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# What controls tropical forest architecture? Testing environmental, structural and floristic drivers

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## ABSTRACT

**Aim** To test the extent to which the vertical structure of tropical forests is determined by environment, forest structure or biogeographical history.

**Location** Pan-tropical.

**Methods** Using height and diameter data from 20,497 trees in 112 non-contiguous plots, asymptotic maximum height ( $H_{AM}$ ) and height–diameter relationships were computed with nonlinear mixed effects (NLME) models to: (1) test for environmental and structural causes of differences among plots, and (2) test if there were continental differences once environment and structure were accounted for; persistence of differences may imply the importance of biogeography for vertical forest structure. NLME analyses for floristic subsets of data (only/excluding Fabaceae and only/excluding Dipterocarpaceae individuals) were used to examine whether family-level patterns revealed biogeographical explanations of cross-continental differences.

**Results**  $H_{AM}$  and allometry were significantly different amongst continents.  $H_{AM}$  was greatest in Asian forests ( $58.3 \pm 7.5$  m, 95% CI), followed by forests in Africa ( $45.1 \pm 2.6$  m), America ( $35.8 \pm 6.0$  m) and Australia ( $35.0 \pm 7.4$  m), and height–diameter relationships varied similarly; for a given diameter, stems were tallest in Asia, followed by Africa, America and Australia. Precipitation seasonality, basal area, stem density, solar radiation and wood density each explained some variation in allometry and  $H_{AM}$  yet continental differences persisted even after these were accounted for. Analyses using floristic subsets showed that significant continental differences in  $H_{AM}$  and allometry persisted in all cases.

**Main conclusions** Tree allometry and maximum height are altered by environmental conditions, forest structure and wood density. Yet, even after accounting for these, tropical forest architecture varies significantly from continent to continent. The greater stature of tropical forests in Asia is not directly determined by the dominance of the family Dipterocarpaceae, as on average non-dipterocarps are equally tall. We hypothesise that dominant large-statured families create conditions in which only tall species can compete, thus perpetuating a forest dominated by tall individuals from diverse families.

## Keywords

Allometry, architecture, Dipterocarpaceae, ecology, Fabaceae, function, height–diameter, maximum height, structure, tropical moist forest.

## INTRODUCTION

Tree architecture and wood anatomy determine light capture, water transport and resistance to mechanical damage. Thus, tree architecture is said to be indicative of 'survival versus growth' life strategy trade-offs (King *et al.*, 2006a). Survival specialists tend to have shorter stems for a given biomass, or higher wood density, to avoid breakage. Growth specialists tend to be tall for a given diameter in an attempt to quickly attain a dominant canopy position. If trees optimise their design in a given environment, we might expect to see predictable trends in architectural traits along environmental gradients, and to see cross-continental similarities in architectural design, despite floristic differences, i.e. ecological convergence. Nevertheless, architectural traits are, in part, genetically pre-determined and studies have demonstrated that height and the relationship between stem height and diameter (allometry) vary among species and in association with various functional traits (e.g. Bohlman & O'Brien, 2006; van Gelder *et al.*, 2006). However, it remains unclear whether this phylogenetic variation drives differences between forest stands as well as individuals within a stand; investigations into variation in vertical structure over continental and global scales have only recently begun (Moles *et al.*, 2009; Feldpausch *et al.*, 2011).

The extent to which maximum tree height and allometry vary along environmental gradients and between floristic and functional groups has been the subject of both theoretical and field-based enquiry. Hypotheses can primarily be grouped around: (1) metabolic theory, which predicts that stem height consistently scales with diameter to the power  $2/3$  (e.g. Niklas & Spatz, 2004); (2) hydraulic limitations to apical growth and the effect of water availability on sapwood cross-sectional area predicting that precipitation, and its seasonality, may affect tree stature and allometry over large scales (Meinzer, 2003; Ryan *et al.*, 2006), and (3) mechanical constraints, because a tree of a given height must avoid buckling under its own weight (McMahon, 1973). Therefore the properties of wood (notably wood density and elasticity), local wind conditions and the density of neighbouring trees are likely to be important determinants of spatial variation in maximum tree heights and allometry (Henry & Aarssen, 1999; King *et al.*, 2009; Anten & Schieving, 2010). We test each hypothesis in our analysis.

Furthermore, biogeographical history establishes the regional pool of species from which forest stands can be composed and therefore may be important in determining large-scale variation in tree allometry. For example, many Southeast Asian forests are dominated by the family Dipterocarpaceae, so this may be anticipated to drive structural differences between forests in Asia and other tropical continents. Here, we test: (1) whether environmental/structural differences alone explain any observed differences in forest architecture, or if (2) the biogeographical pool of species, and limited locally available genetic variation, are the partial cause of differences in vertical structure.

To assess the two major hypotheses we require measurements of individual tree architecture within (1) unmanaged forest stands, to reduce interpretation difficulties, and (2)

across all biogeographical realms in which forests are found, to maximise the biogeographical differences amongst stands. We focus on tropical forests because we could access data from all four realms (the Americas, Africa, Indo-Malaysia, Australasia) in multiple unmanaged forests, thus providing a unique global-scale analysis.

Differences in maximum tree height between tropical regions have been noted, based on 'record-sized trees', with emergent canopy trees in Asia reaching over 60 m in height, whilst heights of only about 50 m have been reported from Africa and central and north-eastern Amazonia, and even shorter 'maximums' being identified elsewhere in Amazonia and Australia (e.g. Yamakura *et al.*, 1986; Ola-Adams & Hall, 1987; Korning *et al.*, 1991; Milliken, 1998; de Gouvenain & Silander, 2003; Liddell *et al.*, 2007). However, these generalisations are largely from localised, individual tree measurements. Thus, while anyone who has walked in both Southeast Asian and central Amazonian forests will recognise that the Asian forests are taller, to our knowledge, the possible differences amongst sites and all continents, and their possible causes, have not been robustly statistically analysed.

In order to explore our key hypothesis, that forests growing in a similar environments develop similar architectural properties, we assess whether the stand-level asymptotic maximum tree height ( $H_{AM}$ ) and the height–diameter allometry of trees (1) vary systematically among the four tropical moist forest continents (Africa, America, Asia and Australia) and (2) are influenced by environment (temperature, precipitation, solar radiation), forest structure, wood density and/or floristic composition, using height and diameter data from 20,497 trees from 112 non-contiguous plots to derive plot-level asymptotic maximum height and allometric coefficients.

The results from this study have two practical applications: firstly, as old-growth tropical forest ecosystems are major stores of carbon (Pan *et al.*, 2011), persistent regional differences in forest stature would indicate that local allometric equations are required to more accurately calculate carbon storage and fluxes. Secondly, significant biogeographical effects on forest structure would indicate that inclusion of phylogenetic history may be an important development in future vegetation modelling.

