by assessing the slope of bivariate trait relationships (Wright *et al.*, 2004). A slope that significantly differs from +1.0 or -1.0 (i.e., disproportionate relationships, log scale) indicates that plants disproportionately allocate resources to specific plant functions.

Studies indicate that there are disproportionate scaling relationships among many leaf traits (e.g., LMA, leaf life span, leaf nitrogen concentration, photosynthetic capacity; Reich *et al.*, 1997; Wright *et al.*, 2004; Onoda *et al.*, 2011; Xiang *et al.*, 2013, etc.), and wood traits (e.g., wood density, conduit diameter, sapwood area conductivity; Chave *et al.*, 2009). Recently Díaz *et al.* (2016) found that trait space occupied by global vascular plants is coordinated and characterized by trade-offs among six traits critical to growth, survival and reproduction. However, these patterns have largely been assessed among species, typically using species mean values (Reich *et al.*, 1997; Wright *et al.*, 2004; Xiang *et al.*, 2013; Díaz *et al.*, 2016). Moreover, comparative studies suggest that in many instances, intraspecific trait variation is comparable to interspecific variation (Albert *et al.*, 2010; Bolnich *et al.*, 2011; Laforest-Lapointe *et al.*, 2014; Siefert *et al.*, 2015), and that intraspecific trait variation can promote species coexistence by enabling species to pass through a broader range of environmental filters (Long, Zang, Schamp, *et al.*, 2011). For example, including intraspecific trait variation can be consequential in tests for significant trait overdispersion among coexisting plant species (e.g., de Bello *et al.*, 2013; Jensen *et al.*, 2019).

In addition to disproportionate scaling relationships at the species and within-species levels, Reich (2014) has proposed that these relationships also exist at the community and ecosystem level. Recent studies demonstrate that community-weighted mean trait values (CWM) can be used to relate functional composition to environmental conditions (Swenson and Weiser, 2010), allowing researchers to examine which environmental filters may drive community assembly (Ackerly *et al.*, 2002; Long, Zang, and Ding, 2011; Domínguez *et al.*, 2012). Our approach of examining these bivariate

relationships at three hierarchical levels allows us to test whether important scaling relationships observed elsewhere are present at the within-species and community levels, whether those bivariate relationships are similar across levels, and whether observed bivariate relationships are influenced similarly by abiotic gradients across the three levels considered (Castro-Díez, 2012; Messier *et al.*, 2017).

Bivariate trait scaling relationships across the individual, species, and community levels can be influenced by genetic effects, plant developmental stages, physiological or biomechanical constraints, plasticity, selective pressure (or species sorting/filtering), ecosystem types, and disturbance (Vasseur *et al.*, 2012; Wright and Sutton-Grier, 2012; Xiang *et al.*, 2013). For example, the interspecific scaling relationships among key leaf traits (morphological, chemical, and metabolic) result from a synergy between physiological, biophysical and evolutionary constraints on leaf phenotypes for species in any terrestrial ecosystem (Field and Mooney, 1986; Díaz *et al.*, 2016). At the individual level, phenotypic plasticity allows plants to adjust their physiological and structural attributes to better match different environmental conditions. Conversely, community-weighted mean trait values, which are closely related to individual plant abundance and species turnover rates (Cornwell and Ackerly, 2009; Castro-Díez, 2012), may exhibit trait relationships that differ from those observed in within- and among-species analyses. This may be due to the effects of environmental filtering, which some evidence suggests is more conspicuous at the community level (Ackerly *et al.*, 2002; Swenson and Weiser, 2010; Domínguez *et al.*, 2012).

Tropical cloud forests experience a unique combination of abiotic conditions that distinguish them from low-altitude tropical forests (Long, Ding, *et al.*, 2011). These abiotic conditions strongly impact trait values of individuals, species, and communities (Long, Zang, and Ding, 2011; Long, Zang, Schamp, *et al.*, 2011) and affect species distributions and community assembly (Long, Schamp, *et al.*, 2015). For example, research has demonstrated that facilitative interactions in tropical cloud forests play a role in tree species assembly and coexistence in the face of important abiotic stresses such as low soil nutrient availability and high winds (Long *et al.*, 2013; Long, Schamp, *et al.*, 2015). It is likely that these same abiotic conditions shape resource allocation strategies at within-species, among-species, and community levels.

