Testing the generality of above-ground biomass allometry across plant functional types at the continent scale

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Abstract

Accurate ground-based estimation of the carbon stored in terrestrial ecosystems is critical to quantifying the global carbon budget. Allometric models provide cost-effective methods for biomass prediction. But do such models vary with ecoregion or plant functional type? We compiled 15 054 measurements of individual tree or shrub biomass from across Australia to examine the generality of allometric models for above-ground biomass prediction. This provided a robust case study because Australia includes ecoregions ranging from arid shrublands to tropical rainforests, and has a rich history of biomass research, particularly in planted forests. Regardless of ecoregion, for five broad categories of plant functional type (shrubs; multistemmed trees; trees of the genus *Eucalyptus* and closely related genera; other trees of high wood density; and other trees of low wood density), relationships between biomass and stem diameter were generic. Simple power-law models explained 84–95% of the variation in biomass, with little improvement in model performance when other plant variables (height, bole wood density), or site characteristics (climate, age, management) were included. Predictions of stand-based biomass from allometric models of varying levels of generalization (species-specific, plant functional type) were validated using whole-plot harvest data from 17 contrasting stands (range: 9–356 Mg ha^{-1}). Losses in efficiency of prediction were <1% if generalized models were used in place of species-specific models. Furthermore, application of generalized multispecies models did not introduce significant bias in biomass prediction in 92% of the 53 species tested. Further, overall efficiency of *stand*-level biomass prediction was 99%, with a mean absolute prediction error of only 13%. Hence, for cost-effective prediction of biomass across a wide range of stands, we recommend use of generic allometric models based on plant functional types. Development of new species-specific models is only warranted when gains in accuracy of stand-based predictions are relatively high (e.g. high-value monocultures).

Introduction

Vegetation is an important sink within the global carbon budget, with carbon storage facilitated by uptake of atmospheric carbon dioxide through photosynthesis (Le Quéré *et al.*, 2015). Ground-based information on the carbon storage in vegetation is critical for calibrating carbon budgets, largely calculated using remote sensing metrics (e.g. Haverd *et al.*, 2013; Mitchard *et al.*, 2013; Chen *et al.*, 2015), or regional carbon accounting models (e.g. Richards & Evans, 2004; Paul *et al.*, 2015a, b). In addition, accurate ground-based estimates of biomass are important for the assessment and management of wood and biomass products (e.g. Canadell & Raupach, 2008), fire hazard (Van der Werf *et al.*, 2010), habitat suitability (e.g. Hatanaka *et al.*, 2011), and water yield and quality within catchments (e.g. George *et al.*, 2012).

Typically, ground-based estimates of biomass are obtained by applying allometric models to field measurements of biometric data such as stem diameter or plant height (e.g. Picard *et al.*, 2012). Two key decisions frame the construction of allometric models to predict total above-ground biomass (AGB$_{Indiv}$, oven-dry weight of an individual plant). The first is deciding which predictor variable(s) to use. Stem diameter (*D*, typically measured over bark at 130 cm height above the ground) is commonly used because it can be easily measured with high accuracy (Husch *et al.*, 2003; but see Clark, 2002 for issues in some tropical forests). Plant height (*H*) and bole wood density (ρ) are also often considered, since $D^2H\rho$ is expected to strongly correlate with AGB$_{Indiv}$ (e.g. Chave *et al.*, 2005). The second decision relates to the level of generalization to be used. Most allometric models are based on relatively small species-specific data sets obtained from local areas and often ignore variation across both species and sites (Henry *et al.*, 2011; de Miranda *et al.*, 2014).

Localized species-specific models provide the most accurate estimates of AGB$_{Indiv}$ for the domain for which they were developed (e.g. Wirth *et al.*, 2004; Williams *et al.*, 2005; Basuki *et al.*, 2009; Paul *et al.*, 2013a,b; Ngomanda *et al.*, 2014), but can generate substantial uncertainty when applied outside the range of calibration, with potential for significant biases (20–200%, e.g. Ketterings *et al.*, 2001; Wirth *et al.*, 2004; Chave *et al.*, 2014; Ishihara *et al.*, 2015). The development of new models for new local area-by-species combinations is costly, particularly for woody ecosystems where there are numerous species.

Generalized allometric models can greatly simplify AGB$_{Indiv}$ estimation by assuming that all individuals, irrespective of species or site, are represented by one allometric relationship. Data from large numbers (100s to 1000s) of destructively sampled plants can be used to reparameterize new broadly applicable models (e.g. Brown *et al.*, 1989; Jenkins *et al.*, 2003; Chave *et al.*, 2005, 2014; Moore, 2010; Paul *et al.*, 2013a,b; Gonzalez-Benecke *et al.*, 2014; Ishihara *et al.*, 2015). Models developed with such relatively large sample sizes have the

added advantage of greatly reducing uncertainty in parameter estimates (Chave *et al.*, 2004; Van Breugel *et al.*, 2011; Roxburgh *et al.*, 2015) when compared to most (~75%) localized species-specific models that are developed with $N < 50$ trees (e.g. Zianis *et al.*, 2005; Genet *et al.*, 2011).

Because it is physically difficult to collect and assemble AGB_{Indiv} data, many questions about the usefulness of generic approaches and models remain unanswered. For example, it is unclear to what extent data should be pooled or separated according to their physical, phylogenetic and/or phenological characteristics; often defined as plant functional types (e.g. trees vs. shrubs (Paul *et al.*, 2013a), multistemmed vs. single-stemmed trees (Paul *et al.*, 2013a,b), angiosperms vs. gymnosperms (Chojnacky *et al.*, 2014)). Similarly, we need to quantify the extent to which the use of multispecies allometric models introduces bias to AGB_{Indiv} predictions for some species relative to others. Finally, we need guidance as to which types and combinations of predictor variables (plant dimensions, bioclimatic variables and stand characteristics) will best predict AGB_{Indiv} using generalized models.

At the scale of individual plants, allometry-predicted AGB_{Indiv} can be validated by independent sampling of new plants. However, it is difficult to ascertain whether sampled plants have been truly selected at random. If specific criteria have been applied for selection (e.g. only healthy trees), the resulting allometric model may be inherently biased. A true test of this possible bias would be a direct validation of stand-based allometric model predictions of above-ground biomass (AGB_{Stand}) against that measured through whole-plot harvesting. Such testing has been undertaken in monoculture hardwood forests (Arthur *et al.*, 2001; Paul *et al.*, 2013b), and in mixed-species vegetation (Búrquez & Martínez-Yrízar, 2011; Paul *et al.*, 2013a), but not using generic allometric models that are representative of a more comprehensive range of vegetation types.

Australia provides a good case study for testing generalized allometric models given that it has both a long history of research contributing to AGB_{Indiv} data sets (e.g. Holland, 1969; Forrest & Ovington, 1970; Attiwill, 1979), and spans a broad range of ecoregions, ranging from arid shrublands to tropical rainforests, with plant functional types varying from shrubs and short multistemmed trees through to some of the largest trees in the world (e.g. Specht & Specht, 2002, 2013; Sillett *et al.*, 2015). Improving methods for quantifying biomass and its carbon content in Australia is also of global significance given high interannual variability in biomass carbon globally (Houghton *et al.*, 2012; Ballantyne *et al.*, 2015), with semi-arid ecosystems in Australia playing a significant role (Poulter *et al.*, 2014).

For this project, an AGB_{Indiv} data set of unprecedented size was compiled, composed of 15 054 destructively measured individuals from both managed (i.e. planted) and natural ecosystems across Australia. This data set was used to assess whether diameter-based allometric models of biomass were improved: (i) by the inclusion of other plant variables (e.g. height, wood density); (ii) by the inclusion of site characteristics (e.g. climate, age, management); and (iii) when based on species rather than broader categories like plant functional groups. Our objectives were first, to recommend the most appropriate allometric model(s) for estimating AGB_{Indiv} in Australian ecosystems, and second, to quantify bias of the recommended model(s) when tested against direct measurements of AGB_{Stand} obtained using whole-plot harvesting across a range of contrasting sites.

Materials and methods

Data set

Data sets of AGB_{Indiv} were obtained from destructive harvesting of 15 054 individual trees and shrubs. Data represented a range of managed and natural woody ecosystems across 826 sites in various ecoregions of Australia (Fig. 1) and were obtained from numerous published and unpublished sources (Table S1; Paul *et al.*, 2015c). They included 274 species, 53 of which had $N > 50$ individuals, sufficient for developing species-specific models that provide a reasonable approximation of AGB_{Indiv} given population level variability (Roxburgh *et al.*, 2015). To utilize the wider data set, we categorized all species into plant functional types as described below.

Plant functional types. Five categories of plant functional types of unique physiognomic growth form (Gitay & Noble, 1997) were included: (i) shrubs or small trees characterized by being relatively short (generally <2 m height) and typically multistemmed or highly branched, with a relatively small (<7 cm) stem diameter (F_{Shrub}); (ii) multistemmed hardwood (angiosperm) trees, including mallees from the genus *Eucalyptus*, and trees from the genus *Acacia* (F_{Multi}); (iii) typically single-stemmed hardwood trees from the genus *Eucalyptus* and closely related genera of *Corymbia* and *Angophora* (F_{Euc}); (iv) other tree species that typically have single stems and relatively high wood density (mean 0.67 g cm^{-3}) ($F_{Other-H}$); and (v) other trees, namely conifers from the genera of *Pinus*, *Araucaria* and *Agathis*, that typically have single stems and relatively low stem wood density (mean 0.40 g cm^{-3}) ($F_{Other-L}$). Each of these five plant functional types could also be further subcategorized as indicated in Fig. S1.

