Leaf mass per area, not total leaf area, drives differences in above-ground biomass distribution among woody plant functional types

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Summary

- Here, we aim to understand differences in biomass distribution between major woody plant functional types (PFTs) (deciduous vs evergreen and gymnosperm vs angiosperm) in terms of underlying traits, in particular the leaf mass per area (LMA) and leaf area per unit stem basal area.
- We used a large compilation of plant biomass and size observations, including observations of 21 084 individuals on 656 species. We used a combination of semiparametric methods and variance partitioning to test the influence of PFT, plant height, LMA, total leaf area, stem basal area and climate on above-ground biomass distribution.
- The ratio of leaf mass to above-ground woody mass (M_F/M_S) varied strongly among PFTs. We found that M_F/M_S at a given plant height was proportional to LMA across PFTs. As a result, the PFTs did not differ in the amount of leaf area supported per unit above-ground biomass or per unit stem basal area. Climate consistently explained very little additional variation in biomass distribution at a given plant size.
- Combined, these results demonstrate consistent patterns in above-ground biomass distribution and leaf area relationships among major woody PFTs, which can be used to further constrain global vegetation models.

Introduction

The distribution of forest biomass among leaves and stems strongly influences the productivity and carbon cycle of the world's vegetation (Ise *et al.*, 2010; De Kauwe *et al.*, 2014; Friend *et al.*, 2014). Biomass stored in woody stems has a long residence time (Luyssaert *et al.*, 2008), whereas leaf biomass turns over quickly, entering the soil carbon cycle where the majority of carbon is released back to the atmosphere (Ryan & Law, 2005). Globally, forests store *c.* 360 pg of carbon in living biomass (Pan *et al.*, 2011), equivalent to almost 40 yr of current anthropogenic CO_2 emissions (Friedlingstein *et al.*, 2014). Reducing uncertainties about biomass distribution and carbon residence times is a priority for understanding the effects of climate and other environmental changes on the global carbon cycle (De Kauwe *et al.*, 2014; Friend *et al.*, 2014; Negrón-Juárez *et al.*, 2015; Bloom *et al.*, 2016), in particular because projections by global vegetation models (GVMs) are particularly sensitive to this component (Ise *et al.*, 2010; Friend *et al.*, 2014).

Perhaps the biggest challenge in understanding and predicting biomass distribution is to capture the combined responses to environmental factors of the > 250 000 plant species comprising the world's vegetation. While most plants have the same basic resource requirements and physiological function, large differences exist among species in the amount of biomass invested in different tissues (leaves, stems, roots) (Poorter *et al.*, 2012). The challenge, therefore, is to identify the key traits driving differences among species. One way to start capturing and understanding the sources of this functional diversity is to consider a few archetypal plant functional types (PFTs) (Harrison *et al.*, 2010; Wullschleger *et al.*, 2014). Previous work has shown that despite widespread variation within PFTs for some traits and outcomes, others – including biomass distribution – vary substantially among PFTs (O'Neill & DeAngelis, 1981; Chabot & Hicks, 1982; Bond, 1989; Enquist & Niklas, 2002; Poorter *et al.*, 2009, 2012, 2015; Reich *et al.*, 2014).

The goal of the current work is to better understand differences among PFTs in their biomass distribution. Past work has shown that gymnosperms tend to hold a much larger leaf mass compared with angiosperms (at a given stem mass) (O'Neill & DeAngelis, 1981; Enquist & Niklas, 2002; Poorter *et al.*, 2012, 2015; Reich *et al.*, 2014). The cause of this difference is not yet fully understood, but could arise from either differences in leaf mass per area (LMA) (Poorter *et al.*, 2009) or the amount of leaf area maintained (Chabot & Hicks, 1982; Bond, 1989), or both. It is also unknown whether there are differences among

finer-scale groupings, for example between evergreen and deciduous angiosperms. While past analyses have often spanned many sites and/or species, researchers have been unable to further investigate the factors underlying observed differences in biomass distribution among PFTs because available data only included a limited number of variables.

Here, we use the recently compiled Biomass and Allometry Database (BAAD) (Falster *et al.*, 2015), which includes observations of biomass and other size metrics for 21 084 individual plants (Fig. 1), to establish the underlying cause of biomass distribution among PFTs, and also to test for systematic shifts in biomass distribution with climate. We focus on the distribution of biomass among leaf and above-ground woody tissues in individual plants. To quantify this distribution we analyse two related metrics: the ratio of leaf mass to stem mass, M_F/M_S, and the ratio of leaf area to stem mass, A_F/M_S. To understand the factors driving variation in these quantities, we decompose these ratios into component variables, each of which can be quantified with our dataset. The ratio of leaf mass to stem mass can be decomposed as:

$$\frac{M_F}{M_S} = \frac{M_F}{A_F} \times \frac{A_F}{A_S} \times \frac{A_S}{M_S}, \qquad \text{Eqn 1}$$

where M_F/A_F is the LMA, A_F/A_S the ratio of total plant leaf area to basal stem area, and A_S/M_S is the ratio of stem basal area to above-ground woody mass. Similarly, the ratio of leaf area to stem mass can decomposed as:

$$\frac{A_F}{M_S} = \frac{A_F}{A_S} \times \frac{A_S}{M_S}. \qquad \text{Eqn 2}$$

The terms M_F/A_F and A_F/A_S are themselves prominent traits known to vary among species (Wright *et al.*, 2004; Togashi *et al.*, 2015), suggesting a potential to explain differences in M_F/M_S among PFTs. The third term is known to vary strongly with individual size, decreasing as a plant grows. However, Chave *et al.* (2014) found that a single model of M_S incorporating A_S, wood density, and H to hold across diverse tropical trees, irrespective of vegetation type, or environmental factors.

