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## **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 prediction above-ground biomass. 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; multi-stemmed 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 generalisation (species-specific, plant functional type) were validated using whole-plot harvest data from 17 contrasting stands (range: 9 to 356 Mg ha<sup>-1</sup>). Losses in efficiency of

prediction were < 1% if generalised models were used in place of species-specific models. Furthermore, application of generalised multi-species 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 ( $AGB_{\text{Indiv}}$ , oven-dry weight of an individual plant). The first is

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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 ( $\rho$ ) are also often considered, since  $D^2H\rho$  is expected to strongly correlate with  $AGB_{\text{Indiv}}$  (e.g. Chave *et al.*, 2005). The second decision relates to the level of generalisation to be used. Most allometric models are based on relatively small species-specific datasets obtained from local areas, and often ignore variation across both species and sites (Henry *et al.*, 2011; de Miranda *et al.*, 2014).

Localised species-specific models provide the most accurate estimates of  $AGB_{\text{Indiv}}$  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.

Generalised allometric models can greatly simplify  $AGB_{\text{Indiv}}$  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 then be used to re-parameterise new broadly applicable models (e.g., Brown *et al.*, 1989; Jenkins *et al.*, 2003; Moore 2010; Paul *et al.*, 2013a,b; Chave *et al.*, 2005, 2014; 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%) localised 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  $AGB_{\text{Indiv}}$  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), multi-stemmed *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 multi-species allometric models introduces bias to  $AGB_{\text{Indiv}}$  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  $AGB_{\text{Indiv}}$  using generalised models.

At the scale of individual plants, allometry-predicted  $AGB_{\text{Indiv}}$  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 ( $AGB_{\text{Stand}}$ ) 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-Yrizar, 2011; Paul *et al.*, 2013a), but not using generic allometric models.

Australia provides a good case study for testing generalised allometric models given it has both a long history of research contributing to  $AGB_{Indiv}$  datasets (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 multi-stemmed trees through to some of the largest trees in the world (e.g. Sillett *et al.*, 2015; Specht & Specht, 2002, Specht & Specht, 2013). Improving methods for quantifying biomass and its carbon content in Australia is also of global significance given high inter-annual 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  $AGB_{Indiv}$  dataset of unprecedented size was compiled, composed of 15,054 destructively-measured individuals from both managed (i.e. planted) and natural ecosystems across Australia. This dataset 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 secondly, 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

### *Dataset*

Datasets of  $AGB_{\text{Indiv}}$  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 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  $AGB_{\text{Indiv}}$  given population level variability (Roxburgh *et al.*, 2015). To utilise the wider dataset, we categorised all species into plant functional types as described below.

### *Plant functional types*

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



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characteristic of species within  $F_{\text{Shrub}}$ , while a unique characteristic of conifer species within  $F_{\text{Other-L}}$  is a relatively low wood density. By comparison, such distinctions were less obvious between the three categories of trees of relatively high wood density ( $F_{\text{Multi}}$ ,  $F_{\text{Euc}}$  and  $F_{\text{Other-H}}$ ), with their categorisation 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  $F_{\text{Multi}}$  category having different predictor variables to that of the other two hardwood tree categories. When compared to single-stemmed trees, multi-stemmed 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  $F_{\text{Other-H}}$  was segregated from the much more widely sampled  $F_{\text{Euc}}$  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 dataset comprised two categories of plant functional types, namely  $F_{\text{Euc}}$  (40%) and  $F_{\text{Multi}}$  (36%), largely representing the ecoregions that supported either ‘Mediterranean forests, woodlands and scrub’, or ‘Temperate broadleaf and mixed forests’ (Fig. 2). Although  $F_{\text{Other-L}}$  represented only 5% of the dataset, this category was also largely found in these two ecoregions. In contrast,  $F_{\text{Shrub}}$  and  $F_{\text{Other-H}}$  comprised 16% and 3% of the dataset, respectively, but were sourced from a wide range of ecoregions.