We measured three functional traits, leaf mass per area (LMA), plant height (H) and wood density (WD); all three are important for plant growth and survival and capture the main strategy axes of

variation. LMA is the leaf dry mass divided by the one-sided area of a fresh leaf and reflects a plant's allocation of resources in leaves (Wright *et al.*, 2004; Poorter *et al.*, 2009). H reflects the ability of a plant to compete for light and space (Long, Schamp, *et al.*, 2015), and is related to a plant's carbon acquisition strategy (Falster and Westoby, 2003). WD, the dry mass per fresh volume of the stem, is often associated with plant stability and defense, and is recognized as a core functional trait (Chave *et al.*, 2009). These three key traits were measured for 4,748 trees belonging to 174 species and 48 community plots in three Chinese tropical cloud forests.

In this paper, we examine: (a) what bivariate trait relationships are found across three key traits, (b) whether these scaling relationships are similar across three hierarchical levels (individuals, species and communities); and (c) to what extent these relationships are shaped by important soil nutrients. Finally, because the functional traits we examine here contribute to important resource allocation strategies among plant species, we tested whether the slopes of bivariate relationships among all three traits would be conserved (i.e., consistent) across the three hierarchical levels.

2 | METHODS

2.1 | Study sites

This study was conducted in the tropical cloud forests of the Bawangling Nature Reserve (BNR), Jianfengling Nature Reserve (JNR) and Limushan Nature Reserve (LNR) on Hainan Island, Southern China. These three forest reserves are composed of undisturbed old-growth forest, mainly distributed as mountaintop islands at altitudes greater than 1,250 m. The rainy season ranges from May to October and the dry season ranges from November to April of the next year. Soils are montane meadow soils developed from sandstone, with inclinations ranging from 3° to 65°. These forests are characterized by low air temperature, strong winds and frequent fog; consequently, trees in these forests are frequently deformed and short in stature. Average tree height is 4.8 m ± 2.8 m (BNR), 4.1 m ± 2.2 m (JNR) and 5.3 m ± 3.4 m (LNR) and tree densities were 9,633 stems ha⁻¹, 2,577 stems ha⁻¹ and 6,325 stems ha⁻¹ respectively (for all trees with DBH [diameter at breast height] ≥ 1 cm). The five most abundant tree species across the three reserves are *Distylium racemosum* Siebold & Zucc., *Syzygium buxifolium* Hook. & Arn., *Xanthophyllum hainanense* Hu, *Camellia sinensis* (L.) O. Ktze. var. *assamica* (J.W.Mast.) Kitam. and *Cyclobalanopsis championii* (Benth.) Oerst. (Appendix S1).

2.2 | Data collection

We collected data from randomly located 20 m × 20 m plots in tropical cloud forests (BNR: 21 plots; JNR: 12 plots; LNR: 15 plots). The distance between any two plots was always greater than 50 m and the total plot area spanned 1.92 ha across the three sites. The

different number of plots in each site reflects the fact that the three study sites differ in overall area. Before vegetation surveys were completed, each 400-m² plot was divided into 4 10 m × 10 m sub-plots and 16 5 m × 5 m quadrats. We measured the height of all individual trees appearing in the study plots with DBH ≥ 5 cm using a clinometer. Measurements excluded stems that were clearly suckering from other trees, and when a dominant stem was less clear, the tallest sucker/stem was measured. Taxonomic identification was in accordance with Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China, 2004). A total of 4,748 individual trees representing 174 species were recorded (BNR: 76 species, JNR: 121 species, LNR: 80 species).

The relatively small stature of trees in the three study forests helped us to accurately measure H, WD and LMA for each of the 4,748 trees in our plots during the rainy season from July to August, 2013 (following the protocol of Pérez-Harguindeguy *et al.*, 2013). These functional traits were chosen to reflect the ways that plants grow and survive (Wright *et al.*, 2004; Chave *et al.*, 2009; Poorter *et al.*, 2009; Baraloto *et al.*, 2010; Onoda *et al.*, 2011). For example, LMA is the dry mass divided by the one-sided area of a fresh leaf; variation in LMA is understood to reflect how different species allocate resources to the production of leaves (Wright *et al.*, 2004; Poorter *et al.*, 2009). LMA is also related to a plant's ability to obtain nutrients and change growth rate (Castro-Díez, 2012). H is the shortest distance from the base of the plant stem to the highest sucker/shoot in the canopy, reflecting the ability of a plant to compete for light and space (Long, Schamp *et al.*, 2015), and is therefore related to carbon acquisition strategy (Falster and Westoby, 2003). WD is the dry mass per fresh volume of the stem. It is often associated with plant stability and defense and is therefore recognized as a core functional trait (Chave *et al.*, 2009). Exploring bivariate relationships among these traits is expected to improve our understanding plants resource allocation in tropical cloud forests.