These decompositions, combined with ideas from past studies, lead us to test the following hypotheses about biomass distribution:

• Individual height captures the majority of variation in M_F/M_S and A_F/M_S, reflecting the fact that height can vary several orders of magnitude within the life span of a single individual and thus represents the dominant form of variation in Eqns 1 and 2.

• Height-related effects on biomass distribution are concentrated in the term A_S/M_S, and while A_S/M_S may vary considerably among individuals, there are no systematic differences in A_S/M_S among PFTs.

• After controlling for the effects of individual height, differences in M_F/M_S among PFTs can arise as a result of differences in either LMA (because PFTs tend to differ LMA; Poorter *et al.*, 2009) or A_F/A_S (because gymnosperms are hypothesized to maintain a greater leaf area than angiosperms; Chabot & Hicks, 1982; Bond, 1989), or both.

• Any differences in A_F/A_S among PFTs also lead to differences in A_F/M_S.

A final aim was to test for shifts in biomass distribution with climate. Little is known about global-scale patterns in biomass distribution in relation to climate, but one might expect biomass distribution to shift with precipitation or mean annual temperature, as small-scale comparisons have shown such responses (Callaway *et al.*, 1994; Berninger *et al.*, 1995; DeLucia *et al.*, 2000; Poyatos *et al.*, 2007). Reich *et al.* (2014) also showed that after controlling for the large size-related variation in biomass distribution, the ratio of leaf to total plant mass (averaged across whole stands, either including or excluding below-ground components) increases with mean annual temperature in both gymnosperms and angiosperms. Thus, we aimed to test for climate-related variation in M_F/M_S and A_F/M_S, and their component terms with PFTs.

Materials and Methods

Data

We used the repetitive statement from the introduction to BAAD (Falster *et al.*, 2015), which includes records for 21 084 individuals of 656 species. The database has very limited overlap ($n = 261$
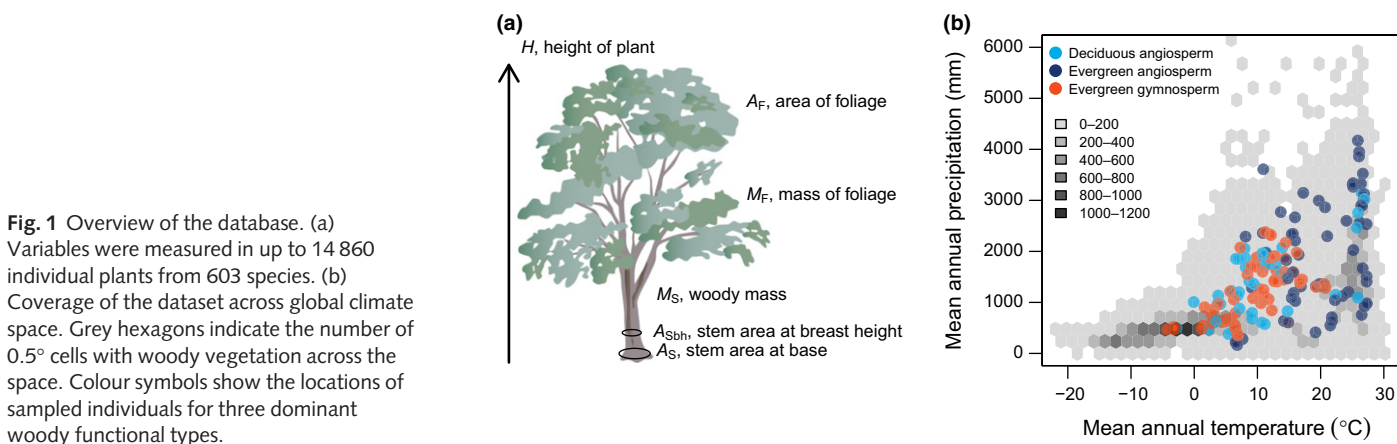

Fig. 1 Overview of the database. (a) Variables were measured in up to 14 860 individual plants from 603 species. (b) Coverage of the dataset across global climate space. Grey hexagons indicate the number of 0.5° cells with woody vegetation across the space. Colour symbols show the locations of sampled individuals for three dominant woody functional types.

individuals; 1.7%) with the recent large compilation of Poorter *et al.* (2015) and differs in that measurements are for individual plants (whereas Poorter *et al.*, 2015 included many stand-based averages) while our dataset also includes other metrics such as leaf area in addition to biomass. We restrict our analysis to records that include leaf mass (M_F), leaf area (A_F), above-ground woody biomass (M_S), plant height (H), and stem area measured at ground level (A_S) or at breast height (typically 1.3 m) (A_{Sbh}) ($n = 14\,860$). Our analysis is in several parts; to maximize the amount of available data for each part we used different subsets of the data, as not all variables were measured in each study. Sample sizes by PFT are summarized in Table 1.