### *Explanatory variables*

The primary set of collated data included three explanatory variables for  $\text{AGB}_{\text{Indiv}}$ : stem diameter ( $D$ , over bark, cm), height ( $H$ , m) and, as described below, measured, estimated or derived basic density of stem wood ( $\rho$ ,  $\text{g cm}^{-3}$ , 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 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,  $\text{mm yr}^{-1}$ ) and mean annual temperature (MAT,  $^{\circ}\text{C}$ ).

### *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 ( $F_{\text{Euc}}$ ,  $F_{\text{Other-H}}$  and  $F_{\text{Other-L}}$ ) had  $D_{130}$  measurements. For species of  $F_{\text{Shrub}}$  and  $F_{\text{Multi}}$ , 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 multi-stemmed 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 dataset,  $D$  was measured at multiple heights, allowing derivation of generic relationships for 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  $\rho$  was measured (or estimated based on local data) in only 8% (or 4%) of individuals in the dataset. For individuals where  $\rho$  was not measured, estimates were derived based on the species (49% of the dataset), or if unavailable, the genus (39% of the dataset) using the global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009).

Very small individuals (i.e.  $D10 < 0.3$  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  $AGB_{\text{Indiv}}$  fell outside the 99.9% confidence interval of prediction of the appropriate plant functional type model. Although the  $AGB_{\text{Indiv}}$  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  $AGB_{\text{Indiv}}$  for the measured dimensions, and were most likely due to errors in data entry of field measurements of fresh weights.

### ***Statistical analysis***

A simple power-law allometric model was used to predict  $AGB_{\text{Indiv}}$  based on the explanatory variable,  $X$  (Eq. 1). Eq. 1 is linearized by logarithmic transformation (Eq. 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 ( $\varepsilon$ ; which becomes a multiplicative error in the power model,  $\varepsilon'$ , Picard *et al.* (2012)).

$$AGB_{\text{Indiv}} = a X^b + \varepsilon' \quad (1)$$

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

Xiao *et al.* (2011) found that Eq. 2 produced more accurate estimates of biomass than alternative nonlinear fitting. Eq. 2 was applied to the entire dataset (universal model,  $All_{Universal}$ ), and to the datasets 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 Eq. 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  $CF$ s were reviewed by Clifford *et al.* (2013), and the MM  $CF$  (Minimise Mean Square Error  $CF$ , Shen and 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  $CF$ 's were consistent, at less two decimal places, due to our 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 standardised 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, 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 Eq. 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 versus 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’ *C<sub>p</sub>* statistics (Mallows, 1973) and Akaike’s information criterion (*AIC*, Burnham & Anderson, 2004). Models of poor fit have *C<sub>p</sub>* 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 by 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 dataset, the change in fit statistics (*RSME*,  $R^2$  and *AIC*) between *D*-alone based model and each of the two alternative compound predictor variables, i.e.:  $D^2H$ , 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 estimates, rather than direct measured, of *H* and  $\rho$  (Sileshi *et al.*, 2014), these analyses were repeated using sub-sets 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  $\rho$  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 Eq. 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 yrs, or >20 yrs), (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 generalisation*

Three approaches were used to determine the impact of the level of generalisation of allometric models (Eq. 2) on accuracy of  $AGB_{\text{indiv}}$  prediction. First, using the entire dataset, general linear model analysis was used to assess whether the fit statistics ( $RSME$ ,  $R^2$  and  $AIC$ ) of  $\ln(AGB_{\text{indiv}})$  prediction from  $\ln(D)$  could be enhanced by accounting for the supplementary categorical variable of plant functional type in the  $All_{\text{Universal}}$  model. Second, using each dataset of the five plant functional types, increases in such fit statistics were assessed when using the less generalised plant functional type model rather than the  $All_{\text{Universal}}$  model. Third, the 53 species that had  $N > 50$  (and which thus provided reasonable prediction of  $AGB_{\text{indiv}}$  given population level variability, Roxburgh *et al.*, 2015) were used to examine improvement in accuracy with decreasing level of generalisation in allometric models. We calculated for each species dataset, the change in fit statistics ( $RSME$ ,  $R^2$  and  $AIC$ ) between the  $All_{\text{universal}}$  model and each of the two levels of generalisations, i.e.: 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  $(F_{\text{Euc}}) - (\text{All}_{\text{universal}})$ , and for (Species-specific model for *E. wandoo*)  $- (\text{All}_{\text{universal}})$ .