To determine leaf traits, we collected and measured three recently expanded sun leaves (current year's growth) from each individual plant (DBH ≥ 5 cm) in each 400-m² plot. Leaf area was quantified using a leaf area meter (LI-COR 3100C Area Meter, LI-COR). Leaves were then dried to a constant weight at 70°C for at least three days and weighed to the nearest 0.01 g; leaf area and dry mass were then used to calculate leaf mass per unit area (mg mm⁻²) for each tree. To characterize species WD (g cm⁻³), which is more laborious, we sampled three branches (diameter 1–2 cm) from each corresponding individual that was sampled for leaf traits (12,348 branches in total). We removed the pith, phloem and bark, measured fresh volume on the rest of the branch using water displacement and determined dry mass after drying for 72 hr at 70°C (Cornwell *et al.*, 2006). Branch density is the dry mass of the rest of the branch (minus the pith, phloem, and bark) divided by its volume, and has been demonstrated to be closely related to core stem density for adult trees in BNR ($R^2 = 0.93$; Bu *et al.*, 2014).

We measured environmental characteristics in each 5 m × 5 m quadrat including soil organic matter (g kg⁻¹), total and available phosphorus (g kg⁻¹ and mg kg⁻¹ respectively), and total and

available nitrogen (g kg^{-1} and mg kg^{-1} respectively). Three soil cores (4 cm in diameter and 20 cm in depth) were collected in each $5 \text{ m} \times 5 \text{ m}$ quadrat. The three soil samples were evenly mixed and air-dried, and then were ground to a fine powder with a mill. Finally, samples were hand-sieved, and analyzed according to Agricultural Chemistry Committee of Soil Society of China (1983) (Appendices S2 and S4). In total, 768 mixed soil samples were obtained for the 48 $20 \text{ m} \times 20 \text{ m}$ plots.

2.3 | Data analyses

2.3.1 | Trait relationships across tree individuals, species and communities

Leaf mass area values at the individual level were calculated as the average of three sampled leaves per individual plant and individual WD values were calculated as the mean of the three branch samples taken per individual. Species-level values for each trait were calculated as the mean of all sampled individual plants per recorded species. Plot-level values for each trait (among species) were calculated as the abundance-weighted mean trait values for each $20 \text{ m} \times 20 \text{ m}$ plot (abundance = number of individual plants) and represent the mean community-level trait values (Long, Zang, Schamp, *et al.*, 2011). All trait values were \log_{10} -transformed to normalize strongly positively skewed distributions.

Bivariate relationships among LMA, H and WD were explored at the individual, species and community levels. Thus, we examined three trait pairs, using regression analyses at each level (nine bivariate relationships in total). When calculating the within-species trait relationships, we quantified bivariate relationships for each trait pair for each species using type II regression as there are no independent or dependent variables and measurement error exists for all traits. We calculated each within-species slope using the standardized major axis approach using the "sma" function in the SMATR package in R. We used Student's *t* tests to determine whether all the within-species slopes differed significantly from zero. The single slope value for each trait pair at the individual-level bivariate relationship was calculated as the mean of all individual species slopes. Among the 174 species investigated, 98 species had over six individuals in the 1.92 ha study areas. Consequently, these species (3,920 individuals) were considered for individual-level trait relationships. When calculating the species- and community-level trait relationships, we also quantified bivariate relationships and slopes of type II regression using the standardized major axis approach. We tested whether these species- and community-level regression slopes differed from +1 or -1 using the sma function (with `slope.test = +1` or `-1`).

Again using the sma function, we tested whether the bivariate trait relationships across individual, species and community levels shared a common slope, with the individual, species and community level as group factors.

2.3.2 | Effects of soil conditions on trait relationships

Five soil variables, including organic matter, total and available phosphorus and nitrogen, were measured in each of our $5 \text{ m} \times 5 \text{ m}$ quadrats, and were accepted as reflecting the soil conditions relevant to the growth of trees in those quadrats. These soil measures were averaged across plots associated with each species to represent the soil conditions specific to each species. The community-level soil conditions were calculated as the mean of each soil factor within each $20 \text{ m} \times 20 \text{ m}$ plot (i.e., mean values in 16 $5 \text{ m} \times 5 \text{ m}$ quadrats).