We included only field-grown woody plants in our analysis (including natural vegetation, unmanaged, and managed plantations), excluding glasshouse and common garden studies. We did not exclude plantations from the analysis because this would have removed many data points for evergreen gymnosperms, and excluding plantations did not affect the main results. We considered three PFTs: evergreen angiosperms, evergreen gymnosperms, and deciduous angiosperms. We excluded deciduous gymnosperms because of insufficient data.

To test for climate effects on biomass distribution, we estimated mean annual temperature (MAT), precipitation (MAP) and potential evapotranspiration (PET) for each study location. MAT and MAP were extracted from WORLDCLIM (Hijmans *et al.*, 2005), PET from the Global-PET database (http://www.cgiar-csi.org; Zomer *et al.* (2008)), and an aridity index was calculated as PET/MAP. To assess the coverage of the global climate space by the dataset, we also extracted MAT and MAP from WORLD-CLIM for each 0.5 cell across the globe but excluding areas without woody vegetation, as assessed from the global land cover database GLC-SHARE (Latham *et al.*, 2014).

We only used LMA directly estimated for the harvested plants (typically for a subsample of leaves; see Falster *et al.* (2015) for details on the methods for each contributed study). For conifers, leaf area was converted to half-total surface area using the average of a set of published conversion factors (Barclay & Goodman, 2000), with different conversion factors applied to pines (*Pinus* spp.) and nonpines. This conversion was necessary because half-total surface area is most appropriate for comparison with flat leaves (Lang, 1991; Chen & Black, 1992).

Table 1 Sample sizes used for the four studied whole-plant variables, by plant functional type

	Deciduous angiosperm	Evergreen angiosperm	Evergreen gymnosperm	Total
M_F/M_S	2548 (142)	4362 (316)	1893 (31)	8803 (489)
A_F/M_S	1585 (86)	3648 (239)	894 (22)	6127 (347)
M_F/A_F	1863 (102)	4348 (257)	1487 (30)	7698 (389)
A_F/A_S	1793 (98)	3509 (236)	1629 (32)	6931 (366)
A_S/M_S	2502 (140)	3544 (290)	1910 (29)	7956 (459)

Numbers indicate individual plants, with the number of unique species given in parentheses. Sample sizes differed between variables because not all included studies measured all variables. M_F, total leaf mass; M_S, above-ground woody mass; A_F, total leaf area; A_S, basal stem area.

In our dataset, stem cross-sectional area was measured either at breast height (1.3–1.34 m) and/or at the base of the plant. In our analyses, we used basal stem area because many plants ($n = 5455$) were < 1.3 m tall. We therefore converted records where area was measured at breast height only to area at base, using a relationship fitted to individuals where both measurements existed. For the subset of the data where both areas were measured, we estimated A_S from A_{Sbh} from the equation:

$$D_S = D_{Sbh}\left(\frac{H}{H - H_{bh}}\right)^c, \qquad \text{Eqn 3}$$

where D_S is the basal stem diameter (m), and D_{Sbh}, the stem diameter at breast height. Stem area and diameter were always related assuming the stem was circular. We chose to estimate missing stem diameter rather than stem area because a much better fit was obtained, with a more constant error variance. The parameter c in Eqn 3 was further expressed as a function of plant height:

$$c = c_0 H^{c_1}. \qquad \text{Eqn 4}$$

The estimated coefficients were $c_0 = 0.424$, $c_1 = 0.719$, root-mean-square error = 0.0287, $R^2 = 0.916$. The relationship was fitted using a total of 1270 observations covering the three major PFTs.

Data analysis

Similar to Poorter *et al.* (2015), we found that none of the studied relationships were linear on a log-log scale. Therefore, we did not use standard allometric equations to study relationships between size and biomass variables. Instead, we used generalized additive models (GAMs), a semiparametric modelling approach that makes no assumption about the shape of the relationships, to visualize the relationships between biomass and plant size variables, and to estimate variables such as M_F/M_S and A_F/M_S at a common plant height. In all fitted GAMs, we used a cubic regression spline. For the smoothed term in the model (plant height), we used up to three or four degrees of freedom, which resulted in biologically realistic smoothed relationships. Within the GAM, we used a penalized regression smoother (Wood, 2006) to allow the final degree of smoothness to be estimated from the data. In all fitted GAMs, we used species–dataset combination as a random effect. To homogenize variance, all variables (except MAP and MAT) were log-transformed before analysis.