### ***Model performance***

One concern with the application of generalised (multi-species) 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  $\text{AGB}_{\text{Indiv}}$  (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 generalised plant functional type or universal models. If the 95% confidence interval of prediction using a generalised 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  $\text{AGB}_{\text{Stand}}$  (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  $\text{AGB}_{\text{Indiv}}$  to facilitate a comparison of observed and predicted  $\text{AGB}_{\text{Stand}}$ . The relationship between observed and predicted  $\text{AGB}_{\text{Stand}}$  was used to determine the overall accuracy and bias of generalised predictions at the stand-scale. These predictions were made using three scenarios where the level of generalisation 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  $\text{AGB}_{\text{Stand}}$ . 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 versus 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 (Eq. 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 generalised 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 generalised models provided reasonable accuracy across the datasets, 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 under-prediction of  $AGB_{Indiv}$  in larger trees and over-prediction 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  $\ln(\text{AGB}_{\text{Indiv}})$  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  $\rho$  in a compound predictor variable in Eq. 2 did not markedly influence model performance compared with the  $D$ -based model in predicting  $\ln(\text{AGB}_{\text{Indiv}})$ , with changes in  $RMSE$  and  $R^2$  less than  $\pm 0.06$  and  $\pm 0.02$ , respectively (Table 4). Similar results were obtained for a sub-set of the data for which  $H$  or  $\rho$  were measured rather than estimated (see values in parentheses, Table 4), noting that tests of  $\rho$  inclusion were based on limited data because only 12% of the dataset had measured or estimated  $\rho$  values.

#### ***Inclusion of site-factor predictor variables***

Since the addition of  $H$  and/or  $\rho$  in a compound predictor did not markedly influence performance of the  $D$ -based model in predicting  $\ln(\text{AGB}_{\text{Indiv}})$ , 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  $\ln(\text{AGB}_{\text{Indiv}})$  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 models based on plant functional types where a majority of the individuals were from young planted stands (e.g.  $F_{\text{Multi}}$ ,  $F_{\text{Other-H}}$ ,  $F_{\text{Other-L}}$ ). Accounting for ecoregion reduced  $RMSE$  by  $< 0.03\%$  and  $AIC$  by  $< 8\%$ . If ecoregion was added as supplementary variable,  $C_p$  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 generalisation***

Addition of plant functional type as a categorical explanatory variable improved performance of the All<sub>Universal</sub> 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 generalisation, 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<sub>Universal</sub> model. When generalising 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 generalising at the plant functional type level were particularly pronounced for F<sub>Other-L</sub> (or F<sub>Multi</sub>) 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 dataset for F<sub>Other-L</sub> (i.e. excluding saplings with  $D_{130} < 10$  cm, N=455), gains in accuracy were similarly larger when using a model specific for that dataset than when applying the All<sub>Universal</sub> model (i.e.  $\Delta RMSE$  of -0.162,  $\Delta R^2$  of 0.150, data not shown).

Although results are not shown here, generalising at the level of sub-categories of plant functional type (Fig. S1) showed little or no improvement in accuracy of  $\ln(AGB_{Indiv})$  predictions when compared to those obtained when using models generalised at the level of plant functional type.