We then assessed the effects of the soil variables on trait relationships using multiple regressions, with one trait serving as the response variable, and with all soil variables as well as a second trait serving as explanatory variables (five explanatory variables in each multiple regression). To understand whether soil variables altered the relationship between the two traits, we examined the standardized regression coefficients for each soil variable. If the significant standardized coefficients for soil variables were positive or negative, the corresponding variables were interpreted as positively or negatively affecting the bivariate trait relationships. All the data were analyzed in the R 3.1.1 environment (R Core Development Team, 2014).

3 | RESULTS

3.1 | Trait relationships across three hierarchical scales

For the 3,920 individual trees, H ranged from 1 to 21 m, and the average height was 7.05 m. LMA ranged from 0.001 mg mm^{-2} to 0.079 mg mm^{-2} , and the average was 0.012 mg mm^{-2} . WD ranged from 0.20 to 0.98 g cm^{-3} , and the average WD was 0.56 g cm^{-3} .

Although trait relationships varied in strength, LMA-H, LMA-WD and H-WD were positively related at the individual, species and community level (Table 1; Figure 1). SMA slopes of these bivariate relationships were generally disproportionate (i.e., differed significantly from +1 or -1). Moreover, for each bivariate relationship, there were no significant differences in SMA slopes across these three scales (Table 1; SMA tests: LMA-H, $p = 0.06$; LMA-WD, $p = 0.35$; H-WD, $p = 0.20$), suggesting similar relationships at the individual, species and community level for each trait pair.

3.2 | Effects of soil variables on trait relationships across the three hierarchical scales

The slopes of the LMA-H, LMA-WD and H-WD relationships across all three hierarchical scales generally increased significantly with soil phosphorus, whereas nitrogen only affected the individual and

TABLE 1 Bivariate relationships for leaf mass per area (LMA), plant height (H) and wood density (WD) across individuals ($n = 3,920$), species ($n = 98$) and communities ($n = 48$)

	H-LMA		H-WD		LMA-WD	
	Slope	R^2	Slope	R^2	Slope	R^2
Individuals	0.41 (0.11, 0.72)	0.10***	0.48 (0.39, 1.37)	0.14***	1.40 (1.06, 1.74)	0.16***
Species	0.80 (0.69, 0.93)	0.08***	1.42 (1.22, 1.64)	0.04**	1.77 (1.54, 2.03)	0.15***
Communities	0.58 (0.45, 0.76)	0.16**	1.19 (0.94, 1.49)	0.40***	2.04 (1.57, 2.64)	0.21**
p	0.08		0.23		0.35	

Standardized major axis (SMA) slope, 95% confidence interval (in parentheses), coefficient of determination (R^2) and significance level (indicated by asterisks) are shown. The first variable mentioned is the Y variable (e.g., H) and the second variable mentioned is the X variable (e.g., LMA). Each trait was \log_{10} -transformed before analysis. Differences in SMA slopes across the individual, species and community levels were assessed using a SMA function in R software and the corresponding p value is given in the bottom row.

** $p < 0.01$.

*** $p < 0.001$.

community-scale relationships, and organic matter only affected the individual and species-scale relationships (Table 2).

4 | DISCUSSION

4.1 | Positive trait-scaling relationships in tropical cloud forests

We found, as expected, positive relationships between LMA and H, LMA and WD and H and WD at all three organizational scales (Figure 1; Table 1). High LMA is related to a plant's ability to resist physical stress, enhance leaf longevity and conserve nutrients (Castro-Díez, 2012). The positive correlation between LMA and H indicates that sun- or wind-exposed tree species make thicker and/or denser leaves to enhance light capture (Gutschick and Wiegel, 1988; Long, Schamp *et al.*, 2015) and resist physical stress.

High WD enhances the stiffness and strength of wood, thus protecting trees against biophysical hazards and enhancing plant survival (van Gelder *et al.*, 2006). Positive correlations between WD and H indicate that taller trees in tropical cloud forests have denser wood, likely to avoid buckling due to self-loading and stem breakage that can result from strong winds.