Using variance partitioning we quantified the contribution of plant height, PFT and climate to the overall variation in M_F/M_S and for all three component variables. The amount of variance explained by quantitative climate variables (MAP and MAT) was assessed with GAMs, with variables sequentially added to the model and the explained variance (R^2) calculated. We also compared this approach to another method using linear mixed-effects models instead of GAMs (calculating the R^2 for linear mixed-effects models for the fixed effects only following Nakagawa & Schielzeth, 2013), as well as third method called 'independent

effects analysis'. The three methods generally agreed on the ranking of variable importance (see Supporting Information Fig. S1).

All analyses were conducted in R 3.2.4 (R Core Team, 2015), using the packages 'MGCV' (Wood, 2006), 'hier.part' (Walsh & Mac Nally, 2013), 'MuMIn' (Barton, 2015), and 'REMAKE' (FitzJohn, 2015). In addition, the code replicating this analysis (and all figures) is available at http://github.com/remkoduursma/baadanalysis (doi: 10.5281/zenodo.50647).
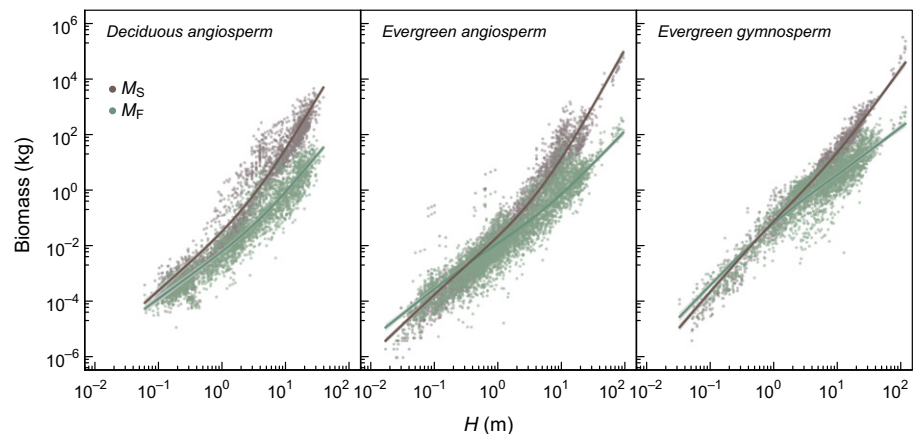
Results

The compiled dataset covered the global climate space well (indicated by coverage across sites classified by MAT and MAP) (Fig. 1; see also Fig. S2). There was some separation between the three major PFTs in terms of climate space occupancy. Evergreen angiosperms occurred, on average, at a higher MAT (50% of studies between 15.5 and 26°C MAT) than deciduous angiosperms (6–12.6°C) and evergreen gymnosperms (3.4–12.4°C). PFT and climate are thus at least partly confounded.

As expected, both M_F and M_S showed a strong dependence on plant height (Fig. 2). For both variables the relationship was nonlinear on a log-log scale, demonstrating departure from simple allometric relationships. It is also evident that M_S increases much more quickly with plant height than M_F. As a result, the ratio M_F/M_S decreased with plant height (Fig. 3a), from an average of 1.5 for very small saplings (< 0.1 m) to an average of 0.01 for large trees (> 30 m). Similarly, A_F/M_S decreased with plant height (Fig. 3c), from an average of 26.7 for very small saplings to an average of 0.045 for large trees.

The composition of M_F/M_S and A_F/M_S into component variables confirmed our second hypothesis, that size-related effects in biomass distribution are heavily concentrated in the A_S/M_S term within Eqns 1 and 2. For M_F/M_S, A_F/M_S and each of the component variables, we estimated the variance explained by individual height, PFT, and climate variables (MAT or aridity) (Table 2). We did this by sequentially adding terms to a GAM and calculating the R^2 for each fitted model. The first model included only plant height and this variable alone explained > 65% of the variation in M_F/M_S, A_F/M_S, and A_S/M_S, but little variation (4–11%) in LMA and A_F/A_S.

We found large differences between the three major PFTs in terms of above-ground biomass distribution, as quantified by the ratio M_F/M_S (Fig. 3a), but not in the ratio A_F/M_S (Fig. 3c). Differences in M_F/M_S were fairly consistent along the range in plant height, with a ranking of evergreen gymnosperm > evergreen angiosperm > deciduous angiosperm. Similar results were obtained when we used above-ground biomass ($M_F + M_S$) instead of plant height as the variable describing plant size (Fig. S3). Next we calculated M_F/M_S at a common plant height of 3 m for each of the PFTs (close to the mean height across all data). These three size-standardized values of M_F/M_S were highly significantly different between PFTs ($P < 0.001$) and were approximately proportional to the average LMA (M_F/A_F) across the PFTs (Fig. 3b). As a result, the amount of leaf area per unit above-ground woody biomass (A_F/M_S) did not differ between PFTs (all pairwise comparisons, $P > 0.05$; see Fig. 3d), because the differences in M_F/M_S were compensated by differences in LMA.