## METHODS

### Study sites and tree data

We collated tree diameter and corresponding height data from lowland, tropical moist forest stands [defined by Sommer (1976) as including both tropical rain and seasonal forests, but excluding dry/transitional forests], with primary data collected from plots associated with the RAINFOR and AfriTRON plot networks (Peacock *et al.* 2007; Lewis *et al.* 2009; Lopez-Gonzalez *et al.* 2011) and Banin (2010) for South America, Africa and Asia, respectively. Sites conform to the following criteria: (1) old-growth tropical forest stands free from large-scale anthropogenic (e.g. industrial logging) or natural disturbances (e.g. major cyclone disturbance or fire); (2)  $\leq 1000$  m above sea level;

(3) six or fewer dry months per year, where a dry month is defined as precipitation  $\leq 100$  mm (using WorldClim datasets; Hijmans *et al.*, 2005); and (4) mean annual precipitation  $\geq 1200$  mm (Hijmans *et al.*, 2005). The 112 non-contiguous forest plots are in Africa (38), South America (49), Asia (14) and Australia (11). Details of data sources, locations and plot conditions are given in Appendices S1 & S2 and Fig. S1 in the Supporting Information.

From each plot we included free-standing woody plants  $\geq 10$  cm diameter at breast height (d.b.h.; default 1.3 m or above all buttresses or stem deformities), but excluded the following: (1) monocotyledonous trees and climbers, because they have substantially different allometries (note that these form a small proportional of the canopy, usually contributing  $< 5\%$ , and  $< 1\%$  of stems  $\geq 10$  cm diameter respectively, in a given stand); (2) stems with snapped boles and/or visible crown damage whenever documented; (3) 48 trees with stem allometry that strongly suggested a snapped bole or data collection error, but were not marked as such in the original data; (4) stems leaning more than  $10^\circ$  from upright when documented, since this affects both the accuracy of height estimates and height growth itself. We chose a lower limit of 10 cm d.b.h. as this is a foresters convention, thus data below this threshold are rare. The number of stems available from each site varied from 10 to 649 (Appendix S1; median 64 stems).

Tree heights were measured one of four ways (Appendix S1): (1) direct measurement from destructively sampled stems; (2) direct measurement from climbing the sampled tree; (3) estimation by a trigonometric approach where the distance from the tree to the observer and the angles from the observer to the base and apex of the tree were measured using either a manual clinometer or hypsometer (Vertex III, Haglof); or (4) estimation using a laser rangefinder to measure distance to the top-most leaf whilst standing below the crown.

Sampling strategies within a given plot were conducted in one of the following five ways.

1. All trees within a delimited area were measured (35 plots).
2. All stems within selected subplots within a plot were measured (four plots).
3. Sampling was 'haphazard' in plots where trees were climbed for collecting leaf samples (seven plots) or harvested for biomass measurements (seven plots).
4. Trees were selected on a stratified-random basis to incorporate the full range of tree diameters (61 plots). The stratified-random sampling approach involved random selection of 10 trees from each of four diameter size classes (10–19.9, 20–29.9, 30–39.9 and  $\geq 40$  cm d.b.h.). Often, but not always, the largest individuals at the site were also measured to improve the parameterisation of height–diameter curves. In 11 Asian plots the five largest individuals from the Dipterocarpaceae and non-Dipterocarpaceae were also measured.
5. In three plots (Pasoh-02, Pasoh-03 and Lambir-01) trees were randomly chosen from common, pre-selected species. In total, diameter and height data from 20,497 trees were analysed: 9394 stems in Africa, 4754 in America, 2108 in Asia and 4241 in Australia.

Climatic conditions, forest structural attributes and mean wood density were estimated for each plot (Appendix S2). Temperature and precipitation data (mean annual temperature,  $T_A$ ; mean annual precipitation,  $P_A$ ; precipitation in the driest three consecutive months,  $P_{D3}$ ; precipitation in the wettest 3 months,  $P_{W3}$ ; precipitation seasonality, given by the coefficient of variation,  $P_{CV}$ ) were obtained from WorldClim global coverage at 2.5' resolution (Hijmans *et al.*, 2005). Altitude was recorded locally and lapse rate corrections ( $0.0065^\circ\text{C m}^{-1}$ ; Barry & Chorley, 1998) were applied to WorldClim temperature data according to the difference between local and WorldClim-derived altitudes. Incoming solar radiation ( $R_S$ ;  $\text{MJ m}^{-2} \text{day}^{-1}$ ), based on station recordings of sunshine hours and cloud percentage cover, was extracted from a  $0.5^\circ$  global dataset (New *et al.*, 1999).

Forest structural properties (plot-level basal area,  $A_B$ ; stem density,  $D_S$ ; mean stem size of all stems  $\geq 10$  cm d.b.h.) and plot-level mean wood density ( $W$ ) were available for 109 plots, so environment/structure analyses were restricted to these plots. Primary forest structure data were obtained from the Forest Plots Database (Lopez-Gonzalez *et al.*, 2009) and the remainder from the literature. For 104 plots, wood density was calculated utilising the Global Wood Density Database (Chave *et al.*, 2009; Zanne *et al.*, 2009). Each stem in the plot was attributed a wood density value; where possible this was the species-level average, and in descending order of precision, a genus-, family- or plot-level average depending on the availability of  $W$  data and level of taxonomic identification of each stem. Plot-level means were computed, weighted by number of stems of each taxon. For the remaining five plots, mean wood density was taken from the available literature. The median and range of key plot-level environmental and structural conditions by continent are shown in Fig. 1. Significant differences (as determined by Wilcoxon pairwise comparisons with Hochberg corrections) are indicated and described further in Appendix S2.

## Statistical analyses

The statistical analyses consisted of three main stages, as detailed below: (1) examining height–diameter functions and continent-level differences using nonlinear mixed effects (NLME) models; (2) testing the impact of environmental and structural variables on height–diameter parameters ( $H_{AM}$  and height at reference diameter 22.5 cm,  $H_{22.5}$ ); and (3) testing for possible taxonomic effects.