As expected, when applied to datasets restricted to focal species, the greatest accuracy of prediction in  $\ln(\text{AGB}_{\text{Indiv}})$  was attained using the least generalised model – i.e. models specific to a given species. Compared to the  $\text{All}_{\text{Universal}}$  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  $\ln(\text{AGB}_{\text{Indiv}})$  predictions could be made by reducing the level of generalisation from functional type to species, especially for  $\text{F}_{\text{Shrub}}$  and  $\text{F}_{\text{Euc}}$ .

### ***Model performance***

Fig. 5 illustrates the overlap of the 95% confidence interval of generalised model prediction with that attained using the species-specific model for predicting  $\ln(\text{AGB}_{\text{Indiv}})$  under the scenarios of assuming an observed  $D_{10}$  of 10, 50 and 100 cm. On average, 74% (SD 14%) of the confidence interval of prediction obtained using the models generalised at the level of plant functional type overlapped with that attained using the species-specific model. Tested against the  $\text{All}_{\text{Universal}}$  model, this figure decreased to 67% (SD 13%), largely because two key species of  $\text{F}_{\text{Other-L}}$  were relatively poorly represented by the  $\text{All}_{\text{Universal}}$  model. However for most tested species, results were similar (with mean  $\pm 8\%$ , SD 5%) when comparisons were made between the confidence intervals of species-specific models and two alternative, more generalised models.

Of the 53 species tested, only four (or 8%) had  $< 55\%$  overlap in confidence intervals of prediction obtained using generalised and species-specific models. These four species were *Eucalyptus vegrandis*, *Acacia calamifolia*, *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 generalised models. However, generalised multi-species models poorly

represented the allometry of all four of these species, indicating potential for significant bias in up to 8% of the tested species generalised models were applied.

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 generalisation 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  $AGB_{Stand}$  introduced significant bias, even when applying species-specific models. However, this bias was largely independent of the level of generalisation of allometry applied. For example, for the Leos site, where measured  $AGB_{Stand}$  was  $113.6 \text{ Mg ha}^{-1}$  (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 generalised 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  $AGB_{Indiv}$  datasets that were larger, and from a broader range of vegetation types than previously collated for Australia, the fit statistics obtained were comparable to generalised allometric

models for  $AGB_{Indiv}$  previously developed for much smaller datasets (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 generalised allometric models for  $AGB_{Indiv}$  (i.e. being based on datasets from a wider range of ecoregions and from a range of plant types etc.) does not substantially jeopardise their accuracy of prediction. Our results provide further evidence of the effectiveness of generic  $AGB_{Indiv}$  allometric models developed from large, compiled datasets, 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 generalised models is an appropriate approach to extending the geographical application range of otherwise limited, and often localised, species-specific models. Collation of datasets to develop such generalised allometric models seems preferable to either: (i) making parameters of existing localised 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 localised species-specific models to generate pseudo-observations to develop more generalised 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 multi-stemmed plant functional types of  $F_{Shrub}$  and  $F_{Multi}$  (Table 3). Many others (e.g. Buech & Rugg, 1995; Chojnacky & Milton, 2008; Paul *et al.*, 2013a,b; Berner *et al.*, 2015) found  $D$  to be the strongest predictor of  $AGB_{Indiv}$  in such multi-stemmed individuals. However in allometric models of  $AGB_{Indiv}$  for multi-stemmed trees, 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 multi-stemmed individuals, and determining the method that provides the highest accuracy of prediction of  $AGB_{\text{Indiv}}$ . 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  $F_{\text{Other-L}}$  category of species, a single simple power-law model did not accurately predict  $AGB_{\text{Indiv}}$  across the full range of tree sizes. For these species, options for weighted non-linear modelling should be investigated as an alternative to the power-law model provided here (i.e. for  $F_{\text{Other-L}}$  trees of  $D_{130} > 10$  cm).