Positive correlations between LMA and WD indicate that under particular conditions, trees in tropical cloud forests employ a resource conservation strategy that enhances both leaf and stem toughness and persistence. For example, plants in low soil phosphorus environments in tropical cloud forests may employ a conservative resource use strategy to accumulate relatively more carbon-rich chemicals in leaves and wood (i.e., high LMA and WD; Niinemets and Kull, 2003; Pérez-Harguindeguy *et al.*, 2013). This increases the lignin and carbon density of the cell wall, contributing to the thickening and hardening of those walls, thus enhancing the longevity of stem and leaves as well as the nutrient residence time in the plant. The disproportionate scaling relationship between LMA and WD may also be mediated by plant height, as taller trees are more exposed to wind and have higher WD and LMA.

Similar positive relationships for these traits have been found across species (Fonseca *et al.*, 2000; Chave *et al.*, 2009; Long, Zang, Schamp, *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013). However, Falster and Westoby (2005) found a negative relationship between WD and maximum species height for tropical rain-forest species. In those rain-forest understories, it is possible that high WD protects against pathogens and falling debris, helping trees avoid tissue loss and enhancing survival and shade tolerance (Alvarez-Clare and Kirajima, 2007). In cloud forests, trees are small in stature (less than 5 m tall), long-lived and light-demanding (Long, Zang, and Ding, 2011), and their higher wood density is clearly beneficial to survival in strong winds and high sun (Peterson, 2000; Poorter, 2008; Thomas *et al.*, 2015).

4.2 | Disproportionate scaling relationships across the three hierarchical scales

As hypothesized, tropical cloud forest trees showed disproportionate scaling relationships between LMA and H, LMA and WD and H and WD, across the individual, species and community levels (Table 1). The slopes of bivariate trait relationships (on log-log axes), also called "scaling exponents," indicate the proportionality or disproportionality of resource allocation to different plant functions. The fact that scaling components of the three trait pairs we studied differed significantly from one (Table 1) indicates unique allocation strategies for tropical cloud forest trees. For example, a 10% increase in H (log) co-occurred with an increase in LMA (log) of 25% at the individual level, 13% at the species level and 17% at the community level. The same increase in H also co-occurred with an increase in WD (log) of 5% at the individual level, 14% at the species level, and 12% at the community level (Figure 1). Thus, we can see that for a given gain in carbon, resource investment at the species and community levels is higher in stem WD than in stem H. Differences in material investments between H and WD probably show that resistance to strong wind stresses is more important than competition for light for tropical cloud forest trees. Thus, our results show that trait