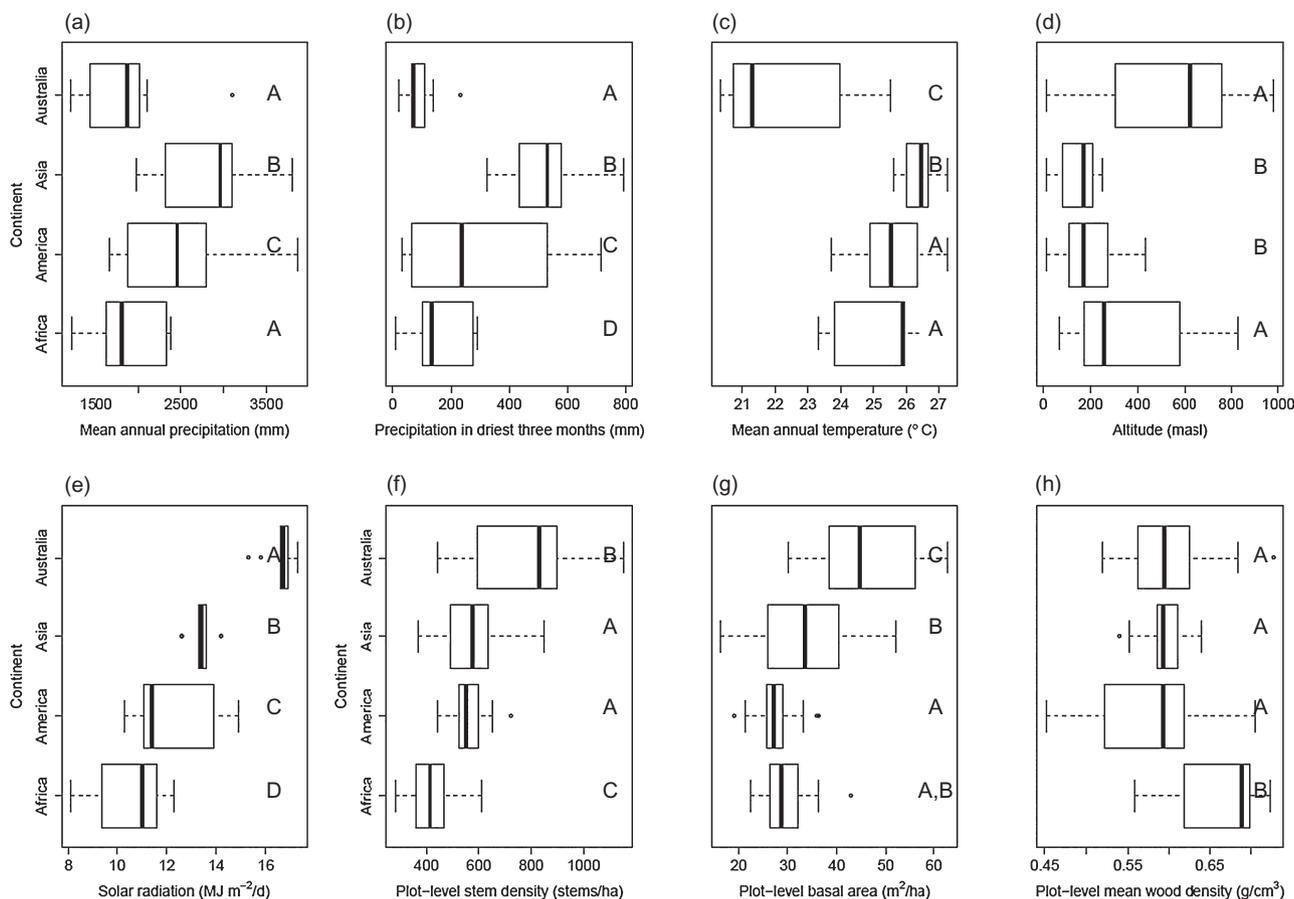
### Height–diameter function forms

At least 75 different equations have been proposed to describe height–age and height–diameter relationships (e.g. Zeide, 1993). We compared six commonly used function forms for the present dataset (equations S1–S6, Appendix S3) to find the best model fit and assess sensitivity of results to the function form used.

The three-parameter exponential equation (equation 1) performed best statistically and was used for subsequent analyses:

$$H = a - b \exp(-cD). \quad (1)$$

In equation 1,  $H$  is individual tree height,  $D$  is diameter, and  $a$ ,  $b$  and  $c$  are estimated curve parameters which represent,



**Figure 1** (a)–(h) Boxplots showing the median, inter-quartile range, maximum and minimum values of environmental variables (a–e) and forest structure and wood density variables (f–h) by continent, calculated on a plot basis. Within each plot, letters A–D are the same where continent medians do not differ significantly (Wilcoxon rank sum tests; Hochberg corrected  $P$ -values < 0.05 are significant).

respectively, the asymptote ( $H_{AM}$ ), the difference between maximum and minimum height ( $b$ ) and the shape of the curve ( $c$ ). Theoretically, parameter  $c$  should be indicative of stem allometry. However, examination of parameters demonstrated that it is not independent of the parameterised asymptote (this study; Thomas, 1996). Therefore, to examine stem allometry of subcanopy stems ( $\leq 40$  cm d.b.h.) we additionally use the power function (equation 2):

$$H = aD^b \quad (2)$$

where  $a$  and  $b$  are parameters to be estimated. The dataset was limited to stems  $\leq 40$  cm d.b.h. to avoid biases in the residuals associated with the largest stems, and since different variables may be important in determining subcanopy stems compared with large, supra-canopy individuals. Results from this equation allowed the calculation of height at a reference diameter (22.5 cm d.b.h.),  $H_{22.5}$ , a measure of stem allometry. Analysis using equation 2 also provided a means to test theoretical predictions from metabolic ecology theory (e.g. Niklas & Spatz, 2004).

#### Cross-continental comparisons of maximum height and allometry

Height–diameter relationships (using both equations 1 & 2) were estimated by NLME models (*nlme* package in R software version 2.9.1, Pinheiro *et al.*, 2009). Since trees within the same plot are likely to be more similar in height–diameter allometry than trees selected at random, residuals are autocorrelated. NLME models account for this non-independence. ‘Plot’ was specified as a random effect and ‘continent’ (referring to America, Africa, Asia or Australia) as a fixed effect. The general model form is given by

$$H = f(D, \alpha_c) + \alpha_p + \epsilon \quad (3)$$

where height ( $H$ ) is modelled by a nonlinear function  $f$  (equation 1 or 2) of diameter ( $D$ ), the fixed effect term ‘continent’ ( $\alpha_c$ ), the random effect term ‘plot’ ( $\alpha_p$ ) and the residual term ( $\epsilon$ ) associated with variability between individuals, species and measurement error. Parameters were estimated using the maximum likelihood (ML) method, allowing comparisons of model fits with different fixed effects structures (Pinheiro &

Bates, 2000). We modelled the variance structure as a power of the covariate ( $D$ ) and this term was allowed to vary by continent; this provided a model of significantly better fit (as determined by the likelihood ratio test,  $P$ -value  $< 0.001$ ) compared with the error term modelled as constant variance. Further details on the NLME method are provided in Appendix S3.