#### ***Compound predictor variables including height and wood density***

We found including  $H$  and  $\rho$  in addition to  $D$  in a compound predictor variable did not markedly improve  $\ln(AGB_{\text{Indiv}})$  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  $AGB_{\text{Indiv}}$  as it minimises costs associated with these additional biometric measurements, and also the uncertainty resulting from measurement and prediction errors of  $H$  and/or  $\rho$ .

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 markedly 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  $AGB_{\text{Indiv}}$ , 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  $\rho$  did not improve the predictive ability of the  $D$ -based model. The first is possible measurement errors. For example,  $\rho$  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  $\rho$  values may have been erroneous due to the height and/or age at which  $\rho$  was measured (e.g. Molto *et al.*, 2013). Second, most of our dataset was obtained from temperate regions, where  $\rho$  is typically less variable than, for example, among tropical trees (Swenson & Enquist, 2007). This is consistent with  $\rho$  having greater predictive potential in  $AGB_{\text{Indiv}}$  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  $AGB_{\text{Indiv}}$  and plant architecture (i.e. the  $D$ - $H$  relationship) may vary with site factors as individuals optimize their growth strategies, the impact on total  $AGB_{\text{Indiv}}$  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; 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  $AGB_{\text{Indiv}}$  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 generalised 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  $AGB_{\text{Indiv}}$  predictions (Callaway *et al.*, 1994; De Lucia *et al.*, 2000; Genet *et al.*, 2011; Alvarez *et al.*, 2012; Lopez-Serrano *et al.*, 2015). Such improvements are often interpreted as climatic impacts influencing predicted  $AGB_{\text{Indiv}}$  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  $AGB_{\text{Indiv}}$  (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 generalisation***

Compared to the most generalized model ( $All_{\text{Universal}}$ ), the largest gains in predictive ability were attained when categorising the dataset at the level of species, but with little loss of accuracy when generalised to the level of plant functional type (Tables 6 & 7). These results were therefore consistent with previous work showing that generic multi-species 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).



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It is often suggested that plant functional attributes (e.g.  $\rho$ , apical dominance, and canopy architecture) may be genetically constrained as a result of adaption to environmental factors (e.g. Onoda *et al.*, 2010; van Gelder *et al.*, 2006; 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, multi-stemmed 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  $\rho$  (Table 1).

Although including  $\rho$  in compound predictor variables offered no measurable improvement to D-based models (Table 4), phylogenesis resulting in divergent stem anatomy and  $\rho$  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  $\rho$  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  $\rho$  measurement and estimates collated due to the high uncertainties in these datasets, such differences in stem anatomy may also be one of the reasons why species of  $F_{Euc}$  (average  $\rho$  0.77 g cm<sup>-3</sup>, 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  $\rho$  0.67 g cm<sup>-3</sup>, Table 1) (Fig. 3).

There is evidence that  $\rho$  varies greatly among species in Australia (e.g. Onoda *et al.*, 2010). Further refinement and consistency in protocols used to measure  $\rho$  is required to confirm whether, as observed by others (e.g. van Breugel *et al.*, 2011; Fayolle *et al.*, 2013; Chojnacky *et al.*, 2014),  $\rho$  may be more similar within than between different plant functional types, resulting in each having a unique  $\text{AGB}_{\text{Indiv}}$  allometry. Hence, although  $\rho$  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 generalised models are developed.