These patterns in biomass distribution reflected differences in the distribution of components of Eqns 1 and 2. In particular, LMA differed substantially among PFTs, whereas A_F/A_S did not (Fig. 4), which is consistent with the large differences between PFTs in LMA shown in Fig. 3(b), and the substantial variance in LMA explained by just PFT (Table 2). When PFT was added to the statistical model (as an intercept term as well as interaction with the smooth plant height term), the R^2 increased substantially for M_F/A_F but not A_F/A_S (Table 2), demonstrating that PFT differences entered largely in leaf mass-based variables.

To confirm the finding that A_F/A_S did not vary appreciably between PFTs, we further examined patterns between A_F and A_S. When these variables are plotted against one another, we see that similar A_F is attained at a given A_S, across the entire plant size range (with the exception of extremely large trees with > 1 m² stem basal area, for which comparatively few data were available) (Fig. 5). We fitted a GAM to A_F as a function of A_S with and without PFT as a covariate, which showed that PFT significantly improved model fit (likelihood ratio test, $P < 0.001$). Nevertheless, the R^2 of the relationship only increased from 0.836 to 0.851, indicating that while significant, PFT had little additional predictive power.

Likewise, the ratio A_S/M_S apparently varied little between PFTs (Table 2). To illustrate this further, a plot of M_S as a

Fig. 2 Raw data for leaf biomass (M_F) and above-ground woody biomass (M_S), for each of the plant functional types, as a function of total plant height (H). Each point is an individual plant. Sample sizes are listed in Table 1. Lines show generalized additive models, fitted to visualize the highly nonlinear relationships. Note the logarithmic scale.
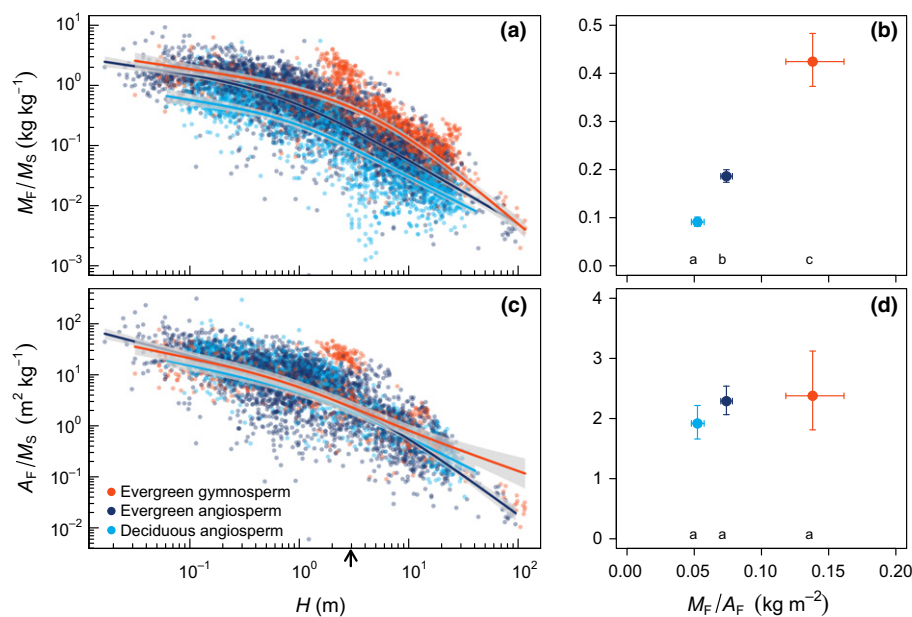
Fig. 3 Dominant woody plant functional types (PFTs) differ in above-ground biomass distribution as a result of underlying differences in leaf mass per area. (a) Leaf mass per unit above-ground woody biomass (M_F/M_S) as a function of plant height (H) by PFT. Each symbol is an individual plant. Lines are generalized additive model fits. The arrow indicates the average plant height in the dataset. (c) Leaf area per unit above-ground woody biomass (A_F/M_S) as a function of H by PFT (symbols and lines as in (a)). (b, d) M_F/M_S and leaf area ratio (A_F/M_S) at the average plant height in the dataset, estimated from fitted models in (a) and (c). Error bars are 95% confidence intervals. Lowercase letters denote significant differences (at $\alpha = 0.05$).

Table 2 Explained variance in four plant biomass variables by plant height (H), plant functional type (PFT) and climate

	H	PFT	H, PFT	H, PFT, MAT	H, PFT, aridity	PFT, MAT	PFT, aridity
M_F/M_S	0.65	0.08	0.76	0.72	0.72	0.06	0.00
A_F/M_S	0.69	−0.04	0.67	0.67	0.62	−0.04	−0.04
M_F/A_F	0.11	0.30	0.45	0.53	0.46	0.35	0.30
A_F/A_S	0.04	0.00	0.05	0.06	0.07	0.02	0.02
A_S/M_S	0.79	0.03	0.79	0.78	0.79	0.02	0.03