#### *Environmental and forest structure covariate modelling*

The relationships between two response variables ( $H_{AM}$  and  $H_{22.5}$ ) and explanatory variables (continent, environment, forest structure and wood density) were examined using ordinary least squares (OLS) regression models. Since some of the precipitation variables, and  $T_A$  and altitude, were strongly correlated, several candidate maximal models were considered for both response variables. All models included  $A_B$ ,  $D_S$ ,  $W$ ,  $R_S$  and  $T_A$  and any of the three non-correlated precipitation combinations ( $P_{DQ} + P_{WQ}$ ;  $P_{WQ} + P_{CV}$  or  $P_{CV} + P_A$ ). All models were repeated with and without 'continent' as a factor to test whether accounting for environmental conditions removed continent-level differences. In each case, the best regression model was selected using an automated stepwise approach ('step' function in R) that compares the model Akaike information criteria (AICs) following the exclusion of each variable individually to determine the model with the lowest possible AIC for the given set of variables. Following selection of the model with the lowest AIC,  $P$ -values and percentage variation explained by terms remaining in the model were evaluated.

NLME models were also constructed to include significant covariates from the OLS analysis, to assess the robustness of results and to test whether the inclusion of covariates in the NLME model negated the significance of the 'continent' term in the NLME models. Results are presented in Appendix S4.

#### *Taxonomic models*

To test whether biogeographical differences are likely determinants of large-scale differences in architecture, four additional analyses were conducted. Firstly, we selected and analysed, using the same NLME procedure outlined for the full dataset, (1) only the most common family in the dataset, the Fabaceae (2442 stems) and (2) the whole dataset excluding the Fabaceae. We hypothesise that if maximum height and allometry are more similar across regions when only the legume clade is considered than when all clades are considered, this would indicate that biogeographical history may be important in determining cross-continental differences. Secondly, we selected and analysed (3) only individuals from the Dipterocarpaceae family (482 stems) in Asia and (4) the Asia dataset excluding the dipterocarps, as their dominance in Asian forests is the clearest biogeographical continental difference in the dataset. We test the hypothesis that the maximum heights of Asian forests are lower once the dipterocarps are excluded, and that this floristic element is an important determinant of vertical structure, testing previous assertions stating that Asian forests are tall due to dipterocarp dominance.

## RESULTS

### **Cross-continental comparisons of maximum height and allometry**

Measured maximum tree heights varied greatly across the continents: the mean height of the tallest 5% of stems ( $\pm$  SD) was 54.9 m (5.9) in Asia, 46.0 m (5.8) in Africa, 41.0 m (5.1) in South America and 36.0 m (3.6) in Australia. Note that the height of the tallest 5% of stems in the present dataset will be greater than that of 5% of all stems  $\geq 10$  cm within a stand due to the increased representation of taller stems from stratified samples. By contrast, measured diameters of the largest tree were similar in Africa, America and Asia, *c.* 200 cm (217, 191, 198 cm d.b.h., respectively), but no tree greater than 120 cm d.b.h. was found in the Australian dataset (Fig. 2).

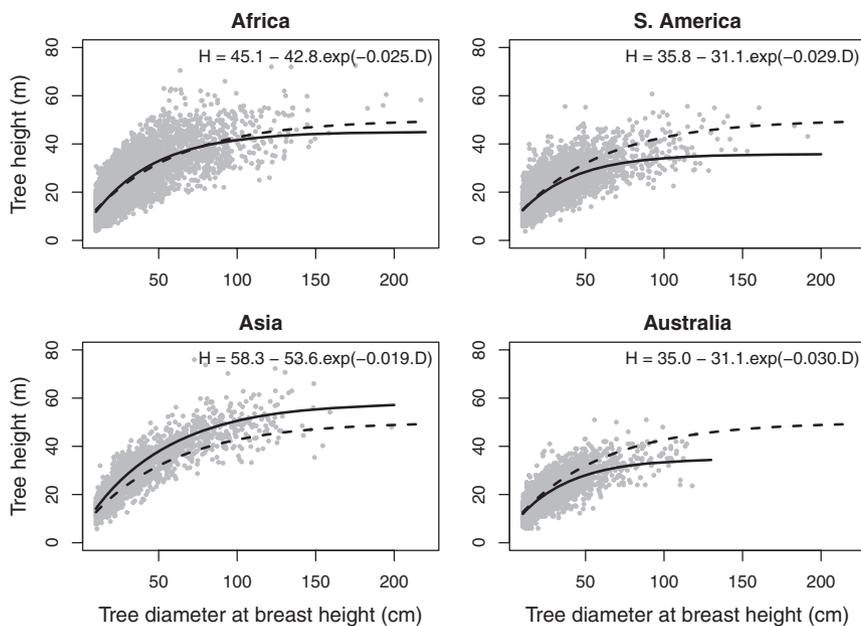
$H_{AM}$  differed significantly amongst continents, using the three-parameter exponential function (equation 1; Fig. 2, Table 1). Height–diameter relationships were significantly different amongst all pairs of continents except South America and Australia (Table 1, Appendix S3). The addition of 'continent' as a fixed factor substantially improved the model when compared with the model with only 'plot' specified, as determined by a reduction in the AIC.  $H_{AM}$  ( $\pm$  95% CI) was greatest in Asia ( $58.3 \pm 7.47$  m) followed by Africa ( $45.1 \pm 2.59$  m), South America ( $35.8 \pm 6.02$  m) and Australia ( $35.0 \pm 7.42$  m). Whilst the absolute value for  $H_{AM}$  depended on form of the function, the order of the continents remained the same for all functions (see Appendix S3).

For a given diameter, trees in Asia were tallest, followed by Africa, South America and Australia in descending order (Fig. 2, Table 1). For the entire range of stem sizes, exponent  $b$  of the power function (equation 2) ranged from 0.486 to 0.589 across the continents; substantially lower than the 0.667 predicted by both the critical buckling limit and metabolic theory.

Similarly,  $H_{22.5}$  also differed significantly amongst continents. Average  $H_{22.5}$  was 23.3 m in Asia, 20.4 m in Africa, 19.2 m in South America and 18.9 m in Australia. Interestingly, stems  $\leq 40$  cm d.b.h. in Africa and Asia grew statistically indistinguishably from the theoretically predicted exponent [0.671 ( $\pm 0.024$  95% CI) and 0.630 ( $\pm 0.067$ ) respectively], compared with South America (0.528  $\pm$  0.058) and Australia (0.556  $\pm$  0.065), which were significantly lower than the theoretically predicted value.