### ***Model performance***

Species datasets for which we had confidence in prediction of  $\text{AGB}_{\text{Indiv}}$  using species-specific models (i.e. 53 species where  $N > 50$ ) provided a test for bias in predictions with the application of more generalised models. Most (92%) demonstrated no significant bias, with the 95% confidence interval of prediction obtained using generalised allometry overlapping with that attained using the species-specific model in 55-85% of the cases (Fig. 5). In contrast, species-specific models appeared to avoid risks of significant bias in  $\text{AGB}_{\text{Indiv}}$  in about 8% of the species studied. Thus, to minimise 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  $\text{AGB}_{\text{Indiv}}$  are generally used to derive  $\text{AGB}_{\text{Stand}}$ , 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  $< 3.2 \text{ Mg ha}^{-1}$  and  $< 5.6\%$ , respectively) of using species-specific models when compared to more generalised models (Fig. 6). The stand of Leos (observed  $AGB_{Stand}$  of  $113.6 \text{ Mg ha}^{-1}$ ) remained an outlier regardless of which level of generalisation 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 minimised through the application of more generalised models that are based on a much smaller number of parameters (e.g. only two when applying the most generalised model), irrespective of the number of species within the stand.

This study has advanced the development and testing of generalised 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 under-sampled 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).

Although species-specific models significantly reduced bias in  $AGB_{\text{Indiv}}$  in about 8% of the species tested, results obtained from validation of allometric models against 17 stands that had  $AGB_{\text{Stand}}$  directly measured showed that a good individual-level model does not necessarily translate into much improved stand-level predictions. Across these contrasting sites where direct measurement (destructive stand harvest), the application of more generalised 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 parameterise, 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 to a single generalised multi-species 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  $AGB_{\text{Stand}}$  prediction when applying multiple species-specific models when compared to a generalised multi-species model.

It is therefore recommended that generalised multi-species models be applied when cost-effective predictions of  $AGB_{\text{Stand}}$  are required across multiple mixed species stands. The most generalised model ( $All_{\text{Universal}}$ ) tested here was based on  $D_{10}$  by necessity, and yet D measurement at this height is known to be sub-optimal for many single-stemmed tree species. Hence for practical reasons, models generalised at the level of plant functional groups (Eq. 4a-e, reported here using the Baskerville  $CF$ ) are recommended for application in both Australia, and for validation in similar ecoregions in other continents.

$$\text{AGB}_{\text{Indiv}} \text{ (kg) of } F_{\text{Shrub}} = \exp [-3.007 + 2.428 \ln(D_{10})] \times 1.128, \quad (4a)$$

$$\text{AGB}_{\text{Indiv}} \text{ (kg) of } F_{\text{Multi}} = \exp [-2.757 + 2.474 \ln(D_{10})] \times 1.079, \quad (4b)$$

$$\text{AGB}_{\text{Indiv}} \text{ (kg) of } F_{\text{Euc}} = \exp [-2.016 + 2.375 \ln(D_{130})] \times 1.067, \quad (4c)$$

$$\text{AGB}_{\text{Indiv}} \text{ (kg) of } F_{\text{Other-H}} = \exp [-1.693 + 2.220 \ln(D_{130})] \times 1.044, \quad (4d)$$

$$\text{AGB}_{\text{Indiv}} \text{ (kg) of } F_{\text{Other-L}} = \exp [-2.573 + 2.460 \ln(D_{130})] \times 1.018, \quad (4e)$$

There are two exceptions to the recommendation of application of Eq. 4. First, where the trade-off between accuracy and cost effectiveness is relatively high, such as when estimating  $\text{AGB}_{\text{Stand}}$  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  $\text{AGB}_{\text{Stand}}$  prediction. Second, where  $\text{AGB}_{\text{Stand}}$  is required for stands dominated by species suspected of not conforming to the generalised 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 generalised plant functional type models.

As with all allometric models, to avoid bias in  $\text{AGB}_{\text{Indiv}}$  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 to both increase the replication (and confidence) of prediction of larger sized trees ( $D_{130} > 50$  cm), and to account for some of the variation in  $\text{AGB}_{\text{Indiv}}$  due to hollows or piping of larger over-mature trees or trees affected by termites (e.g. Rayner *et al.*, 2014; Monda *et al.*, 2015).

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## List of Figures

**Fig 1** Location of trees or shrubs sampled for live aboveground biomass by terrestrial ecoregion across Australia (DSWPC, 2015).