Shown are adjusted R^2 values estimated with generalized additive models (GAMs), with four sets of predictors. All variables except PFT were added as smooth terms to the GAMs, avoiding the need to assume linear partial responses to the predictor variables or to search for best-fitting transformations. Climate variables included were either mean annual temperature (MAT) or aridity index (calculated as the potential evapotranspiration (PET) to mean annual precipitation (MAP)). P-values are not shown because all smooth terms were always significant ($P < 0.01$), with the exception of the aridity index in the model for M_F/M_S ($P = 0.057$). In some cases, the R^2 value decreases after adding variables to the model, which is possible because it is adjusted for the number of model parameters. M_F, total leaf mass; M_S, above-ground woody mass; A_F, total leaf area; A_S, basal stem area.

function of A_S revealed a tight relationship, with little apparent difference between PFTs (Fig. 6a). The only exception was for large gymnosperm trees, which consistently showed a lower M_S at a given A_S (Fig. 6b). We fitted a GAM of M_S as a function of A_S (added as a smooth term) with or without PFT as a covariate. Again PFT was formally significant (likelihood ratio test, $P < 0.001$), but the R^2 increased only marginally from 0.802 to 0.82, again showing little practical significance of PFT in explaining this variable.

Taken together, these results demonstrate that the majority of PFT-related variation in M_F/M_S results from variation in LMA, not A_F/A_S or A_S/M_S, and the majority of height-related variation in M_F/M_S results from variation in A_S/M_S, not LMA or A_F/A_S.

Nevertheless, it is important to note that there is also very large variation between individuals within PFTs (Fig. 4), and within all species as plant species grow from seedlings to adults.

Climate variables consistently added little explanatory power when added to a statistical model that included PFT and height (the adjusted R^2 frequently decreased), or to a model that included only PFT (see Table 2). The only exception was LMA, for which a model that included MAT, PFT and height explained 53% of the variation, compared with a model including height and PFT (45%). As the lack of climate effects on biomass distribution is in contrast with recent finding of Reich *et al.* (2014), we also analysed climate effects with methods similar to that study. When we tested for MAT effects on M_F/M_S when only considering gymnosperms and angiosperms (thus grouping deciduous and evergreen species), we found a significant and consistent positive relationship with MAT (Fig. S4) for angiosperms for most size classes (but never for gymnosperms). We found, however, that this was largely because of the fact that at higher MAT, an increasing proportion of angiosperms are evergreen (Fig. 1), which have higher M_F/M_S. When analysed separately for deciduous and evergreen angiosperms, few and weaker significant relationships were found (Fig. S5).

Discussion

Using the largest database of individual woody plant allometry to date, we studied patterns in above-ground biomass distribution among major woody PFTs, plant size, and climate. Our compilation is the first of its kind that also includes leaf area estimates on the same plants, allowing a direct test of the hypothesis that leaf and stem biomass distribution is driven by component traits, LMA and A_F/A_S. We found that at a common plant height, the ratio M_F/M_S varied as a result of underlying differences in LMA across three PFTs, but that there were no differences among PFTs in A_F/A_S. As a result, leaf area per unit above-ground

Fig. 4 Histograms (as probability density functions) of (a) leaf mass per area (M_F/A_F) and (b) leaf area per unit basal stem area (A_F/A_S) grouped by the three plant functional types (PFTs). Arrows indicate means by PFT.
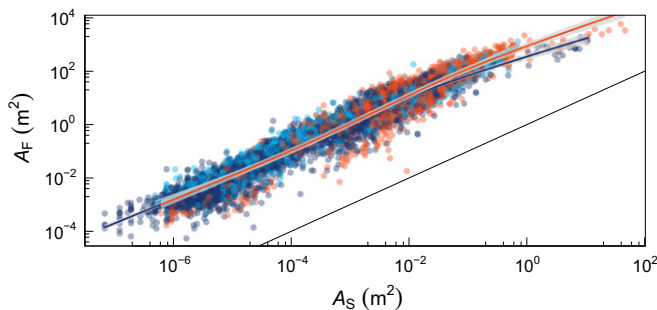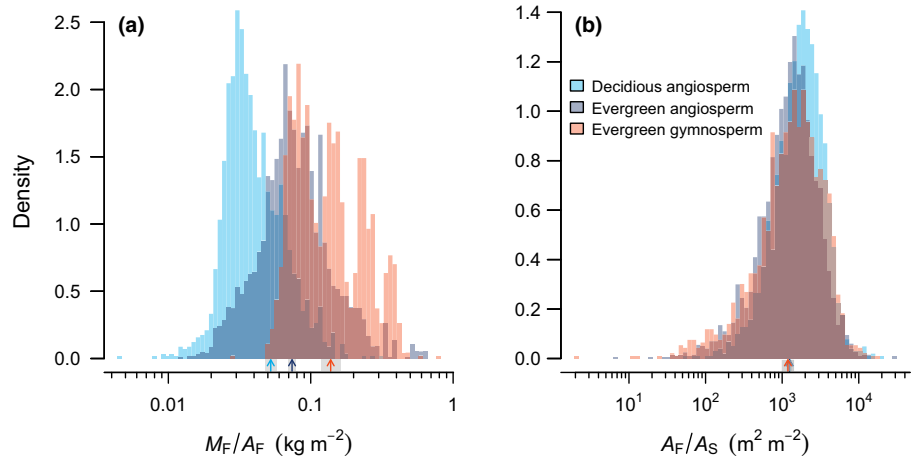