Most of these plant functional types include plant species with distinctive branch architecture and/or stem wood density. A highly branched architecture is a unique characteristic of species within F_{Shrub}, while a unique characteristic of conifer species within $F_{Other-L}$ is a relatively low wood density. By comparison, such distinctions were less obvious between
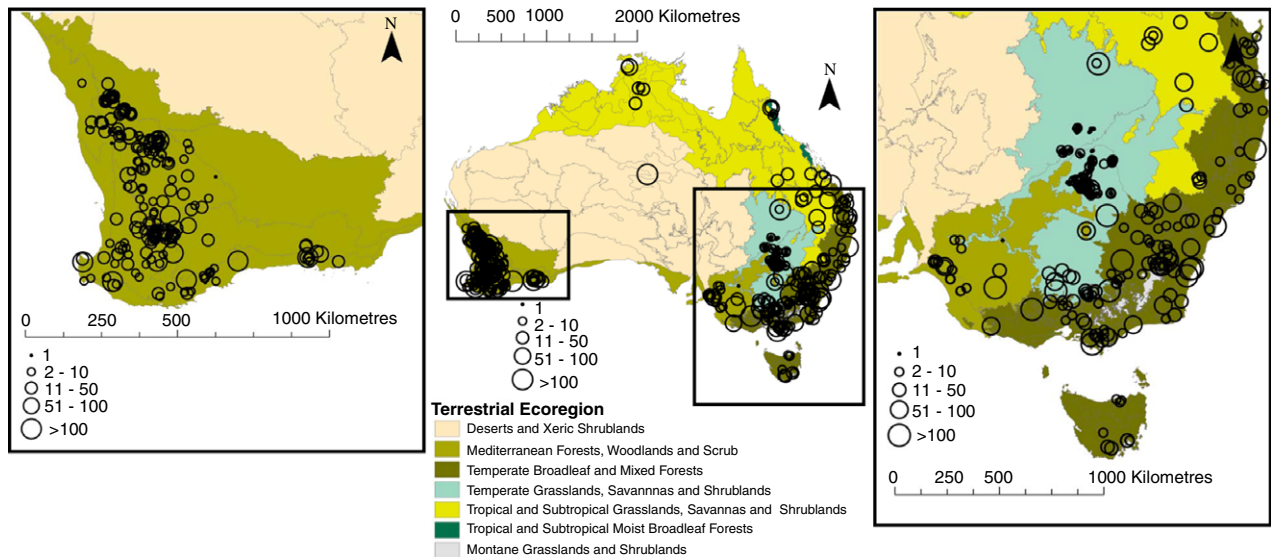
Fig. 1 Location of trees or shrubs sampled for live above-ground biomass by terrestrial ecoregion across Australia (DSWPC, 2015).

the three categories of trees of relatively high wood density (F_{Multi}, F_{Euc} and $F_{Other-H}$), with their categorization based on two issues of practicality. The first related to the height at which stem diameter was typically measured in multi- and single-stemmed trees, resulting in the F_{Multi} category having different predictor variables to that of the other two hardwood tree categories. When compared to single-stemmed trees, multistemmed mallee eucalypts and shrubs have stem diameter measurements taken closer to the ground (usually 10 cm height) below the point at which the stem forks (e.g. Paul *et al.*, 2013a,b). Second, for practicality, the relatively heterogeneous category of $F_{Other-H}$ was segregated from the much more widely sampled F_{Euc} category that solely represented typically single-stemmed *Eucalyptus* trees of relatively high wood densities (Ilic *et al.*, 2000).

The majority of the 15 054-tree data set comprised two categories of plant functional types, namely F_{Euc} (40%) and F_{Multi} (36%), largely representing the ecoregions that supported either 'Mediterranean forests, woodlands and scrub', or 'Temperate broadleaf and mixed forests' (Fig. 2). Although $F_{Other-L}$ represented only 5% of the data set, this category was also largely found in these two ecoregions. In contrast, F_{Shrub} and $F_{Other-H}$ comprised 16% and 3% of the data set, respectively, but were sourced from a wide range of ecoregions.

Explanatory variables. The primary set of collated data included three explanatory variables for AGB_{Indiv}: stem diameter (D, over bark, cm), height (H, m) and, as described below, measured, estimated or derived basic density of stem wood (ρ, g cm^{-3}, typically measured as oven-dry mass per green volume of stem at a standard height of 130 cm, Table 1). Secondary data relating to the site from which an individual was sampled were also collated (Table 1). These included whether the site was 'natural' (i.e. naturally
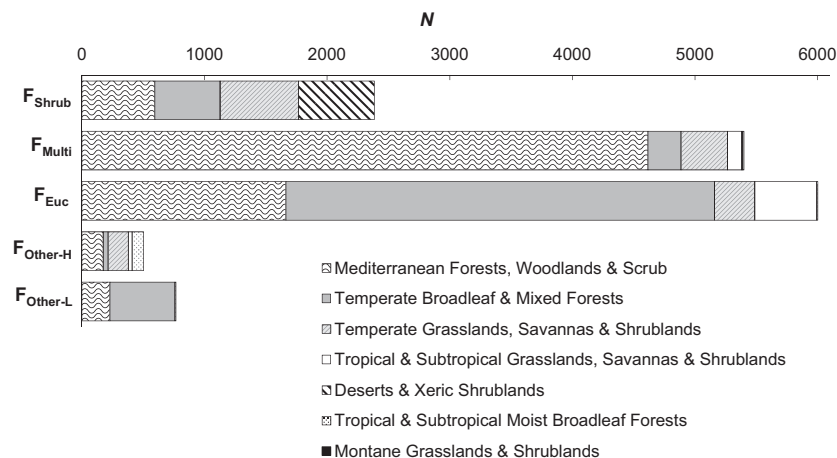

Fig. 2 Number of individuals (*N*) of each of the five plant functional types by ecoregion (Fig. 1).

Table 1 Characteristics of the entire data set (All$_{Universal}$), or for each of the five plant functional types. Abbreviations as follows: 'N', total number of individuals; 'D_{10}' or 'D_{130}', mean stem diameter measured over bark at 10 cm or 130 cm height above the ground, respectively; 'H', mean height of the tallest part of a tree or shrub, irrespective of branch architecture; 'ρ', mean stem wood density (based on limited direct measures with 88% derived from a global wood density database, see text); 'N sites', number of field sites from which the trees or shrubs were harvested; 'N spp.', number of species that were harvested; '%Age < 20 years', percentage of individuals from stands where age was known to be <20 years old; '%Managed', percentage of individuals from stands that were managed rather than naturally regenerated without human intervention; 'MAT', long-term mean annual temperature, averaged across sites from which individuals were harvested; and 'MAP', long-term mean annual precipitation, averaged across from which individuals were harvested. Where relevant, standard deviations (and for D_{10} and D_{130} the range in values) are provided in parentheses

Type	N	D_{10} (cm)	D_{130} (cm)	H (m)	ρ (g cm^{-3})	N spp.	N sites	%Age < 20 years	%Managed	MAT (°C)	MAP (mm yr^{-1})
All$_{Universal}$	15 054	15.2 (15.9; 0.3–203.4)	NA	7.0 (6.5)	0.77 (0.15)	274	826	64.4	71.6	16.8 (2.9)	619 (341)
F_{Shrub}	2383	7.2 (6.7; 0.3–50.0)	NA	2.4 (1.7)	0.74 (0.10)	77	144	51.0	41.4	18.2 (2.6)	539 (343)
F_{Multi}	5397	10.7 (6.8; 0.5–61.5)	NA	4.6 (2.5)	0.86 (0.11)	64	363	81.9	92.1	17.1 (1.9)	432 (158)
F_{Euc}	6004	21.7 (21.0; 0.9–203.4)	16.9 (17.5; 0.5–169.0)	10.5 (8.0)	0.77 (0.11)	95	225	53.2	62.7	16.1 (3.3)	791 (344)
$F_{Other-H}$	503	20.2 (17.2; 1.6–123.4)	16.0 (14.0; 0.9–102.0)	8.8 (5.7)	0.67 (0.17)	33	59	39.6	57.6	19.0 (3.3)	779 (572)
$F_{Other-L}$	767	17.1 (10.4; 2.3–60.4)	13.0 (9.1; 0.7–49.3)	9.2 (6.2)	0.40 (0.02)	5	35	90.0	100.0	14.2 (2.3)	733 (281)

regenerated shrubland, woodland, or forest) or managed (i.e. human-induced establishment via either nursery stock, direct seeding or human-induced natural regeneration). If the stand was managed, it was also recorded whether or not the stand was relatively young, defined as <20 years since establishment. Climatic data were collated (BoM, 2015; mean data based on 30-year period 1961–1990, resolution of approximately 2.5 km) and included long-term mean annual precipitation (MAP, mm yr^{-1}) and mean annual temperature (MAT, °C).

Measurements and data cleaning. Conventionally, tree diameter is measured at 130 cm (D_{130}) height above ground level to avoid marked stem buttress swelling or exposed lignotubers in some species and thus better represents the diameter of a log above the stump. Consequently, most trees (F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$) had D_{130} measurements. For species of F_{Shrub} and F_{Multi}, where D_{130} measurements introduced errors due to the presence of multiple stems at this height, or where the individual was too small to have a measurable D_{130}, D was typically measured at 10 cm height above the ground (D_{10}). For such multistemmed individuals, a single, pooled D estimate was obtained from the quadratic mean – representing the sum of the cross-sectional areas of individual stems (Chojnacky & Milton, 2008).

For many individuals in the data set, D was measured at multiple heights, allowing derivation of generic relationships for the prediction of D at a given height based on D measured at another height (Table S2). These relationships were used to 'gap-fill' D estimates where required, with D_{10} and D_{130} estimated for 33% and 14% of the 15 054 individuals, respectively. Similarly, generic relationships were derived to 'gap-fill' H estimates of an individual through the development of generic relationships between H and either D_{10} or D_{130} (Table S2). In this way, H was estimated for 15% of the individuals in the database. The wood specific gravity ρ was measured (or estimated based on local data) in only 8% (or 4%) of individuals in the data set. For individuals where ρ was unknown, values were derived based on the species (49% of the data set), or if unavailable, the genus (39% of the data set) using the global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009).

Very small individuals (i.e. D_{10} < 0.3 cm) were not included in the database. Such individuals are unlikely to conform to biomass scaling laws typical of woody plants given relatively little secondary thickening (e.g. Niklas, 2004; Enquist *et al.*, 2007). Data for a further 72 individuals from 51 sites (and 24 sources) were also excluded as outliers. Here, individuals were defined as outliers if their measured AGB$_{Indiv}$ fell outside the 99.9% confidence interval of prediction of the appropriate plant functional type model. Although the AGB$_{Indiv}$ of these outliers were assumed to come from a normally distributed population and had no major influence on model fit, they were nonetheless removed on the basis that they were highly unlikely values of AGB$_{Indiv}$ for the measured dimensions, and were most likely due to errors in data entry of field measurements.