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

**Fig 3** Generic allometric equations for prediction of total above-ground biomass ( $\ln(\text{AGB}_{\text{Indiv}})$ ) from stem diameter ( $\ln(D)$ , at 10 cm,  $D_{10}$ , or at 130 cm,  $D_{130}$ ) of: (a) all individuals  $\text{All}_{\text{Universal}}$ ; (b) shrubs and small trees ( $F_{\text{Shrub}}$ ); (c) multi-stemmed trees ( $F_{\text{Multi}}$ ); (d) single-stemmed eucalypt trees ( $F_{\text{Euc}}$ ); (e) single-stemmed other hardwood trees ( $F_{\text{Other-H}}$ ); and (f) softwood trees ( $F_{\text{Other-L}}$ ). 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 sub-categories of plant functional types (b-g) as defined in Fig. S1. Grey dashed lines in plots b-g represent predictions obtained using the  $\text{All}_{\text{Universal}}$  model based on  $D_{10}$ . Datasets with  $D_{130} < 10$  cm were not used in the  $F_{\text{Other-L}}$  model.

**Fig 4** Generic allometric equations for prediction of total above-ground biomass ( $\text{AGB}_{\text{Indiv}}$ ) from stem diameter ( $D$  at 10 cm,  $D_{10}$ , or at 130 cm,  $D_{130}$ ) of: (a) all individuals  $\text{All}_{\text{Universal}}$ ; (b)

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shrubs and small trees ( $F_{\text{Shrub}}$ ); (c) multi-stemmed trees ( $F_{\text{Multi}}$ ); (d) single-stemmed eucalypt trees ( $F_{\text{Euc}}$ ); (e) single-stemmed other hardwood trees ( $F_{\text{Other-H}}$ ); and (f) softwood trees ( $F_{\text{Other-L}}$ ). 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 sub-categories of plant functional types (b-f) as defined in Fig. S1. Datasets with  $D_{130} < 10$  cm were not used in the  $F_{\text{Other-L}}$  model.  $R^2$  and RMSE refer to the linear regression of predicted vs. observed AGB.

**Fig 5** Box plots describing the Proportion of the 95% confidence interval (CI) of generalised allometry prediction overlapped by the 95% CI of species-specific allometry prediction when the level of generalisation was; (a) plant functional type, or (b) universal,  $All_{\text{Universal}}$ . These results are for prediction of  $\ln(\text{AGB}_{\text{Indiv}})$  using models (Eq. 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 scenario of  $D_{10}$  of 50 and 100 cm.

**Fig 6** Relationship between total above-ground biomass ( $\text{AGB}_{\text{Stand}}$ ) from whole-plot harvesting at 17 contrasting stands (Table 2) and that predicted for those stands through the application of three scenarios of increasing generalisation of allometric models applied: (a) information on species identity of each individual at each of the test sites was utilised, and for

species that were represented by the 53 available species-specific models, these were applied (Eq. 2 using parameters given in Table S3), while for all other species, the appropriate plant functional type model was applied (Eq. 2 using parameters given for  $F_{\text{Shrub}}$ ,  $F_{\text{Multi}}$ ,  $F_{\text{Euc}}$ ,  $F_{\text{Other-H}}$  and  $F_{\text{Other-L}}$  in Table 3), (b) species identification and/or species-specific models were assumed to be unavailable, and so plant functional type models were applied (Eq. 2 using parameters given for  $F_{\text{Shrub}}$ ,  $F_{\text{Multi}}$ ,  $F_{\text{Euc}}$ ,  $F_{\text{Other-H}}$  and  $F_{\text{Other-L}}$  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 ( $All_{\text{Universal}}$ ) was applied (Eq. 2 using parameters given for  $All_{\text{Universal}}$  in Table 3). In all scenarios, the MM correction factor was applied when back-transforming predictions. Grey dashed line represents the 1:1 line. *EF* indicates model efficiency. 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.