Fig. 5 Total plant leaf area (A_F) is approximately proportional to basal stem area (A_S), and this relationship is similar between plant functional types (PFTs). Coloured lines are generalized additive model fits, with grey areas approximate 95% confidence intervals. The black solid line is a 1/1 line. Blue, deciduous angiosperm; purple, evergreen angiosperm; orange, evergreen gymnosperm.

woody biomass did not vary between PFTs. We found very weak effects of climate (MAT and aridity) on biomass distribution, so that the vast majority of the variation in biomass distribution was explained by plant size and PFT.

We found that M_F/M_S declined steeply with plant height. It is well known that it is necessary to correct for plant size when comparing biomass distribution among groups (McConnaughay & Coleman, 1999). We used a semiparametric approach to account for plant size, which has the advantage that it does not require an *a priori* assumption on the functional relationship. This was useful because both M_F and M_S showed nonlinear patterns with plant height (Fig. 2) and among biomass pools, even on a logarithmic scale. This is consistent with recent results on an independently compiled large database of plant allometry (Poorter *et al.*, 2015), and further calls into question the generality of the often-assumed log-linear relationships between plant biomass pools and size metrics.

A significant implication of our results is that the amount of leaf area supported per plant is less variable between PFTs than the amount of leaf mass, at least at the level of individual plants. Poorter *et al.* (2015) hypothesized that such a result might arise at the scale of entire stands, because forests would converge to a similar leaf area index (LAI). Yet this idea is inconsistent with results reported by Iio *et al.* (2014), who found a much higher

LAI for evergreen gymnosperms compared with evergreen angiosperms, with deciduous angiosperms having intermediate and more variable LAI. Although we found remarkably similar values for A_F/M_S (Fig. 3c), this does not in itself imply that LAI is equally similar. In fact, we would expect LAI to change with LMA, not because of changes in the amount of leaf area maintained by individual plants, but because LMA correlates with the shade tolerance of seedlings (Poorter & Bongers, 2006; Falster *et al.*, 2011), and thereby the LAI of the community (Falster *et al.*, 2011). The ultimate reason why LMA might affect shade tolerance is most likely because of its correlation with leaf life span (LL; Wright *et al.*, 2004). For whole stands, we can therefore expect total stand leaf mass to be correlated with LMA (e.g. Reich *et al.*, 1992), both because of greater leaf mass per plant and the greater density of plants arising from increased LL. Previous interpretations of differences in M_F/M_S between gymnosperms and angiosperms have focused on differences in LL (Enquist & Niklas, 2002; Poorter *et al.*, 2012). We suggest that there are in fact two effects occurring simultaneously: differences in LMA cause differences in the M_F/M_S of individual plants, while differences in LL (and thereby LMA) also cause differences in the LAI of whole stands.

After accounting for PFT and plant height, we found very weak and inconsistent effects of climate on all variables studied, with some exception for LMA (Table 2). Climate was represented as either MAT or an aridity index (PET/MAP); however, results were similarly inconclusive when studying other climate variables such as composite drought indices, growing season length or MAP (results not shown). This result appears to contradict Reich *et al.* (2014), who reported consistent increases in M_F with MAT, when corrected for M_S. We were able to partly reconcile our findings with those of Reich *et al.* (2014): when we categorized our species as only angiosperms vs gymnosperms (thus grouping deciduous and evergreens, as did Reich *et al.*, 2014), M_F/M_S increased consistently with MAT for most size classes within angiosperms (Fig. S4), in line with the findings of Reich *et al.* (2014); on the other hand, we found no comparable relationship for gymnosperms. Moreover, we found that in our dataset, the significant relationships observed for angiosperms as a whole, could be explained via differences between the LMA of deciduous
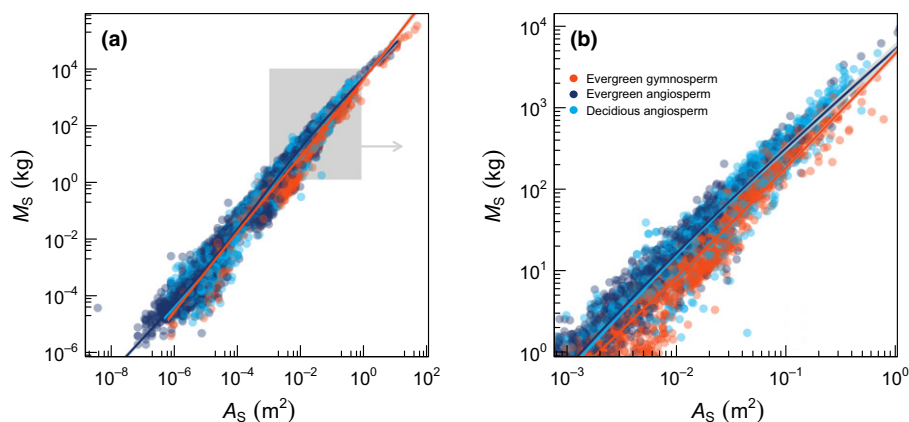
Fig. 6 Above-ground woody biomass (M_S) scales with basal stem area (A_S), similarly for the three plant functional types. (a) M_S as a function of A_S for the entire dataset. Lines are generalized additive model fits. (b) A close-up view of a portion of the data shown in (a), where evergreen gymnosperms displayed significantly lower woody biomass at a given stem basal area.