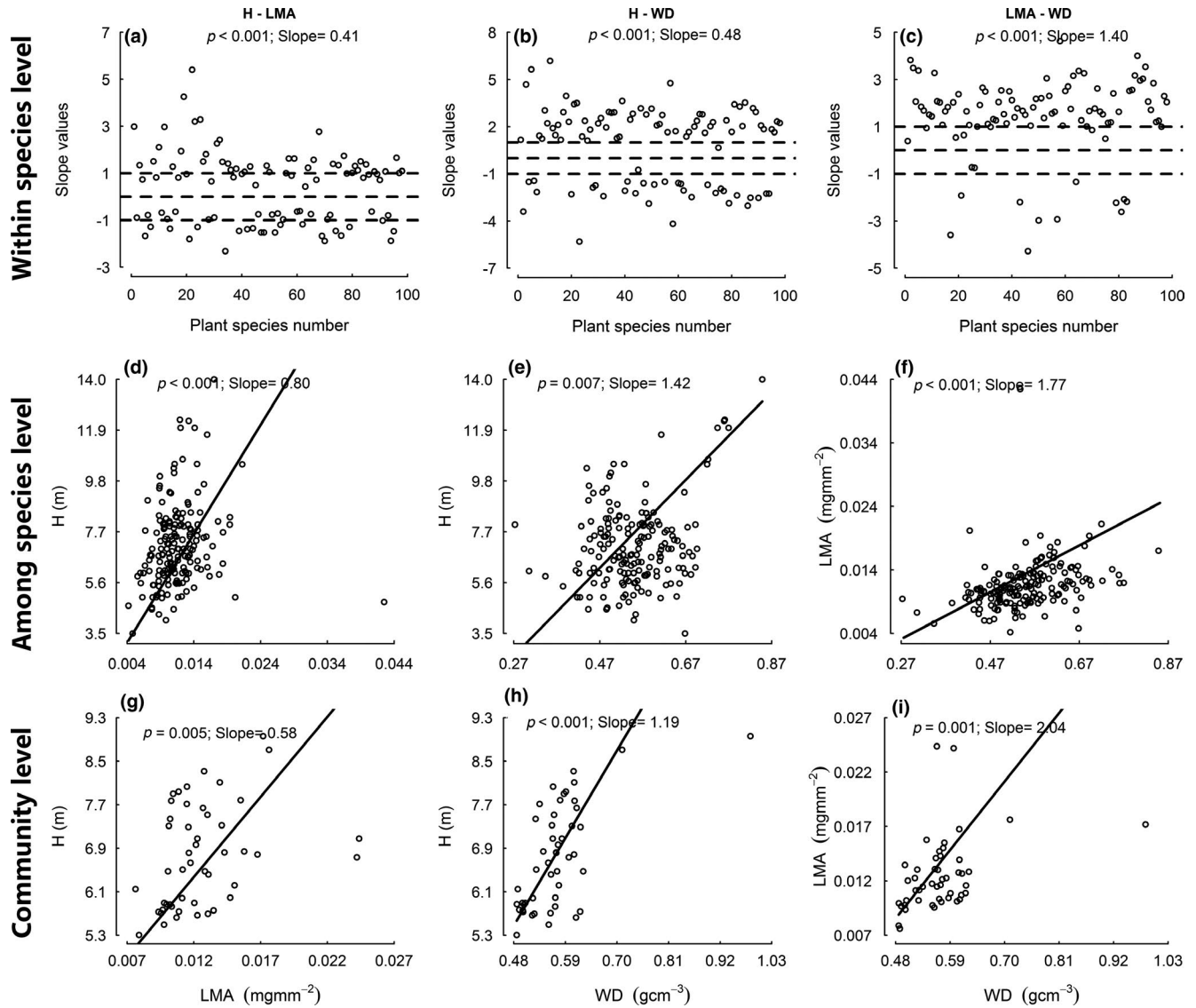


FIGURE 1 Mean standardized major axis (SMA) slopes for (a, d, g) plant height (H) and leaf mass per area (LMA), (b, e, h) H and wood density (WD), (c, f, i) LMA and WD across within-species (a–c), among-species (d–f) and community levels (g–i). The slope values in panels a–c were calculated as the mean value for each trait pair across all species at the within-species level, and the p value was derived from a Student's t test which determines whether slopes differed significantly from zero. The slope values and p values in panels d–i derived from those in the SMA analyses. The dashed horizontal lines in panels a–c indicate slopes equal to +1 and –1. Each trait was \log_{10} -transformed before analysis

functional relationships can vary across tropical systems, and differences between our results and those from lowland tropical forests are most likely driven by differences in environmental stresses in the two systems. In tropical cloud forests, trees are regularly exposed to high winds, which may explain the small stature of trees in these forests (Long, Zang, Schamp, *et al.*, 2011).

Our findings reinforce that these three functional trait pairs represent core plant strategies for maximizing growth while tolerating the environmental stresses in tropical cloud forests (i.e., low soil phosphorus and strong winds). One potential explanation for similar trait relationships across the three levels is that phosphorus is a limiting nutrient in this system, affecting the resource strategies of individuals, species and communities in similar ways (Table 2). Our

results support the general view that these functional traits, along with other unmeasured but correlated functional traits, capture primary dimensions of functional variation (Witkowski and Lamont, 1991; Wright *et al.*, 2004; Poorter *et al.*, 2009; Baraloto *et al.*, 2010; Grady *et al.*, 2013).

The similar scaling relationships for each trait pair across the individual, species and community levels (Table 1), suggest that there is a similar allocation strategy operating across hierarchical scales. The within-species bivariate relationships for some species, however, have negative slopes (Figure 1a–c). This suggests that these scaling relationships are highly variable, and may be constrained under particular environmental conditions (e.g., air temperature; Long, Zang, and Ding, 2011). Tree species in tropical cloud forests

TABLE 2 Effects of soil variables (available nitrogen, AN; total nitrogen, TN; total phosphorus, TP; available phosphorus, AP; organic matter, OM) on the allometric relationships among leaf mass per area (LMA), plant height (H) and wood density (WD), across the individual, species and community levels, using multiple regression