Statistical analysis

A simple power-law allometric model was used to predict AGB_{Indiv} based on the explanatory variable, X (Eqn 1). Eqn 1 is linearized by logarithmic transformation (Eqn 2) so that coefficients (a and b) may be estimated using ordinary least squares linear regression analyses, with data corrected for heteroscedasticity, such that residual errors were normally distributed on the logarithmic scale (ε; which becomes a multiplicative error in the power model, ε', Picard *et al.* (2012)).

$$AGB_{Indiv} = aX^b + \varepsilon' \qquad (1)$$

$$\ln(AGB_{Indiv}) = \ln(a) + b\ln(X) + \varepsilon \qquad (2)$$

Xiao *et al.* (2011) found that Eqn 2 produced more accurate estimates of biomass than alternative nonlinear fitting. Equation 2 was applied to the entire data set (universal model, $All_{Universal}$) and to the data sets for each of the five plant functional types: F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$. The simplest versions of the models depicted by Eqn 2 had $X = D$, where D was D_{130} (or D_{10}) for F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$, and by necessity, D_{10} for F_{Shrub}, F_{Multi}, and hence, $All_{Universal}$.

When back-transforming from logarithmic to natural scales (i.e. to obtain the estimate of AGB_{Indiv}), a correction factor (CF) is required to remove bias. Nine different CFs were reviewed by Clifford *et al.* (2013), and the MM CF (Minimize Mean Square Error CF, Shen & Zhu, 2008) was recommended for predicting biomass of new trees or shrubs as it gave relatively low prediction bias. Because the value of the MM CF varies with D, a range of MM CF values are reported here. The more commonly used Baskerville CF (Baskerville, 1972, which assumes the variability is constant across D) may lead to biased AGB_{Indiv} estimates, particularly for individuals that have a D that is appreciably larger or smaller than the mean D used to develop the allometric model. But in this study the MM and Baskerville CFs were consistent, at least to two decimal places, due to our large sample sizes. Therefore, although the MM CF is recommended, we also report the Baskerville CF for reference.

To confirm the validity of tested models, we checked: (i) that there was no heteroscedasticity by confirming standardized residuals were not correlated with the $\ln(AGB_{Indiv})$, and (ii) for influential points (i.e. data points having a Cook's D value >1; Cook, 1979). Then, the performance of valid models was quantified using five fit statistics: (i) standard errors of the coefficients $\ln(a)$ and b, (ii) residual standard error of Eqn 2, RMSE, (iii) adjusted coefficient of determination, R^2, (iv) 95% confidence interval of the slope and intercept of the line of best fit to the plot of observed vs. predicted back-transformed AGB_{Indiv}, and (v) average bias, or mean of the residuals expressed in absolute terms and provided as a proportion (%) of the observed value (i.e. mean absolute prediction error 'MAPE', using back-transformed AGB_{Indiv} predictions) (Sileshi, 2014).

Additional measures of accuracy were used to aid comparisons among alternative models with differing numbers of variables. These included Mallows' Cp statistics (Mallows, 1973) and Akaike's information criterion (AIC, Burnham & Anderson, 2004). Models of poor fit have Cp values greater than the number of model parameters (including the intercept), while the lowest AIC indicates the most parsimonious model. The Bayesian information criterion (BIC) was also assessed (Burnham & Anderson, 2004), but not reported as it provided very similar indications to AIC.

Testing compound predictor variables including height and wood density. To explore whether accuracy of AGB_{Indiv} prediction could be improved using a compound predictor variable *cf.* D-alone, we tested three alternatives of X: (i) D-alone, based on a simple geometrical argument that should hold across forests (Chave *et al.*, 2005), (ii) the compound stem volume index D^2H, and (iii) the compound stem mass index $D^2H\rho$. We calculated for each data set, the change in fit statistics (*RSME*, R^2 and AIC) between the D-alone based model and each of the two alternative compound predictor variables, that is D^2H and $D^2H\rho$. For example, for the F_{Euc} model, changes in fit statistics were assessed for (F_{Euc} using D-alone) – (F_{Euc} using D^2H), and for (F_{Euc} using D-alone) – (F_{Euc} using $D^2H\rho$). To examine uncertainties associated with the inclusion of database-derived estimates, of H and ρ (Sileshi 2014), these analyses were repeated using subsets of data that only included individuals for which H was measured (when testing the D^2H predictor variable), or that only included individuals for which both H and ρ were measured (when testing the $D^2H\rho$ predictor variable).

Testing inclusion of site-factor predictor variables. General linear model analyses were used to assess whether accounting for site factors improved the performance of Eqn 2, as indicated by an improvement in the fit statistics of *RSME*, R^2 and AIC. The site factors tested included: (i) stand age (<20 years, or >20 years), (ii) management (natural or managed vegetation), (iii) ecoregion (Fig. 1), (iv) MAT, and (v) MAP. Interactions of these site factors with $\ln(D)$ were included in the model only where they were significant.

Testing levels of generalization. Three approaches were used to determine the impact of the level of generalization of allometric models (Eqn 2) on accuracy of AGB_{Indiv} prediction. First, using the entire data set, general linear model analysis was used to assess whether the fit statistics (*RSME*, R^2 and AIC) of $\ln(AGB_{Indiv})$ prediction from $\ln(D)$ could be enhanced by accounting for the supplementary categorical variable of plant functional type in the $All_{Universal}$ model. Second, using each data set of the five plant functional types, increases in such fit statistics were assessed when using the less generalized plant functional type model rather than the $All_{Universal}$ model. Third, the 53 species that had $N > 50$ (and which thus provided reasonable prediction of AGB_{Indiv} given population level variability, Roxburgh *et al.*, 2015) were used to examine improvement in accuracy with decreasing level of generalization in allometric models. We calculated for each species data set, the change in fit statistics (*RSME*, R^2 and AIC) between the $All_{universal}$ model and each of the two levels of generalizations, that is functional types model and species-specific model. For example, for a species of eucalypt such as

E. wandoo, changes in fit statistics were assessed for (F_{Euc}) – (All_{universal}), and for (Species-specific model for *E. wandoo*) – (All_{universal}).

Model performance

One concern with the application of generalized (multispecies) allometric models, such as those based on plant functional type, is that not all species are well represented by the model. In some cases, this may lead to significant bias. To test bias frequency, predicted AGB_{Indiv} (and its associated 95% confidence interval) was attained at D_{10} values of 10, 50 and 100 cm using both species-specific models and the more generalized plant functional type or universal models. If the 95% confidence interval of prediction using a generalized model largely overlapped with that from the most accurate model (species-specific) for that species, then it was assumed that significant bias had not been introduced.

As a final test of accuracy of allometric models, results were collated from 17 stands of contrasting structure and environment where whole plots of vegetation were harvested to obtain 'true' and direct measurements of stand-based AGB_{Stand} (Table 2). Inventories of species and D from each of these 17 stands were used to apply the models of best fit identified in this study and to sum the predicted AGB_{Indiv} to facilitate a comparison of observed and predicted AGB_{Stand}. The relationship between observed and predicted AGB_{Stand} was used to determine the overall accuracy and bias of generalized predictions at the stand-scale. These predictions were made using three scenarios where the level of generalization of the applied models differed. In the first scenario, we used species identity of each individual to apply the relevant species-specific model and then sum individual tree biomass to estimate AGB_{Stand}. For species where no species-specific model was available, the appropriate plant functional type model was applied. Second, species identification and/or species-specific models were assumed to be unavailable, and so only plant functional type models were applied. Third, species identification, and models based on species or plant functional type models were assumed to be unavailable, and so the universal model (All_{universal}) was applied. Using plots of observed vs. predicted AGB_{Stand}, the 1:1 line was used to indicate the distribution of residuals, and display any bias. Model efficiencies (*EF*, Soares *et al.*, 1995, expressed as a percentage) were used to assess whether the prediction performance differed among the three scenarios. In addition, we calculated slope and intercept of the line of best fit between observed and predicted AGB_{Stand}, and the resulting prediction quality statistics RMSE and MAPE, for each of the three scenarios.

Results

Allometric models

Even when based on D-alone, the model (Eqn 2) precisely predicted AGB_{Indiv} across the entire database using either All_{universal}, or any of the five categories of plant functional types: F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ (Fig. 3). The amount of variation in $\ln(AGB_{Indiv})$ explained by these simple generalized models was 94–98%, with errors (RMSE) of 0.19–0.49 (Table 3). Back-transformation of $\ln(AGB_{Indiv})$ predictions (using the MM correction factor) indicated relatively high uncertainty in the prediction of AGB_{Indiv} for any given tree or shrub of a given D (see 95% confidence intervals of prediction, Fig. 4). However, these individual errors largely cancel out when predictions are made across a wide range of data. Thus, these generalized models provided reasonable accuracy across the data sets, explaining 84–96% of variation in AGB_{Indiv} (Fig. 4), with a MAPE range of 15–41% (Table 3).

There was some evidence that the simple power-law allometric model was not appropriate for $F_{Other-L}$ plant functional types, with underprediction of AGB_{Indiv} in larger trees and overprediction of AGB_{Indiv} in smaller trees. However, if small saplings ($D_{130} < 10$ cm) were excluded, the performance of the power-law model was satisfactory, with the RMSE of $\ln(AGB_{Indiv})$ prediction decreasing from 0.273 (data not shown) to 0.189 (Fig. 3).

Compound predictor variables including height and wood density

Addition of H and/or ρ in a compound predictor variable in Eqn 2 did not markedly influence model performance compared with the D-based model in predicting $\ln(AGB_{Indiv})$, with changes in RMSE and R^2 less than ± 0.06 and ± 0.02, respectively (Table 4). Similar results were obtained for a subset of the data for which H or ρ were measured rather than derived from the global database (see values in parentheses, Table 4), noting that tests of ρ inclusion were based on limited data because only 12% of the data set had measured ρ values.