and evergreen species: evergreen angiosperms occurred at higher MAT (Fig. 1) and had a higher LMA (Fig. 2), resulting in a correlation between M_F/M_S and MAT. We also re-analysed the data in Reich *et al.*, 2014 (not shown) to determine whether this shift in PFT with climate could also explain their finding of an increase in M_F/M_S with MAT, but found the pattern still held within gymnosperms and deciduous angiosperms.

The result that A_F/A_S did not correlate with climate seems to contradict reports, from studies on one or few species, that the ratio of sapwood area to leaf area (the 'Huber value') varies across climate gradients as quantified by summer evaporative demand (DeLucia *et al.*, 2000; Poyatos *et al.*, 2007), rainfall and temperature (Callaway *et al.*, 1994), and temperature (Berninger *et al.*, 1995). Possible reasons for the discrepancy include the following: we studied A_S including the sapwood and heartwood; small-scale climate effects may have been present in our dataset but average out on large climate gradients; climate effects may be highly species-specific; and the majority of reported correlations between the Huber value and climate were for species in the genus *Pinus*.

Although we found no consistent effects of climate on biomass distribution after PFT and plant height were accounted for, effects of climate may also arise by altering the average height of a stand. At a global scale, average plant height is clearly related to climate via water availability (Simard *et al.*, 2011; Klein *et al.*, 2015). As biomass distribution itself is steeply related to plant height (Figs 2, 3), we expect correlations between climate variables and observed biomass distribution when plant height is not first accounted for. However, our database did not lend itself well to a direct test of this hypothesis, and indeed we did not find any correlations between any of the studied variables and climate when height was not first accounted for (Table 2).

We stress that although our results show some convergence between PFTs in leaf area relationships, we do not dismiss the very large variation within PFTs (Fig. 4). Our purpose was to test hypotheses related to first-order differences between PFTs, plant height, and climate, yet clearly more work is needed to understand the variation between species and sites within groups. Some of the residual variation is probably explained by site fertility (Vanninen & Mäkelä, 2005), differences in stand density (Ilomäki *et al.*, 2003), social status within stands (Mäkelä & Valentine, 2006), or

local differences in water availability (possibly mediated by seasonality at a given MAP). It is also likely that the relationship between LMA and biomass distribution reported here among PFTs also operates among species within PFTs. As LMA is known to vary widely within PFTs (Fig. 4), such variation could underpin the equivalent variation in biomass distribution.

Global vegetation models assume or predict differences in biomass distribution between PFTs. However, these differences are currently poorly constrained, as a result of limited available empirical data. Moreover, there is little consensus on how biomass distribution (and allocation) should be modelled in GVMs (Franklin *et al.*, 2012; De Kauwe *et al.*, 2014; Friend *et al.*, 2014). A recent study compared allocation routines in a number of leading ecosystem models (De Kauwe *et al.*, 2014) and recommended constraining allocation by observed biomass distribution instead of using constant allocation fractions. Indeed, the growing availability of large datasets on stand biomass and individual plant construction (Reich *et al.*, 2014; Falster *et al.*, 2015; Poorter *et al.*, 2015) suggests the time is ripe for rigorous benchmarking (Abramowitz, 2012; De Kauwe *et al.*, 2014) of GVMs against empirical data. Our results also suggest a rethink in the way LMA is handled in most growth models. In most existing models, biomass allocation is determined first (by some means or another) and then the amount of leaf area is calculated by multiplying leaf biomass allocation by LMA. Our results suggest that the chain of causation should be reversed: first decide the amount of leaf area, then let LMA determine the cost of building this leaf. Such an approach has already been implemented in at least two vegetation models (Sitch *et al.*, 2003; Falster *et al.*, 2016). Other algorithms are, of course, possible, but this is at least one way to ensure model predictions recover the patterns reported in this paper.

Acknowledgements

reviewers for suggestions that greatly improved the paper. Special thanks to Steve Zissou for advice on colour schemes.

Author contributions

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Comparison of three methods for variance partitioning of the four studied variables.

Fig. S2 Global coverage of the climate space by the dataset, labelled by vegetation type.

Fig. S3 Whole-plant leaf mass (M_F) and leaf area (A_F) as a function of total above-ground biomass.

Fig. S4 Relationships between leaf–stem biomass distribution (M_F/M_S) and mean annual temperature (MAT).

Fig. S5 As Fig. S4 but with angiosperms split up into evergreen and deciduous.

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