Hierarchical levels	Parameters	H-LMA					LMA-WD					H-WD					R ²		
		AN	TN	OM	AP	TP	R ²	AN	TN	OM	AP	TP	R ²	AN	TN	OM		AP	TP
Individuals	<i>p</i>	0.99	0.14	0.01	<0.001	<0.001	0.10	0.001	0.15	0.88	<0.001	<0.001	<0.001	0.67	0.25	0.01	<0.001	<0.001	0.07
	β	-0.0003	-0.04	0.07	-0.20	0.20	0.20	0.08	0.04	0.004	0.10	-0.16	0.11	0.01	-0.03	0.07	-0.18	0.17	0.30
Species	<i>p</i>	0.34	0.10	0.04	0.40	0.03	0.37	0.63	0.82	0.10	0.09	0.01	0.22	0.41	0.20	0.83	0.01	0.02	0.30
	β	0.21	-0.41	0.48	-0.19	0.46	0.46	0.12	-0.06	0.42	-0.39	-0.65	0.19	0.19	-0.33	-0.05	-0.55	0.57	0.74
Communities	<i>p</i>	0.08	0.83	0.36	0.31	<0.001	0.74	0.007	0.62	0.89	0.16	0.02	0.29	0.16	0.54	0.36	0.43	<0.001	0.74
	β	-0.30	-0.04	-0.13	-0.17	1.10	1.10	0.74	-0.16	-0.03	0.39	-0.74	0.29	-0.23	-0.11	-0.14	-0.13	1.08	0.74

β indicates standardized regression coefficients. *p* values of multiple regressions are listed below each soil variable and significant standardized regression coefficients are indicated in bold. The first variable mentioned is the Y variable (e.g., H) and the second variable mentioned is the X variable (e.g., LMA).

have a high structural plasticity to cope with variable environments (Long, Zang, and Ding, 2011), and thus may show a fairly flexible allocation strategy responding to temperature constraints. Trait variation at the individual and community levels is comparable to species-level variation (Wright *et al.*, 2004; Chave *et al.*, 2009), indicating that they are likely to be important for plant and community performance (Albert *et al.*, 2010; Bolnich *et al.*, 2011; Long, Zang, Schamp, *et al.*, 2011; Laforest-Lapointe *et al.*, 2014). Additionally, our findings show that scale choice for investigating these bivariate relationships may be less important for some of these three trait pairs than for others.

Although our results suggest similar trait relationships across the three hierarchical levels, the slopes of bivariate relationships of the three trait pairs at the species level were consistently, although not significantly, steeper than at the individual level (Table 1). This suggests that stronger variation in plant allocation strategies is possible at the species level than at the individual level (e.g., species can vary more markedly in maximum H and WD than individuals within species), as species come from different phylogenetic origins and can display a wide range of strategies. Another explanation for the differences in scaling slopes between the individual and species levels in this study may be that the intra- and interspecific level analysis occurs across different portions of environmental gradients because individual trees and species occupy different parts of the prevailing gradients. That is, the selection pressure that shapes differential resource allocation to these traits at the within-species level might differ from those at the among-species level. For the community-level analysis, however, community-weighted values for pairs of traits are not fully independent as abundance weightings are used for both variables. This issue can inflate *p* values and impact interpretations. We interpreted these analyses with caution, and focused on slopes, rather than the significance of the relationships (Zeleny, 2018).

4.3 | Soil nutrient effects on scaling relationships

Interestingly, we found that the LMA-H, WD-H and LMA-WD relationships across all three hierarchical levels were modified by soil phosphorus. The individual- and community-scale relationships were also affected by soil nitrogen, and the individual and species-scale relationships were significantly impacted by organic matter levels (Table 2). In tropical forests, nitrogen is thought to limit plant performance (Santiago *et al.*, 2012); however, these tropical cloud forests grow on strongly weathered soils, where rock-derived nutrients such as phosphorus are limiting (Table 2; Vitousek *et al.*, 2010). The significant effects of soil phosphorus on trait relationships in this study suggest that soil phosphorus may act as an important determinant of variation in LMA, H and WD at the individual, species and community levels. This leads to slow-growing individual trees and species with low LMA, high H, and high WD values that are favored under the low soil phosphorus conditions in tropical cloud forests. Additionally, the similar