### **Environment, forest structure, wood density and architecture**

Plot-level  $H_{AM}$  varied from 23.8 to 72.1 m, and OLS regression models demonstrated that both environmental and forest structural variables explain some variation in  $H_{AM}$  (Table 2, Fig. 3). The most parsimonious model (lowest AIC and all terms significant at the 5% level,  $R^2 = 0.738$ , d.f. = 105,  $P$ -value  $< 0.0001$ ) included the continent term (explaining 46.7% of variation in plot-level  $H_{AM}$ ), indicating that even when environmental/structural variables were accounted for they did not entirely



**Figure 2** Relationships between total tree height and diameter at breast height (d.b.h.) for living, intact trees  $\geq 10$  cm d.b.h., on four continents. In each plot, the dashed curve shows equation 1 (three-parameter exponential) with parameters estimated for the global dataset. The solid curve demonstrates parameters estimated for each continent separately, and the continent-specific equation given, for nonlinear mixed effects models with ‘continent’ specified as a fixed effect and ‘plot’ as a random effect. See Appendix S3 for further discussion on model performance.

explain continental differences.  $H_{AM}$  was negatively related to  $D_S$  and  $P_{DQ}$ , and positively related to  $A_B$ ,  $T_A$ ,  $R_S$  and  $W$  were not significant in explaining variation in  $H_{AM}$ .

Stem allometry, quantified by  $H_{22.5}$ , also varied substantially between plots, from 15.0 to 25.6 m. Differences were, in part, explained by environment, forest structure, wood density and continent in the most parsimonious model ( $R^2 = 0.594$ , d.f. = 103,  $P$ -value  $< 0.0001$ ). Stems were significantly taller for a given diameter where  $A_B$  and  $P_{CV}$  were greater and shorter where  $D_S$  and  $R_S$  were higher.  $W$  was positively related to  $H_{22.5}$ , indicating that higher wood density may provide mechanical stability for trees to attain a greater height for a given diameter. In the best model,  $T_A$  was not significant in explaining stem allometry. The continent term was significant, explaining 35.5% of variation in plot-level  $H_{22.5}$ . The allometry of African stems became statistically indistinguishable from South American and Australian stems once environmental/structural variables were controlled for, but all other continent pairs remained significantly different. Variables present in the best model and the direction of effect were consistent across a range of reference diameters (10, 20, 30 and 40 cm) and whether the nonlinear power function or log–log linear form were used.

Notably, while some environmental and structural variables explain some of the plot-level variation in allometry and maximum tree height, there remains variation in height–diameter curves associated with continent that cannot be explained by any of the environmental or structural parameters that we considered.

### Taxonomic models

Repeating analyses for stems belonging to the pan-tropical family Fabaceae alone (12% of all trees in the dataset) gave results consistent with those reported above: height–diameter

allometry remained significantly different amongst continents. Considering only the Fabaceae, Asian stands have the greatest  $H_{AM}$  ( $60.4 \pm 8.36$  m, 95% CI), followed by Africa ( $42.3 \pm 2.37$  m), South America ( $36.6 \pm 6.13$  m) and lastly, Australia ( $33.1 \pm 7.68$  m) (Table 1). The Fabaceae clade in a tall forest tends to be tall and in a short forest tends to be short. The non-legumes show similar patterns again (Table 1).

The Dipterocarpaceae in Asia show similar  $H_{AM}$  when compared with Asian data excluding the dipterocarps.  $H_{AM}$  was 57.2 m ( $\pm 7.98$ , 95% CI) without dipterocarps, 58.5 m ( $\pm 4.82$ ) for dipterocarps alone and 58.3 m ( $\pm 7.47$ ) for the whole Asian dataset. These results indicate that the Dipterocarpaceae do not *directly* determine differences in vertical structure observed between Asian forests and other continents.

### DISCUSSION

We hypothesised that, once environmental conditions were controlled for, similar forest architecture (maximum height and stem allometry) would be found on all continents.  $H_{AM}$  did differ greatly, by *c.* 22 m between Asian and Australian forests. Asian and African forests are taller than South American and Australian forests, which corroborates previous *ad hoc* comparisons (e.g. Yamakura *et al.*, 1986; Ola-Adams & Hall, 1987; Milliken, 1998; de Gouvenain & Silander, 2003). For a given diameter, trees are taller in Asia and Africa than they are in South America and Australia. In addition, trees in Africa and Asia apparently grow closer to their mechanical limits than those in South American and Australian forests. Whilst environment, forest structure and wood density explained some plot-to-plot variation in architecture, once these terms were controlled for there were still significant differences in stature, with ‘continent’ explaining 47% and 36% of variation in  $H_{AM}$  and  $H_{22.5}$ , respectively (Table 2). This indicates that there is substantial residual variation, and this may

**Table 1** Nonlinear mixed effects models for equation 1 [ $H = a - b \exp(-cD)$ ] and equation 2 ( $H = aDb$ ) with 'continent' as the fixed effect, 'plot' as the random effect and curve parameters  $a$ ,  $b$  and  $c$  as mixed effects. The  $\pm$  95% confidence intervals are given in parentheses beside the estimated curve parameters.

Equation and dataset	Fixed effects											
	Africa			South America			Asia			Australia		
	$a$	$b$	$c$	$a$	$b$	$c$	$a$	$b$	$c$	$a$	$b$	$c$
1, all stems	45.08 (2.59)	42.80 (2.47)	0.025 (0.002)	35.83 (6.02)	31.15 (5.72)	0.029 (0.006)	58.25 (7.47)	53.58 (7.06)	0.019 (0.006)	34.97 (7.42)	31.08 (7.16)	0.030 (0.007)
2, all stems	3.21 (0.25)	0.59 (0.02)	n.a.	4.20 (0.62)	0.49 (0.04)	n.a.	4.04 (0.71)	0.56 (0.05)	n.a.	3.83 (0.74)	0.51 (0.05)	n.a.
2, stems $\leq$ 40 cm d.b.h.	2.52 (0.21)	0.67 (0.02)	n.a.	3.72 (0.57)	0.53 (0.06)	n.a.	3.27 (0.65)	0.63 (0.07)	n.a.	3.34 (0.62)	0.56 (0.06)	n.a.
1, Fabaceae	42.34 (2.37)	40.84 (2.28)	0.031 (0.003)	36.60 (6.13)	30.09 (5.84)	0.028 (0.010)	60.45 (8.36)	54.62 (8.01)	0.019 (0.008)	33.06 (7.68)	31.10 (7.72)	0.040 (0.019)
1, non-legumes	44.78 (2.64)	42.31 (2.45)	0.024 (0.002)	36.16 (6.10)	31.24 (5.66)	0.027 (0.006)	57.17 (7.70)	52.04 (7.13)	0.019 (0.006)	35.42 (6.85)	31.36 (6.58)	0.028 (0.006)
1, Dipterocarpaceae	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	58.53 (4.82)	52.42 (5.81)	0.019 (0.002)	n.a.	n.a.	n.a.
1, non-dipterocarps	44.43 (2.14)	41.99 (2.03)	0.025 (0.002)	37.24 (5.15)	31.73 (4.86)	0.025 (0.005)	57.20 (7.98)	51.93 (7.35)	0.018 (0.005)	35.42 (5.98)	31.35 (5.80)	0.029 (0.005)

n.a., not applicable.