Inclusion of site-factor predictor variables

Since the addition of H and/or ρ in a compound predictor did not markedly influence performance of the D-based model in predicting $\ln(AGB_{Indiv})$, only models based on D were used to test the benefits of including site-factor predictor variables. When compared to using D-alone, accounting for site factors resulted in negligible model improvements, with the increase in explained variation of $\ln(AGB_{Indiv})$ being consistently <0.4% (Table 5). For example, accounting for whether or not the individual was from a young (<20 years old) stand, or whether or not the individual was from a stand that was managed, resulted in RMSE and AIC decreases of <0.03 and <5%, respectively. Furthermore, these site factors had negligible influence across all

Table 2 Summary of the main characteristics of 17 contrasting stands where whole-plot AGB_{Stand} harvesting was used to test the accuracy of generalized allometric models

Site	Location (decimal degrees)	AGB_{Stand} (Mg ha^{-1})	MAP (mm)	Plot N	Area (ha)	Stand density (individuals ha^{-1})	BA (m^2 ha^{-1})	Tree N	Age (year)	Type of stand
Pepal*	−33.4865 S, 117.7912 E	20.87	406	3	0.04	1863	8.71	77	11	A
Bird*	−32.8515 S, 117.5892 E	37.68	376	3	0.03	1356	11.92	38	11	A
Quicke*	−32.6736 S, 118.2361 E	77.63	339	3	0.02	1894	25.55	29	14	A
Temby*	−33.1457 S, 117.7187 E	22.61	353	3	0.03	1433	6.92	44	16	C
Angel*	−30.1970 S, 117.1160 E	9.93	297	3	0.03	1100	3.45	34	16	C
Brotherony*	−33.1368 S, 146.6380 E	20.60	378	6	0.09	1233	4.92	107	7	D
Gumbinnen†	−36.2447 S, 141.8148 E	19.13	347	6	0.22	2282	4.38	523	10	E
Moorland B†	−35.3377 S, 139.6317 E	18.63	370	4	0.25	244	2.88	88	15	E
Moorland A†	−35.3377 S, 139.6317 E	19.95	370	4	0.25	139	2.52	50	20	E
Strathearn†	−35.0485 S, 149.2325 E	38.88	637	12	0.48	2827	11.37	1499	15	E
Moir†	−34.2809 S, 118.1820 E	42.38	439	12	0.48	2708	4.72	1449	20	E
Jenharwill†	−36.3958 S, 144.4304 E	69.12	406	6	0.05	6456	16.92	304	12	B
Leos†	−37.8381 S, 147.7582 E	113.60	626	10	0.11	845	26.61	96	16	B
McFall†	−33.7290 S, 117.3217 E	189.55	438	3	0.03	2440	30.50	111	22	B
Mogo‡	−35.7333 S, 150.0667 E	212.87	1090	1	0.51	410	29.70	209	MA	F
Clyde‡	−35.4500 S, 150.2000 E	270.48	1173	1	0.63	248	32.10	156	MA	F
Flat Rock‡	−35.4167 S, 150.3000 E	355.53	1226	1	0.45	360	42.91	162	MA	F

Abbreviations included: Location, latitude and longitude; AGB_{Stand}, measured stand-based above-ground biomass; MAP, mean annual precipitation; Plot N, plot area and number; Area, total area harvested across all plots within the stand; Stand density, number of individuals per hectare of the stand, often based on measurements taken from a larger number of plots than those used for direct measurement of biomass; BA, site average basal area; Tree N, number of live trees measured, including relatively small shrubs that were measured in bulk; Age, age of the stand, where 'MA' refers to mixed aged stands; Type of Stand, where A refers to 'Belt monoculture planting of *E. loxophleba*', B refers to 'Belt planting of mixed species', C refers to 'Block monoculture planting of *E. loxophleba*', D refers to 'Block monoculture planting of *E. polybractea*', E refers to 'Block planting of mixed species', and F refers to 'Block native forest of mixed species'. Regardless of whether stands were established in belts or block configuration, plot area calculations (ha) were based on the assumption that the outer edge of the plot was ½ the between-row distance out from the outer row of trees.

*Paul *et al.* (2013b); †Paul *et al.* (2013a); ‡Ximenes *et al.* (2006) and R. Waterworth, in preparation.

models based on plant functional types where a majority of the individuals were from young planted stands (e.g. F_{Multi}, $F_{Other-H}$, $F_{Other-L}$). Accounting for ecoregion reduced RMSE by <0.03% and AIC by <8%. If ecoregion was added as supplementary variable, Cp was sometimes greater than the number of explanatory variables used, suggesting a poor model fit. Inclusion of numerical variables of MAT or MAP led to even less improvement in predictions, with RMSE reduced by <0.01%, AIC reduced by <3%.

Levels of generalization

Addition of plant functional type as a categorical explanatory variable improved performance of the $All_{Universal}$ model (RMSE reduced by 0.04, R^2 increased by 0.01%, and negative changes in AIC, Table 6). As further evidence of improvements in prediction accuracy by reducing level of generalization, there was a

consistent increase in fit statistics when, for each plant functional type, the relevant plant functional type model was applied in place of the $All_{Universal}$ model. When generalizing at the level of plant functional type, there was a decrease in the RMSE of 0.01–0.25, with R^2 increasing by 0.00–0.05% (Table 6). Gains in accuracy when generalizing at the plant functional type level were particularly pronounced for $F_{Other-L}$ (or F_{Multi}) where increases in RMSE were 0.25 (or 0.05), compared to <0.02 for the other categories of plant functional type. When considering the reduced data set for $F_{Other-L}$ (i.e. excluding saplings with $D_{130} < 10$ cm, $N = 455$), gains in accuracy were similarly large when using a model specific for that data set than when applying the $All_{Universal}$ model (i.e. ΔRMSE of −0.162, ΔR^2 of 0.150, data not shown).

Although results are not shown here, generalizing at the level of subcategories of plant functional type (Fig. S1) showed little or no improvement in accuracy
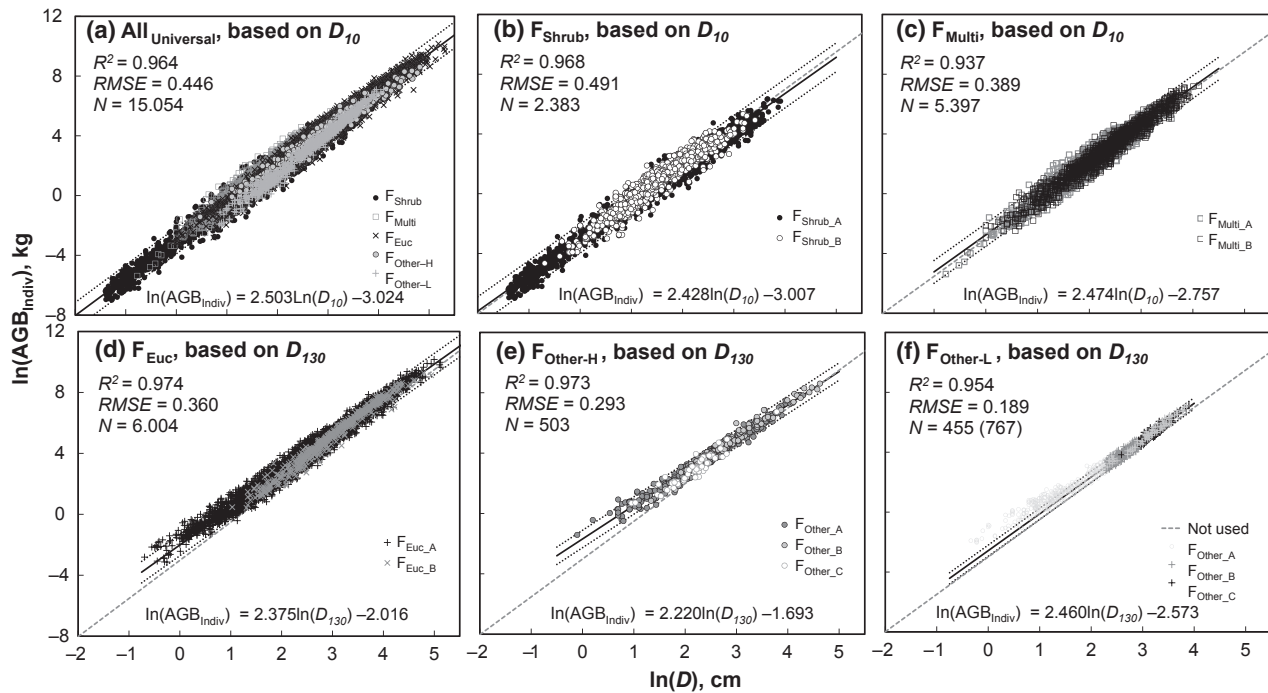
Fig. 3 Generic allometric equations for prediction of total above-ground biomass (ln(AGB$_{Indiv}$)) from stem diameter (ln(D), at 10 cm, D_{10}, or at 130 cm, D_{130}) of: (a) all individuals All$_{Universal}$; (b) shrubs and small trees (F_{Shrub}); (c) multistemmed trees (F_{Multi}); (d) single-stemmed eucalypt trees (F_{Euc}); (e) other single-stemmed trees of relatively high wood density ($F_{Other-H}$); and (f) other single-stemmed trees of relatively low wood density ($F_{Other-L}$). Black solid lines represent the model of best fit, and dotted lines the 95% prediction interval. Different symbols for the scatter points represent the different categories of plant functional types (in (a)) or subcategories of plant functional types (b-g) as defined in Fig. S1. Grey dashed lines in plots b-g represent predictions obtained using the All$_{Universal}$ model based on D_{10}. Data sets with D_{130} < 10 cm were not used in the $F_{Other-L}$ model.

of ln(AGB$_{Indiv}$) predictions when compared to those obtained when using models generalized at the level of plant functional type.

As expected, when applied to data sets restricted to focal species, the greatest accuracy of prediction in ln(AGB$_{Indiv}$) was attained using the least generalized model – that is models specific to a given species. Compared to the All$_{Universal}$ model, plant functional type models yielded some modest improvements, but were still not as good as species-specific models (Table 7). Gains in accuracy of ln(AGB$_{Indiv}$) predictions could be made by reducing the level of generalization from functional type to species, especially for F_{Shrub} and F_{Euc}.