resource allocation strategies across the individual, species and community levels observed here are responsive to multiple abiotic stresses such as low soil phosphorus, (Table 2; Long *et al.*, 2013; Long, Schamp, *et al.*, 2015, Long, Xiong, *et al.*, 2015). Similar spectra in resource use strategies across these three levels may help forest trees partition the phosphorus gradient and persist under this environmental constraint. That is, the positive effect of P on the H–LMA slope may indicate that plants in tropical cloud forests preferentially invest in H over LMA at high soil P, to capture more light and grow faster. The positive effect of P on the H–WD slope, as well as the negative effect of P on the LMA–WD slope, however, may indicate that plants in tropical cloud forests invest in high WD over H and LMA to resist strong wind stresses. Additionally, this scaling relationship adds evidence of a strategy of disproportional nutrient allocation between leaf and stem as a means of adapting to stress related to low soil phosphorus. That is, woody biomass could provide a well-defended storage organ for phosphorus (Chapin *et al.*, 1990), whereas leaves are a poorer storage organ due to their relatively short lifespan and increased vulnerability to herbivores. This resource use strategy most likely enables trees in tropical cloud forests to store two times more phosphorus in wood than in leaves, promoting the nutrient use efficiency of trees, and enhancing their survival in these tropical forests. We also found that the effects of total and available phosphorus on trait relationships were opposite (Table 2). This probably results from the fact that there is a negative relationship between total and available phosphorus (Appendix S4). For example, there was no clear difference in total phosphorus between BNR and JNR ($p = 0.06$), while available phosphorus in BNR was significantly higher than in JNR (BNR, 16.85 ± 7.15 ; JNR, 1.06 ± 1.18 ; $p < 0.001$). The differences in available phosphorus between BNR and JNR may be due to the observed higher topographic slopes for forest plots in JNR compared to BNR. Steep slopes may allow soil clay components with rich soil mineral (e.g., available phosphorus) in JNR to be lost downslope, reducing the available components in soils. Large changes in available soil components with plot slope suggest that this parameter may poorly represent soil conditions in tropical cloud forests.

Finally, species co-occurrence patterns in these systems, which have been linked to facilitation, are accentuated in low soil phosphorus conditions (Long, Xiong, *et al.*, 2015). As such, trees species in these environments have likely evolved a common strategy for dealing with low phosphorus conditions that is successful relative to allocation by other species (Field and Mooney, 1986). This co-evolution increases survival chances not only for individual trees, but for tree species and even the whole community. Trees in competitive environments, however, may not experience a similar co-evolutionary pathway, particularly if functional traits under selection become divergent (i.e., niche differentiation). This may be one reason that consistent scaling relationships across different hierarchical levels are not more commonly observed in natural systems (e.g., Ackerly *et al.*, 2002; Domínguez *et al.*, 2012).

5 | Conclusions

We found positive relationships for LMA–H, LMA–WD and H–WD. Relationships between the three trait pairs were disproportionate, suggesting differential resource investments between H and WD and LMA. The disproportionate scaling relationship between stem density and stem height suggests that resource investment is higher in stem density than stem height, which indicates that resistance to strong wind stresses is a primary driver of resource allocation patterns in tropical cloud forests (Thomas *et al.*, 2015). The scaling components for the studied trait pairs were statistically similar across the individual, species and community levels, suggesting a similar allocation strategy operating at different hierarchical levels. Finally, we found that scaling relationships across all three hierarchical scales are strongly affected by soil phosphorus. This suggests that resource allocation patterns for these important functional traits, which define important plant strategies, are driven by a combination of extreme conditions related to solar irradiance and soil nutrient levels.

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AUTHOR CONTRIBUTIONS

WL, YZ and RZ conceived the ideas and designed methodology; WL and MX collected the data; WL and BSS analyzed the data; WL, BSS, XY, LP and CX led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are stored at the Data center of the College of Forestry and are available in Appendices S1, S2, S3 and S4.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Dominant tree species and individual number in the tropical cloud forest plots of the Bawangling Nature Reserve (BNR), Jianfengling Nature Reserve (JNR) and Limushan Nature Reserve (LNR) on Hainan Island, Southern China

Appendix S2. The mean soil nutrient contents of 48 tropical cloud forest plots in Bawangling Nature Reserve (BNR), Jianfengling Nature Reserve (JNR) and Limushan Nature Reserve (LNR)

Appendix S3. The mean values for each species of the height, leaf mass per area and wood density measured in tropical cloud forests

Appendix S4. Correlations among the five soil factors and methods of soil measurements in tropical cloud forests

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