**Table 2** Best ordinary least squares models explaining variability in (a) plot-level asymptotic height ( $H_{AM}$ ) and (b) plot-level allometry (height at reference diameter,  $H_{22.5}$ ) of stems  $\leq$  40 cm d.b.h.

Variable	Coefficient	SE	Percentage of variation explained
(a)			
Continent			46.7
Africa	44.893***	3.077	
America	39.879***	1.431	
Asia	62.101***	2.044	
Australia	36.335***	2.777	
$P_{DQ}$	-0.006*	0.003	1.0
$D_S$	-0.022***	0.005	4.6
$A_B$	0.357***	0.086	4.3
(b)			
Continent			35.5
Africa	14.417***	2.788	
America	16.373**	0.579	
Asia	20.967***	0.830	
Australia	13.875(n.s.)	1.222	
$P_{CV}$	0.0524***	0.011	9.8
$R_S$	-0.643***	0.138	8.6
$D_S$	-0.003*	0.002	1.5
$A_B$	0.170***	0.028	14.4
$W$	9.465**	3.083	3.7

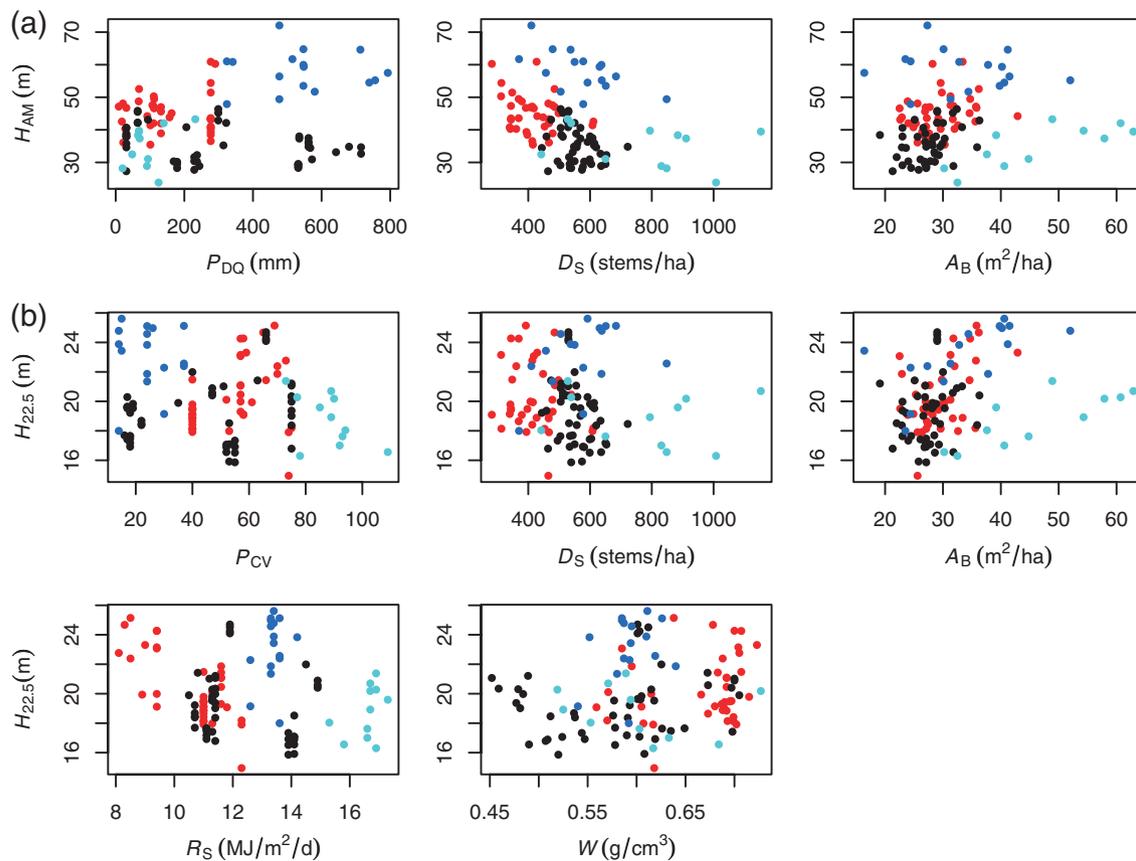
Significant environmental and forest structural covariates are:  $P_{DQ}$  (precipitation in the driest quarter, mm);  $P_{CV}$  (precipitation seasonality, coefficient of variation);  $R_S$  (incoming solar radiation, MJ m<sup>2</sup> ha<sup>-1</sup>);  $D_S$  (stem density, stems ha<sup>-1</sup>);  $A_B$  (basal area, m<sup>2</sup> ha<sup>-1</sup>);  $W$  (mean wood density, g cm<sup>-3</sup>).

\*\*\* $P \leq 0.001$ ; \*\* $P \leq 0.01$ ; \* $P \leq 0.05$ ; n.s.  $P > 0.1$ . The percentage variation explained by each term was calculated as the difference in  $R^2$  between the best model and model without that term.

be, in part, explained by biogeographical differences, or other unmeasured environmental factors. Below we consider, in turn, the potential explanations for the relationships observed and opportunities for further research.