Model performance

Figure 5 illustrates the overlap of the 95% confidence interval of generalized model prediction with that attained using the species-specific model for predicting ln(AGB$_{Indiv}$) under the scenarios of assuming an observed D_{10} of 10 cm, and where available, also, 50 and 100 cm. On average, 74% (SD 14%) of the confidence interval of prediction obtained using the models

generalized at the level of plant functional type overlapped with that attained using the species-specific model. Tested against the All$_{Universal}$ model, this figure decreased to 67% (SD 13%), largely because two key species of $F_{Other-L}$ were relatively poorly represented by the All$_{Universal}$ model. However for most tested species, results were similar (with mean ±8%, SD 5%) when comparisons were made between the confidence intervals of species-specific models and two alternative, more generalized models.

Of the 53 species tested, only four (or 8%) had <55% overlap in confidence intervals of prediction obtained using generalized and species-specific models under the scenario common for all test species; D10 of 10 cm. These four species were *Acacia calamifolia*, *Eucalyptus vegrandis*, *E. pilularis* and *E. muelleriana*. For *Acacia calamifolia*, this was partly attributable to the relatively low RMSE of prediction of the species-specific model resulting in relatively small confidence intervals of prediction relative to the more generalized models. However, generalized multispecies models poorly represented the allometry of all four of these species, indicating potential for significant bias in up to 8% of the tested species.

Table 3 Fitted coefficients (and standard errors) and fit statistics of three levels of generalized allometric models for AGB_{Indiv} of the form given in Eq. 2, and using a predictor of D measured at either 10 or 130 cm height. Here RMSE, R^2, CF, MAPE and N refer to the standard error of the linear regression, adjusted coefficient of determination, bias correction factor, mean absolute percentage error (based on back-transformed AGB_{Indiv} predictions) and sample size, respectively. All equations fitted were highly significant ($P < 0.001$). The diameter range relevant to each model is indicated in brackets (assuming a D_{10} of 0.3 cm). Parameters and performance of the species-specific allometric models are provided in the Table S3

Model	D	ln(a)	b	RMSE	R^2	CF*	CF†	MAPE	N
$All_{Universal}$ ($D_{10} < 203$ cm)	D_{10}	−3.024 (0.010)	2.503 (0.004)	0.446	0.964	1.1042–1.1046	1.1013	40.7	15 054
F_{Shrub} ($D_{10} < 50$ cm)	D_{10}	−3.007 (0.017)	2.428 (0.009)	0.491	0.968	1.1268–1.1279	1.1281	39.3	2383
F_{Multi} ($D_{10} < 62$ cm)	D_{10}	−2.757 (0.020)	2.474 (0.009)	0.389	0.937	1.0775–1.0785	1.0787	33.5	5397
F_{Euc} ($D_{130} < 169$ cm)	D_{130}	−2.016 (0.013)	2.375 (0.005)	0.360	0.974	1.0664–1.0668	1.0668	34.5	6004
$F_{Other-H}$ ($D_{130} < 102$ cm)	D_{130}	−1.693 (0.043)	2.220 (0.016)	0.293	0.973	1.0407–1.0433	1.0436	25.3	503
$F_{Other-L}$ ($D_{130} < 49$ cm)	D_{130}	−2.573 (0.073)	2.460 (0.025)	0.189	0.954	1.0169–1.0179	1.0180	15.4	455‡

*Recommended MM CF.
†Simpler Baskerville CF for reference.
‡312 data sets with $D_{130} < 10$ cm excluded in this model.
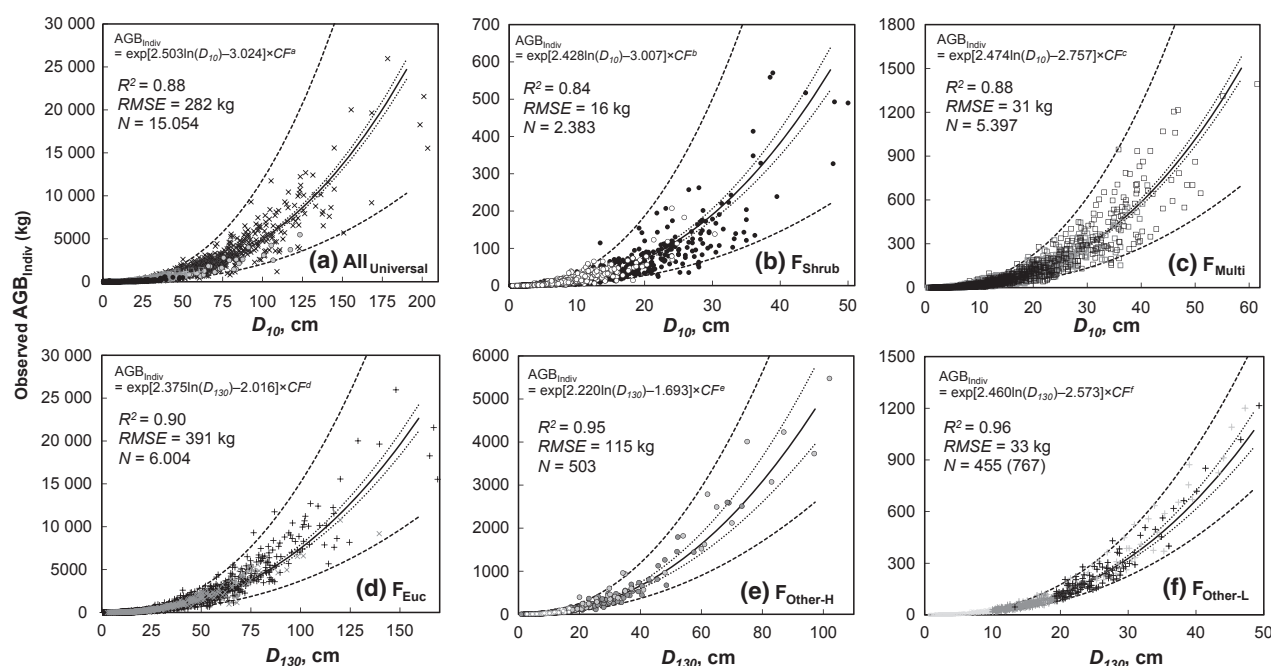
Fig. 4 Generic allometric equations for prediction of total above-ground biomass (AGB_{Indiv}) from stem diameter (D at 10 cm, D_{10}, or at 130 cm, D_{130}) of: (a) all individuals $All_{Universal}$; (b) shrubs and small trees (F_{Shrub}); (c) multistemmed trees (F_{Multi}); (d) single-stemmed eucalypt trees (F_{Euc}); (e) other single-stemmed trees of relatively high wood density ($F_{Other-H}$); and (f) other single-stemmed trees of relatively low wood density ($F_{Other-L}$). Back-transformed predictions were derived by applying the MM correction factor (CF), with superscripts a, b, c, d, e and f indicating CF ranges of 1.1042–1.1046, 1.268–1.1279, 1.0775–1.078, 1.0664–1.0668, 1.0407–1.0433, 1.0366–1.0378, respectively. Black solid lines represent the model of best fit, dotted lines represent the 95% confidence interval of fitting the model, and dashed lines represent the 95% confidence interval of prediction when applying the model. Different symbols for the scatter points represent the different categories of plant functional types (in (a)) or subcategories of plant functional types (b-f) as defined in Fig. S1. Data sets with $D_{130} < 10$ cm were not used in the $F_{Other-L}$ model. R^2 and RMSE refer to the linear regression of predicted vs. observed AGB.

When allometry-predicted AGB_{Stand} was compared to that observed by direct whole-plot harvesting across 17 contrasting stands (Table 2), prediction quality was not affected by increasing the level of generalization of models. Differences in efficiency of prediction of AGB_{Stand} were <1% between scenarios, while

differences in MAPE were <5.61% between scenarios (Fig. 6).

Despite good overall prediction quality, allometry-predicted AGB_{Stand} sometimes introduced significant bias, even when applying species-specific models. However, this bias was largely independent of the level of generalization of allometry applied. For example, for the Leos site, where measured AGB_{Stand} was 113.6 Mg ha^{-1} (Table 2), the absolute prediction error (or bias) was 24–36% regardless of the model applied.

Discussion

Allometric models

Results obtained here confirmed that a simple power-law model largely encapsulated scaling laws common to most woody plants (e.g. Niklas, 2004). There may be bias in AGB_{Indiv} prediction for any given individual tree or shrub. But across a wide range of individuals, AGB_{Indiv} may be predicted using generalized allometric models with reasonable accuracy (i.e. MAPE of 15–41% (Table 3), and RMSE of 16–391 kg and R^2= 0.84–0.96

(Fig. 4)) using D as an explanatory variable. Despite these models being based on AGB_{Indiv} data sets that were larger, and from a broader range of vegetation types than previously collated for Australia, the fit statistics obtained were comparable to generalized allometric models for AGB_{Indiv} previously developed for much smaller data sets (e.g. Williams *et al.*, 2005; Montagu *et al.*, 2005; Jonson & Freudenberger, 2011; Paul *et al.*, 2013a,b).

Our results suggest that increasing the domain of application of generalized allometric models for AGB_{Indiv} (i.e. being based on data sets from a wider range of ecoregions and from a range of plant types etc.) does not substantially jeopardize their accuracy of prediction. Our results provide further evidence of the effectiveness of generic AGB_{Indiv} allometric models developed from large, compiled data sets, consistent with comparable studies in tropical forests (Chave *et al.*, 2005, 2014; Vieilledent *et al.*, 2012); for different forest types in the U.S.A (Chojnacky *et al.*, 2014); and for different forest types in China (Ali *et al.*, 2015). Development of such generalized models is an appropriate approach to extending the geographical application

Table 4 Difference in fit statistics (RMSE, R^2 and AIC) when models based on D-alone were compared with models that used compound predictor variables. Values in parentheses are results obtained when only a subset of the data were used: those for which H was measured (for application in the models based on D^2H), or for which both H and ρ were measured (for application in the models based on $D^2H\rho$); these comparisons were based on relatively low N, particularly in relation to ρ (12% of all data). A negative change in AIC (ΔAIC) indicates that the first model is better than the second, and *vice versa* for positive ΔAIC values

Model	Comparison of models made	ΔRMSE	ΔR^2	ΔAIC	N
$All_{Universal}$	($All_{Universal}$ using D_{10}-alone) – ($All_{Universal}$ using D_{10}^2H)	−0.056 (−0.053)	0.010 (0.008)	−3539 (−2831)	15 054 (12 746)
	($All_{Universal}$ using D_{10}-alone) – ($All_{Universal}$ using $D_{10}^2H\rho$)	−0.027 (−0.062)	0.004 (0.003)	−1753 (−519)	15 054 (1723)
F_{Shrub}	(F_{Shrub} using D_{10}-alone) – (F_{Shrub} using D_{10}^2H)	−0.007 (0.003)	0.001 (0.000)	−72 (26)	2 383 (2191)
	(F_{Shrub} using D_{10}-alone) – (F_{Shrub} using $D_{10}^2H\rho$)	−0.013 (−0.044)	0.002 (0.005)	−121 (−73)	2383 (405)
F_{Multi}	(F_{Multi} using D_{10}-alone) – (F_{Multi} using D_{10}^2H)	0.013 (0.016)	−0.004 (−0.005)	370 (352)	5397 (4102)
	(F_{Multi} using D_{10}-alone) – (F_{Multi} using $D_{10}^2H\rho$)	0.013 (−0.062)	−0.004 (0.003)	364 (−519)	5397 (1723)
F_{Euc}	(F_{Euc} using D_{130}-alone) – (F_{Euc} using D_{130}^2H)	−0.048 (−0.048)	0.008 (0.007)	−1518 (−1306)	6004 (5326)
	(F_{Euc} using D_{130}-alone) – (F_{Euc} using $D_{130}^2H\rho$)	−0.042 (−0.004)	0.007 (0.001)	−1327 (−26)	6004 (947)
$F_{Other-H}$	($F_{Other-H}$ using D_{130}-alone) – ($F_{Other-H}$ using D_{130}^2H)	−0.080 (−0.095)	0.017 (0.020)	−244 (−249)	503 (440)
	($F_{Other-H}$ using D_{130}-alone) – ($F_{Other-H}$ using $D_{130}^2H\rho$)	−0.056 (−0.158)	0.011 (0.050)	−176 (−43)	503 (55)
$F_{Other-L}$	(F_{Other_L} using D_{130}-alone) – ($F_{Other-L}$ using D_{130}^2H)	−0.022 (−0.014)	0.003 (0.002)	−117 (−68)	767 (687)
	($F_{Other-L}$ using D_{130}-alone) – ($F_{Other-L}$ using $D_{130}^2H\rho$)	−0.013 (0.036)	0.002 (−0.012)	−71 (9)	767 (26)

Table 5 Fit statistics from general linear model analysis for assessing whether the allometric model represented by Eqn. 2 was improved by the inclusion of individual site factors (and their interactions with $\ln(D)$) as supplementary predictor variables. Factors tested included: (i) binary categorical variable {0,1} of stand age (Age < $20_{\{1,0\}}$: relatively young at <20 years, or older), (ii) binary categorical variable {0,1} of stand management (Managed$_{\{1,0\}}$: managed or 'natural'), (iii) categorical variable ecoregion (see Fig. 1), (iv) numerical variable of mean annual temperature (MAT), and (v) numerical variable of mean annual precipitation (MAP). Interactions of these site factors with $\ln(D)$ were included in the model only where they were significant. Numbers in parentheses are the number of parameters in the model (Cp values greater than this number indicate models of poor fit). 'n.s' indicates the variable effects were not statistically significant ($P > 0.05$). Note AIC can only be compared across categories where N is the same

Model	Variables	RMSE	R^2	Cp	AIC	N
All$_{Universal}$	$\ln(D_{10})$ alone	0.446	0.964	2.00 (2)	−24 334	15 054
	+ Age < $20_{\{1,0\}}$	0.444	0.965	4.00 (3)	−24 490	15 054
	+ Managed$_{\{1,0\}}$	0.444	0.965	4.00 (3)	−24 492	15 054
	+ Ecoregion	0.421	0.968	6.93 (9)	−26 097	15 054
	+ MAT	0.446	0.964	4.00 (3)	−24 385	15 054
	+ MAP	0.443	0.965	4.00 (3)	−24 573	15 054
F_{Shrub}	$\ln(D_{10})$ alone	0.492	0.968	2.00 (2)	−3383	2383
	+ Age < $20_{\{1,0\}}$	0.480	0.970	2.05 (3)	−3495	2383
	+ Managed$_{\{1,0\}}$	0.473	0.971	4.00 (4)	−3564	2383
	+ Ecoregion	0.465	0.972	6.77 (7)	−3644	2383
	+ MAT	0.483	0.969	4.00 (4)	−3470	2383
	+ MAP	0.486	0.969	4.00 (4)	−3441	2383
F_{Multi}	$\ln(D_{10})$ alone	0.389	0.937	2.00 (2)	−10 177	5397
	+ Age < $20_{\{1,0\}}$	n.s				
	+ Managed$_{\{1,0\}}$	n.s				
	+ Ecoregion	0.386	0.938	3.49 (6)	−10 263	5397
	+ MAT	0.384	0.939	4.00 (4)	−10 317	5397
	+ MAP	0.388	0.938	4.00 (4)	−10 211	5397
F_{Euc}	$\ln(D_{130})$ alone	0.360	0.974	2.00 (2)	−12 275	6004
	+ Age < $20_{\{1,0\}}$	0.331	0.978	2.61 (3)	−13 291	6004
	+ Managed$_{\{1,0\}}$	0.352	0.975	4.00 (4)	−12 532	6004
	+ Ecoregion	0.350	0.975	11.6 (7)	−12 591	6004
	+ MAT	0.359	0.974	4.00 (4)	−12 291	6004
	+ MAP	0.359	0.974	4.00 (4)	−12 312	6004
$F_{Other-H}$	$\ln(D_{130})$ alone	0.293	0.973	2.00 (2)	−1234	503
	+ Age < $20_{\{1,0\}}$	n.s				
	+ Managed$_{\{1,0\}}$	n.s				
	+ Ecoregion	0.290	0.974	5.92 (3)	−1244	503
	+ MAT	0.289	0.974	4.00 (4)	−1244	503
	+ MAP	0.290	0.974	4.00 (4)	−1241	503
$F_{Other-L}$	$\ln(D_{130})$ alone	0.273	0.979	2.00 (2)	−1987	767
	+ Age < $20_{\{1,0\}}$	0.257	0.982	4.00 (4)	−2078	767
	+ Managed$_{\{1,0\}}$	n.s				
	+ Ecoregion	0.272	0.980	6.12 (3)	−1996	767
	+ MAT	0.272	0.980	4.00 (4)	−1992	767
	+ MAP	0.264	0.981	4.00 (4)	−2038	767

range of otherwise limited, and often localized, species-specific models. Collation of data sets to develop such generalized allometric models seems preferable to either: (i) making parameters of existing localized species-specific models available in a database to facilitate the selection of the most appropriate models for new specific areas of interest (e.g. Ter-Mikaelian & Korzukhin, 1997; Zianis *et al.*, 2005; Henry *et al.*, 2013), or (ii) applying existing localized species-specific models to generate pseudo-observations to develop more generalized models (e.g. Pastor *et al.*, 1984; Zianis & Mencuccini, 2004; Muukkonen, 2007; Chojnacky *et al.*, 2014).

In the present study, allometry-predicted AGB$_{Indiv}$ tended to be least accurate for the multistemmed plant functional types of F_{Shrub} and F_{Multi} (Table 3). Although others (e.g. Buech & Rugg, 1995; Chojnacky & Milton, 2008; Paul *et al.*, 2013a,b; Berner *et al.*, 2015) also found D to be the strongest predictor of AGB$_{Indiv}$ in such multistemmed individuals, there are differences between studies in the way in which the

Table 6 Change in fit statistics (RMSE, R^2 and AIC) when the All$_{Universal}$ model was compared with either: (i) All$_{Universal}$ model with the inclusion of a categorical variables for the five categories of plant functional type, using the entire data set (first row), or (ii) less generalized models of plant functional type (F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ or $F_{Other-L}$) when applied against each of the plant functional type data sets. By necessity, all models here were based on D_{10}. A negative change in AIC (ΔAIC) indicates that the model being tested is better than the All$_{Universa}$ model

Data set	Model comparison	ΔRMSE	ΔR^2	ΔAIC	N
All$_{Universal}$	(All$_{Universal}$ + Types) – (All$_{Universal}$)	−0.040	0.006	−2836	15 054
F_{Shrub}	(F_{Shrub}) – (All$_{Universal}$)	−0.016	0.002	−155	2383
F_{Multi}	(F_{Multi}) – (All$_{Universal}$)	−0.050	0.017	−1311	5397
F_{Euc}	(F_{Euc}) – (All$_{Universal}$)	−0.020	0.004	−602	6004
$F_{Other-H}$	($F_{Other-H}$) – (All$_{Universal}$)	−0.008	0.002	−25	503
$F_{Other-L}$	($F_{Other-L}$) – (All$_{Universal}$)	−0.252	0.054	−1019	767

D of multistemmed individuals is estimated. Some workers (e.g. Mosseler *et al.*, 2014; Matula *et al.*, 2015) used D of only a given number (e.g. 3 or 5 stems) of the largest stems, yet did not test whether it resulted in an increased accuracy of prediction above that obtained if an equivalent D was calculated and applied. Hence, further work is required to assess alternative methods for calculating D in multistemmed individuals and determine the method that provides the highest accuracy of prediction of AGB$_{Indiv}$. There is also a need to have clear and consistent protocols for measurement of D.

Another aspect of these results that requires further investigation is whether there may be improvement on the simple power-law model for tree species of relatively low wood density. For the $F_{Other-L}$ category of species, a single simple power-law model did not accurately predict AGB$_{Indiv}$ across the full range of tree sizes. For these species, options for weighted nonlinear modelling should be investigated as an alternative to the power-law model provided here (i.e. for $F_{Other-L}$ trees of $D_{130} > 10$ cm).

Compound predictor variables including height and wood density

We found including H and ρ in addition to D in a compound predictor variable did not markedly improve ln (AGB$_{Indiv}$) predictions, even when using only measured values (Table 4). This finding supports the conclusions of others (e.g. Molto *et al.*, 2013; Sileshi, 2014; Kuyah & Rosenstock, 2015) that using D-alone is an appropriate predictor of AGB$_{Indiv}$ as it minimizes costs associated with these additional biometric measurements, and also the uncertainty resulting from measurement and prediction errors of H and/or ρ.