### Environment, forest structure, wood density and architecture

Contrary to expectations from hydraulic theories of maximum tree height, which suggest that height is ultimately limited by water availability (Ryan *et al.*, 2006), we found that  $H_{AM}$  showed a weak inverse relationship to dry season rainfall ( $P_{DQ}$ ) amongst the plots studied. This relationship could have arisen for several reasons. Firstly, hydraulic limitation may only limit apical growth when trees are very tall, perhaps even taller than the c. 60 m exhibited by very tall trees that occur in tropical forests (Koch *et al.*, 2004). Secondly, the plots considered in this study are perhaps too wet for an effect of drought to be detected, particularly if deep, well-structured soils provide some buffering against periodic water shortages. A threshold may occur at the



**Figure 3** Relationships between response variables (a) plot-level asymptotic maximum height ( $H_{AM}$ ), (b) plot-level height at reference diameter, 22.5 cm ( $H_{22.5}$ ) and significant environmental/structural covariates: precipitation in the driest quarter ( $P_{DQ}$ ), precipitation coefficient of variation ( $P_{CV}$ ), solar radiation ( $R_S$ ), stem density ( $D_S$ ), basal area ( $A_B$ ) and wood density ( $W$ ). Points are coloured by continent: Africa (red), South America (black), Asia (blue) and Australia (cyan). The bivariate relations displayed here sometimes differ from the multivariate coefficients in Table 2 because the latter apply to remaining variation not explained by other variables.

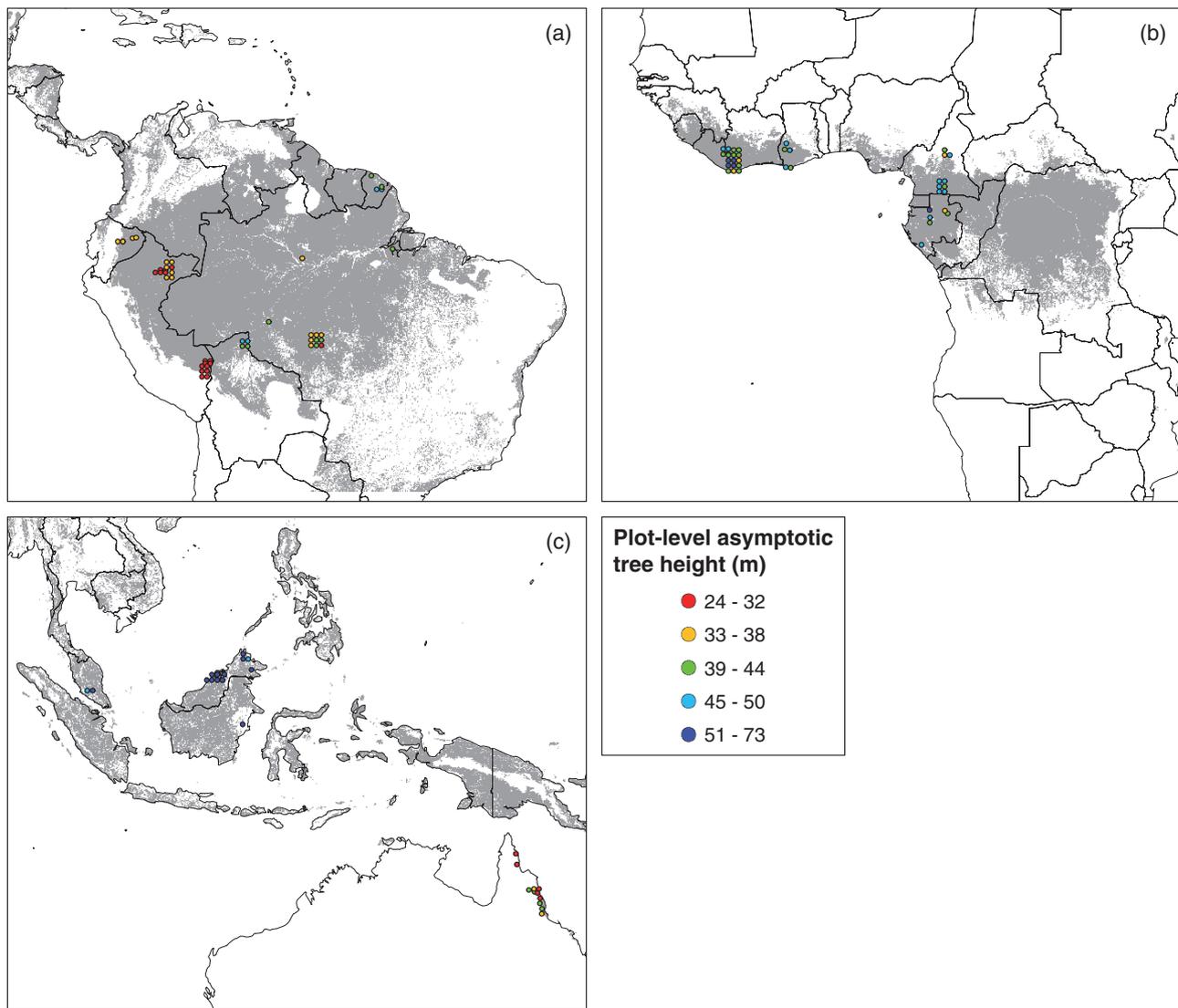
boundary between tropical seasonal forests and other vegetation formations, such as savanna or tropical dry forest, where water availability and soil interactions become much more important determinants of forest physiognomy and tree height (e.g. Feldpausch *et al.*, 2011). Thirdly, other unmeasured covarying environmental or forest structure variables may be determining maximum tree height. For example, in the Amazon, wetter forests also tend to be more dynamic (Phillips *et al.*, 2004) and therefore factors other than hydraulic limitation may determine the maximum height trees tend to attain. Wind disturbance may be a particularly important determinant of tree height – the relatively short stature of Australian tropical forests has previously been attributed to greater wind disturbance there (de Gouvenain & Silander, 2003). Nevertheless, Australian forests experience the most seasonal climate and are the shortest, whilst Asian forests are the least seasonal and the tallest; increased sample sizes and studies incorporating longer environmental gradients in each region are needed to better elucidate these patterns.

The results indicate, however, that regions with wetter periods allow stems to grow tall for a given diameter. Precipitation seasonality ( $P_{CV}$ ) was positively related to  $H_{22.5}$  (Table 2, Fig. 3).

This effect was also observed by Feldpausch *et al.* (2011). Investigating the likely basis of this relationship in detail, the authors argued that the somewhat counter-intuitive association arises because, for a given dry season length, sites with a high  $P_{CV}$  have higher wet season precipitation. This replenishes water held in the soil profile, allowing trees to access water even during the dry season, and may reduce water lost through runoff. Therefore, other things being equal, a variable precipitation regime may reduce hydraulic constraints to trees.

Relationships between architecture and forest structure were stronger than those with climatic variables (Table 2). Other studies have also shown that forest structural characteristics can improve the estimation of height–diameter curve parameters (Fang & Bailey, 1998).  $A_B$  is positively related to  $H_{AM}$ , and  $D_S$  negatively so.