The fact that H is often correlated with D (e.g. Pérez-Cruzado & Rodríguez-Soalleiro, 2011; Mugasha *et al.*, 2013; Ishihara *et al.*, 2015) may largely explain why inclusion of H as an additional predictor did not mark-

edly influence the performance of the D-based models. Indeed, scaling theory of larger woody plants predicts that H scales with diameter to the 2/3 power (Niklas & Spatz, 2004). Nonetheless, although the inclusion of H may not be necessary to accurately predict AGB$_{Indiv}$, there is evidence that it may be beneficial to include in allometric models of foliage biomass, which tends to be influenced by plant architecture (e.g. Picard *et al.*, 2015).
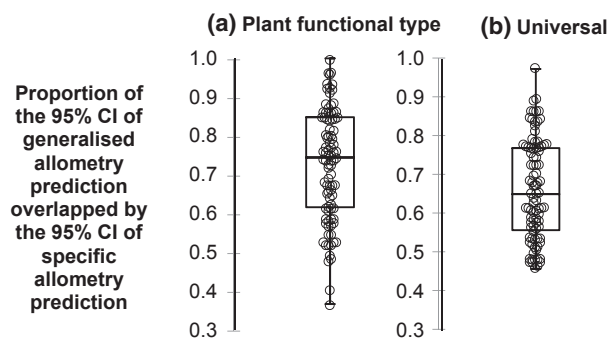
We make two suggestions as to why inclusion of ρ did not improve the predictive ability of the D-based model. The first is possible measurement errors. For example, ρ varies with height (e.g. Pérez-Cruzado & Rodríguez-Soalleiro, 2011; Wiemann & Williamson, 2014), and with stand age or rates of growth (e.g. Ilic *et al.*, 2000). Hence database-derived ρ values may have been erroneous due to the height and/or age at which ρ was measured (e.g. Molto *et al.*, 2013). Second, most of our data set was obtained from temperate regions, where ρ is typically less variable than, for example, among tropical trees (Swenson & Enquist, 2007). This is consistent with ρ having greater predictive potential in AGB$_{Indiv}$ models for tropical trees (Chave *et al.*, 2014) than was found in this study.

Inclusion of site-factor predictor variables

Our study indicated that including site-related factors such as characteristics of the stand (stand age and management), and climatic characteristics (e.g. MAP, MAT), did not markedly improve the predictive ability of D-based models (increased R^2 of <1%, Table 5). These results provided support to findings that while the allocation of AGB$_{Indiv}$ and plant architecture (i.e. the D-H relationship) may vary with site factors as individuals optimize their growth strategies, the impact on total AGB$_{Indiv}$ allometry appears to be negligible (e.g. António *et al.*, 2007; Peichl & Arain, 2007; Feldpausch *et al.*, 2011, 2012; Banin *et al.*, 2012; De Miguel *et al.*, 2014;

Table 7 Median changes in fit statistics (RMSE, R^2 and AIC) when the All$_{Universal}$ model was compared with less generalized models of either the relevant: (i) plant functional type model (F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ or $F_{Other-L}$), or (iii) model specific to the species level. These models relate to data from 53 species having sufficient data for species-specific allometric models ('N Species'), and by necessity, were based on D_{10}. Values in parentheses are standard deviations. N indicates the median number of individuals represented by each species within each grouping of the data set. A negative change in AIC (ΔAIC) indicates that the model being tested is better than the All$_{Universal}$ model, and *vice versa* for positive ΔAIC values

Data set	Model comparison	N Species	ΔRMSE	ΔR^2	ΔAIC	N
All$_{Universal}$	(Types) – (All$_{Universal}$)	53	−0.026 (0.072)	0.006 (0.052)	−12 (146)	111
	(Species) – (All$_{Universal}$)	53	−0.080 (0.095)	0.027 (0.049)	−43 (184)	111
F_{Shrub}	(F_{Shrub}) – (All$_{Universal}$)	8	−0.015 (0.066)	0.004 (0.036)	−9 (30)	115
	(Species) – (All$_{Universal}$)	8	−0.088 (0.122)	0.039 (0.059)	−65 (52)	115
F_{Multi}	(F_{Multi}) – (All$_{Universal}$)	12	−0.062 (0.091)	0.019 (0.043)	−31 (277)	130
	(Species) – (All$_{Universal}$)	12	−0.068 (0.085)	0.028 (0.039)	−40 (294)	130
F_{Euc}	(F_{Euc}) – (All$_{Universal}$)	28	−0.025 (0.057)	0.006 (0.022)	−12 (74)	81
	(Species) – (All$_{Universal}$)	28	−0.101 (0.090)	0.019 (0.042)	−42 (144)	81
$F_{Other-H}$	($F_{Other-H}$) – (All$_{Universal}$)	3	0.005 (0.016)	−0.003 (0.003)	4 (12)	84
	(Species) – (All$_{Universal}$)	3	−0.014 (0.013)	0.003 (0.002)	−5 (12)	84
$F_{Other-L}$	($F_{Other-L}$) – (All$_{Universal}$)	2	−0.168 (0.018)	0.127 (0.044)	−49 (6)	219
	(Species) – (All$_{Universal}$)	2	−0.182 (0.008)	0.133 (0.040)	−55 (2)	219

(a) Plant functional type **(b) Universal**

Proportion of the 95% CI of generalised allometry prediction overlapped by the 95% CI of specific allometry prediction

Fig. 5 Box plots describing the Proportion of the 95% confidence interval (CI) of generalized allometry prediction overlapped by the 95% CI of species-specific allometry prediction when the level of generalization was; (a) plant functional type, or (b) universal, All$_{Universal}$. These results are for prediction of ln (AGB$_{Indiv}$) using models (Eqn. 2) across 53 species and a total of 92 scenarios where D_{10} was assumed to be 10 cm ($N = 53$), 50 cm ($N = 28$), or 100 cm ($N = 11$). Note, species presented here are those reported in Table S3, each of which had an $N > 50$. Only species sampled to these larger sizes were represented in scenarios of D_{10} of 50 and 100 cm.

Gonzalez-Benecke *et al.*, 2014; Moncrieff *et al.*, 2014; Hulshof *et al.*, 2015). This may be due to the compensatory relationship between stem and canopy mass resulting in similar AGB$_{Indiv}$ for trees of the same D, but different partitioning to leaves, branches and stems (e.g. Kuyah *et al.*, 2013). Hence, results obtained here support the claim that generalized models can be based on plant functional types rather than site factors such as climatic zones (Ngomanda *et al.*, 2014).

These findings contrast with previous research showing that the inclusion of additional stand-related variables such as stand age, density and/or productivity in allometric models may provide more accurate AGB$_{Indiv}$ predictions (Callaway *et al.*, 1994; De Lucia *et al.*, 2000; Lopez-Serrano *et al.*, 2005; Genet *et al.*, 2011; Alvarez *et al.*, 2012). Such improvements are often interpreted as climatic impacts influencing predicted AGB$_{Indiv}$ via changes in the tree architecture (*H-D* relationship, e.g. Chave *et al.*, 2014) and have led to recent debates over potential trade-offs between practical application and loss of accuracy when simple power-law models are used in preference to more complex models of AGB$_{Indiv}$ (e.g. Sileshi, 2014; Picard *et al.*, 2015). Results obtained here indicate that this trade-off of loss of accuracy with the application of simple power-law models was relatively minor.

Levels of generalization

Compared with the most generalized model (All$_{Universal}$), the largest gains in predictive ability were attained when categorizing the data set at the level of species, but with little loss of accuracy when generalized to the level of plant functional type (Tables 6 and 7). These results were therefore consistent with previous work showing that generic multispecies models perform almost as well as the species-specific ones developed for that region (e.g. Feller, 1992; Williams *et al.*, 2005; Montagu *et al.*, 2005; Mugasha *et al.*, 2013; Paul *et al.*, 2013a,b; Mbow *et al.*, 2014; Ali *et al.*, 2015).

It is often suggested that plant functional attributes (e.g. ρ, apical dominance and canopy architecture) may
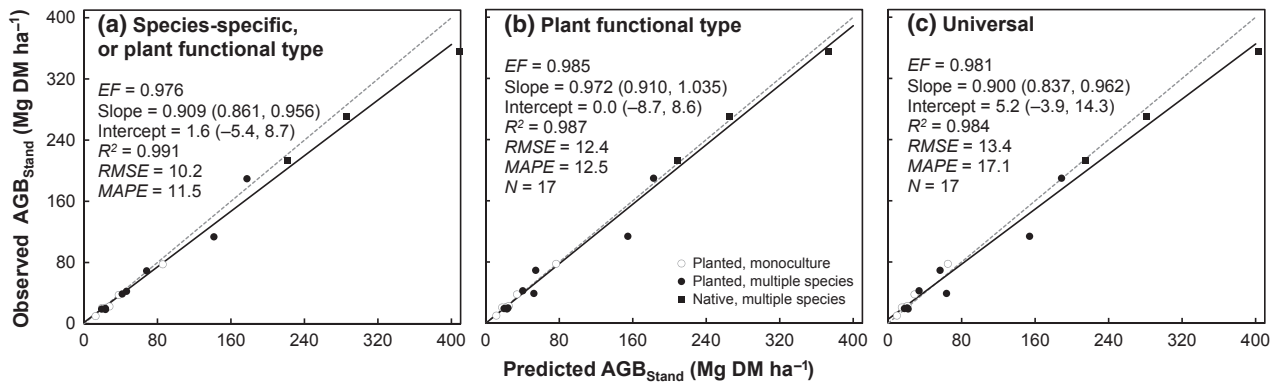
Fig. 6 Relationship between total above-ground biomass (AGB$_{Stand}$) from whole-plot harvesting at 17 contrasting stands (Table 2) and that predicted for those stands through the application of three scenarios of increasing generalization of allometric models applied. (a) information on species identity of each individual at each of the test sites was utilized, and for species that were represented by the 53 available species-specific models, these were applied (Eqn. 2 using parameters given in Table S3), while for all other species, the appropriate plant functional type model was applied (Eqn. 2 using parameters given for F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ in Table 3), (b) species identification and/or species-specific models were assumed to be unavailable, and so plant functional type models were applied (Eqn. 2 using parameters given for F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ in Table 3), and (c) species identification, species-specific models and plant functional type models were assumed to be unavailable, and so the universal model (All$_{Universal}$) was applied (Eqn. 2 using parameters given for All$_{Universal}$ in Table 3). In all scenarios, the MM correction factor was applied when back-transforming predictions. Grey dashed line represents the 1:1 line. Black solid line represents the line of best fit, with slope, intercept and fit statistics as shown. Values in parentheses are the 95% prediction interval of the slope and intercept.

be genetically constrained as a result of adaption to environmental factors (e.g. Van Gelder *et al.*, 2006; Onoda *et al.*, 2010; Banin *et al.*, 2012). Such phylogenesis may account for differences in the AGB$_{Indiv}$ allometry between trees and shrubs found here, and by others (e.g. Paul *et al.*, 2013a). Species of F_{Shrub} of relatively large size (e.g. D_{10} ca. 30–90 cm) had slightly lesser AGB$_{Indiv}$ than trees of the same D (Fig. 3). In contrast, multistemmed species (F_{Multi}) tended to have relatively high AGB$_{Indiv}$ for a given D (Fig. 3). This may be attributable to their typical architecture of a large proportion of relatively heavy branches/small stems (e.g. Paul *et al.*, 2013b) of relatively high ρ (Table 1).

Although including ρ in compound predictor variables offered no measurable improvement to D-based models (Table 4), phylogenesis resulting in divergent stem anatomy and ρ may also largely account for the differences in AGB$_{Indiv}$ allometry between angiosperms and gymnosperms found here (i.e. $F_{Other-L}$ departing strongly from the All$_{Universal}$ model, Tables 6 & 7) and by others (e.g. Chojnacky *et al.*, 2014; Hulshof *et al.*, 2015). Lower average values of ρ for species of $F_{Other-L}$ (Table 1) explain why, for a given D, the AGB$_{Indiv}$ was relatively low when compared to most other tree species, particularly F_{Euc} (Fig. 3). Although less evident from ρ measurement and estimates collated due to the high uncertainties in these data sets, such differences in stem anatomy may also be one of the reasons why species of F_{Euc} (average ρ 0.77 g cm^{-3}, Table 1) of large

size (e.g. $D_{10} > 50$ cm) had relatively high AGB$_{Indiv}$ for a given D when compared to species of $F_{Other-H}$ (average ρ 0.67 g cm^{-3}, Table 1) (Fig. 3).

There is evidence that ρ varies greatly among species in Australia (e.g. Onoda *et al.*, 2010). Further refinement and consistency in protocols used to measure ρ is required to confirm whether, as observed by others (e.g. Van Breugel *et al.*, 2011; Fayolle *et al.*, 2013; Chojnacky *et al.*, 2014), ρ may be more similar within than between different plant functional types, resulting in each having a unique AGB$_{Indiv}$ allometry. Hence, although ρ was found not to impact the model directly via a compound predictor variable, it may nonetheless have an indirect impact via influencing categories (i.e. groups of species, or plant functional types) upon which generalized models are developed.

Model performance

Species data sets for which we had confidence in prediction of AGB$_{Indiv}$ using species-specific models (i.e. 53 species where $N > 50$) provided a test for bias in predictions with the application of more generalized models. Most (92%) demonstrated no significant bias, with the 95% confidence interval of prediction obtained using generalized allometry largely overlapping with that attained using the species-specific model (Fig. 5). In contrast, species-specific models appeared to avoid risks of significant bias in AGB$_{Indiv}$ in about 8% of the

species studied. Thus, to minimize the potential for significant bias when accurate predictions are required at the *individual* level, representative species-specific models (i.e. $N > 50$, Roxburgh *et al.*, 2015) should be used when these are available (e.g. Table S3). However because allometry-predicted AGB_{Indiv} are generally used to derive AGB_{Stand}, user decision on whether the additional costs associated with developing new species-specific models is justified should be based on the extent to which these more specific models improve accuracy (and particularly, reduce bias) at the *stand* level.

Stand-level validation of allometric models showed that there was relatively little added benefit (*EF* of AGB_{Stand} prediction increasing by <1%, and RMSE and MAPE decreasing by <3.2 Mg ha^{-1} and <5.6%, respectively) of using species-specific models when compared to more generalized models (Fig. 6). The stand of Leos (observed AGB_{Stand} of 113.6 Mg ha^{-1}) remained an outlier regardless of which level of generalization was used in the allometric models applied to individuals in this stand. These results indicate that a good *individual*-level model does not necessarily translate into much improved *stand*-level predictions. Hence, when allometry-predicted AGB_{Stand} estimates are required for new stands, added field-measurement costs and model uncertainty associated with obtaining species-specific data and calibrating model coefficients for each new species-specific model are generally unwarranted. Costs and possible uncertainties in stand-based estimates can be minimized through the application of more generalized models that are based on a much smaller number of parameters (e.g. only two when applying the most generalized model), irrespective of the number of species within the stand.

In summary, this study has advanced the development and testing of generalized allometric models for prediction of total AGB_{Indiv} for a wide range of plant functional types found across a diversity of ecoregions in Australia. Simple power-law generic models were precise, even when based on trunk diameter as the sole predictive variable. Given the insubstantial influence of site factors (e.g. whether the stand was relatively young or managed, ecoregion, MAP and MAT) on AGB_{Indiv} allometry, a next line of enquiry is to rigorously evaluate this finding by extending the replication of individuals from some of the relatively undersampled combinations of plant functional type and ecoregion (e.g. individuals of $F_{Other-H}$ from tropical and subtropical regions, Fig. 2) or stand-types (e.g. individuals of F_{Multi} from relatively mature and unmanaged stands).

Results obtained from validation of allometric models against 17 stands that had AGB_{Stand} directly measured showed that the application of more generalized

allometric models resulted in predictions of stand-level AGB that were almost as accurate as species-specific models. Furthermore, it is possible that for stands of mixed species, due to the smaller sample size and larger overall number of model coefficients to parameterize, uncertainties associated with the propagation of errors (including measurement, model-fitting and prediction errors) may be larger with the application of multiple species-specific models compared with a single generalized multispecies model. This hypothesis is being tested in a forthcoming paper. Additionally, sample sizes of >50 are required for constructing each species-specific model (Roxburgh *et al.*, 2015), resulting in significant costs associated with development of models for each new species. For such mixed-species stands, likely higher uncertainties and costs negate the slight gain in average accuracy of AGB_{Stand} prediction when applying multiple species-specific models when compared to a generalized multispecies model.

It is therefore recommended that generalized multispecies models be applied when cost-effective predictions of AGB_{Stand} are required across multiple mixed-species stands. The most generalized model ($All_{Universal}$) tested here was based on D_{10} by necessity, and yet D measurement at this height is known to be suboptimal for many single-stemmed tree species. Hence for practical reasons, models generalized at the level of plant functional groups (Eqn 3a–e, reported here using the Baskerville CF) are recommended for application in both Australia and for validation in similar ecoregions in other continents.

$$AGB_{Indiv}(kg) \text{ of } F_{Shrub} = \exp[-3.007 + 2.428 \ln(D_{10})] \times 1.128,$$
$$(3a)$$

$$AGB_{Indiv}(kg) \text{ of } F_{Multi} = \exp[-2.757 + 2.474 \ln(D_{10})] \times 1.079,$$
$$(3b)$$

$$AGB_{Indiv}(kg) \text{ of } F_{Euc} = \exp[-2.016 + 2.375 \ln(D_{130})] \times 1.067,$$
$$(3c)$$

$$AGB_{Indiv}(kg) \text{ of } F_{Other-H} = \exp[-1.693 + 2.220 \ln(D_{130})] \times 1.044,$$
$$(3d)$$

$$AGB_{Indiv}(kg) \text{ of } F_{Other-L} = \exp[-2.573 + 2.460 \ln(D_{130})] \times 1.018,$$
$$(3e)$$

There are two exceptions to the recommendation of application of Eqn. 3. First, where the trade-off between accuracy and cost effectiveness is relatively high, such

as when estimating AGB$_{Stand}$ for a given high carbon stand comprising only one or two dominant species. In such circumstances, additional costs associated with obtaining species-specific models may warrant the improved accuracy of AGB$_{Stand}$ prediction. Second, where AGB$_{Stand}$ is required for stands dominated by species suspected of not conforming to the generalized plant functional groups models. Another line of enquiry to pursue is to build improved species-specific models to expand the testing done here that found 8% of species did not conform to generalized plant functional type models.

As with all allometric models, to avoid bias in AGB$_{Indiv}$ predictions, recommended models in this study should only be applied within their valid diameter range as indicated by the maximum D sampled (e.g. Table 3, Table S3). Further sampling is required to extend the D range of allometric models both to increase the replication (and confidence) of prediction of larger sized trees ($D_{130} > 50$ cm) and to account for some of the variation in AGB$_{Indiv}$ due to hollows or piping of larger overmature trees or trees affected by termites (e.g. Rayner *et al.*, 2014; Monda *et al.*, 2015).

Acknowledgements

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Supporting Information

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

Table S1 Number of individuals obtained for each plant functional type from various sources.

Table S2. Empirical relationships used to 'gap fill' missing D and H measurements using the equation $Y = c + d\, X$, where X may be D (cm) or H (m).

Table S3. The fitted coefficient (and their standard errors) and fit statistics of each of the 53 species in the dataset that had $N > 50$, and thus, for which species-specific allometric models for AGB_{Indiv} of the form given in Eq. 2 could be developed.

Fig S1 Diagram depicting the categorization of vegetation into five categories of functional type, and how these were further subdivided into subcategories and species in order to assess four levels of generalization of allometric models of AGB; (i) universal ($All_{Universal}$), (ii) functional type (F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$), (iii) functional type subcategory (F_{Shrub_A}, F_{Shrub_B}, F_{Multi_A}, F_{Multi_B}, F_{Euc_A}, F_{Euc_B}, $F_{Other-H\_A}$, $F_{Other-H\_B}$, $F_{Other-H\_C}$, $F_{Other-L\_A}$, $F_{Other-L\_B}$, and $F_{Other-L\_C}$), and (iv) species, of which only 53 species of the 274 studied were adequately sampled (i.e. $N > 50$).