There is a distinct spatial patterning of  $H_{AM}$  within South America (Fig. 4), with forests in eastern Amazonia being taller than those in the west, and also more similar to those in Africa and Asia (Fig. 4). Interestingly, a similar pattern also exists for stem turnover rates, with trees in eastern Amazon typically having much longer lifespans (Phillips *et al.*, 2004; Chao *et al.*, 2009) and with mortality rates also more akin to those of



**Figure 4** (a)–(c) Map of plot-level asymptotic maximum height ( $H_{AM}$ ) in metres in (a) South America, (b) Africa and (c) Asia and Australia. Note, points are dispersed for visibility and are not in precise locations. Estimated lowland moist forest cover is indicated by grey shading (delimited as described in Fig. S1).

African and Asian forests than their more proximal western Amazon neighbours (Gale & Barford, 1999; Gale & Hall, 2001; Phillips *et al.*, 2004; Lewis *et al.*, 2004). These similar geographical patterns suggest that large scale variations in stem turnover rates and  $H_{AM}$  have similar causes. Underlying explanations for this  $H_{AM}$ /turnover covariance include poor substrate stability and/or more intense winds during storm events (Feldpausch *et al.*, 2011; Quesada *et al.*, 2012). However, we consider it unlikely that variations in these factors explain all the documented cross-continental differences in tree height.

$A_B$  was also positively related to  $H_{22.5}$ , while  $D_S$  was negatively related. This suggests that it is the presence of large canopy trees – rather than packing of stems per se – which induces a competitive effect. This is consistent with ‘neighbour’ theories that predict that a race for light and shelter from wind drives individuals to grow close to their critical buckling limits, and thus

to be more slender for a given height when crowded by tall individuals (Henry & Aarssen, 1999; King *et al.*, 2009). Plots with high  $A_B$  and large mean stem size feature in African and Asian regions (Fig. 1), and under these conditions the sub-canopy trees are more slender and are growing closer to the theoretical buckling limit than in America and Australia. This also indicates that the height–diameter relationship is not invariant, corroborating findings from more spatially restricted datasets (Muller-Landau *et al.*, 2006; King *et al.*, 2009).

Wood density moderates height–diameter relationships, since denser wood can more safely bear a given crown mass, allowing stems to be more slender. Our results support this, demonstrating that wood density is positively related to  $H_{22.5}$ , but did not explain all the continent-level variation in allometry. This may be because other aspects of forest architecture, such as crown geometry, and wood anatomy were not included in the analyses

due to a lack of available data. For example, narrower crowns require less wood to support a tree of a given height (Iida *et al.*, 2012). Other wood properties such as Young's modulus of elasticity and wood lignin content may also be important in moderating the trade-off in architectural traits.

### Biogeography and architecture

Large cross-continental differences in  $H_{AM}$  and  $H_{22.5}$  remained after statistically accounting for environmental and structural variation amongst plots. This implies that biogeographical differences may be important. However, when compared, the Dipterocarpaceae had very similar height–diameter relationships to the non-dipterocarps in Asian forests and cross-continental differences in  $H_{AM}$  and allometry persisted, demonstrating that the observed differences in vertical structure cannot be directly attributed to the stature of this dominant family. Yet this does not exclude an indirect effect of the family: a high level of dominance may competitively exclude species that are not functionally similar. Furthermore, once Dipterocarpaceae individuals are removed from the dataset, the tallest 10% of individuals (152 stems) are represented by 28 families, showing that many taxa have the propensity to be tall (Fig. S5). Similarly, the Fabaceae, a common pan-tropical family, share similar cross-continental differences in  $H_{AM}$  and allometry as found in the whole dataset. No direct family-level effects on architecture were found.

Cross-continental differences in architecture may also reflect differences in the functional composition of the understorey and canopy that we did not measure. Firstly, the understorey of Neotropical forests is reported to have a greater proportion of subcanopy species with a smaller adult stature than Asian forests where the understorey is dominated by juveniles of canopy species (LaFrankie *et al.*, 2006). Subcanopy species are adapted to shade and tend to be shorter for a given diameter since there is less competitive advantage in gaining height quickly (King 1996), while stems that are 'passing through' the understorey *en route* to their final destination in the canopy are slender. This apparent difference in functional composition may explain differences in allometry between Asian/African and American/Australian forests for smaller stems, as has been shown to be the case when comparing the vertical structure of some temperate and tropical forests (King *et al.*, 2006b). This explanation is supported further by the regional differences found *within* South America in the present study (Fig. 4a); trees are both taller and more slender in the Guyanan Shield region of north-east Amazonia, where juveniles of canopy taxa dominate (Baker *et al.*, 2009). Secondly, we excluded monocots and lianas (structural parasites) from our analyses: if these differ systematically amongst the continents (e.g. fewer lianas in Asian forests; Gentry & Emmons, 1987), then these may affect our results. However, as monocots and lianas usually constitute < 5% and < 1%, respectively, of stems  $\geq 10$  cm diameter in a plot, we anticipate that any impact will be small. Alternatively, differences *within* families could be more important in determining regional differences. Perhaps ecological traits, such as stem architecture, are not well conserved at the family level (partially due to long histories of isolation between

regions) and thus differences at the genus or species level perpetuate the differences observed.

Manifestly, the tropical moist forest ecosystem has different structural expressions on different continents. Why do stems achieve such different allometries in apparently similar environmental settings? The continental differences are not directly driven by differences in biogeographical history, but we hypothesise that dominant large-statured families create conditions in which only tall species can compete, thus perpetuating a forest dominated by tall individuals from diverse families. Future work to elucidate the drivers of the differences we find will need to develop and exploit large multicontinental datasets, such as crown geometry, leaf mass and wood traits, coupled with the replication of height–diameter curves for common genera and species. Further expansion of these datasets into drier areas and cooler forests, and inclusion of detailed information on soil physical and chemical properties, may also yield important insights into the causes of differences in vertical forest structure globally.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Table S1: data sources and methodology by site.

**Appendix S2** Table S2: sites and ancillary data. Figure S1: map of sites. Environmental and forest structural differences across continents.

**Appendix S3** Height–diameter model evaluation. Table S3: description of six height–diameter function forms for comparison. Table S4: nonlinear mixed effects (NLME) analysis for six function forms. Table S5: Pairwise comparison of continent-level height–diameter relationships. Figure S2: Continent-level height–diameter functions resulting from NLME analysis of six function forms. Figure S3: analysis of residuals from NLME models for six function forms. Figure S4: analysis of residuals by continent for best fit NLME model.

**Appendix S4** Analysis of environment, forest structure and wood density covariates. Table S6: nonlinear mixed effects models including environmental/structural covariates.

**Appendix S5** Figure S5: abundance of non-Dipterocarpaceae in Asian forest plots.

**Appendix S6** References for Supporting Information.

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## BIOSKETCH

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