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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.

80 Regardless of ecoregion, for five broad categories of plant functional type (shrubs; multi-
81 stemmed trees; trees of the genus *Eucalyptus* and closely related genera; other trees of high wood
82 density; and other trees of low wood density), relationships between biomass and stem diameter
83 were generic. Simple power-law models explained 84-95% of the variation in biomass, with little
84 improvement in model performance when other plant variables (height, bole wood density), or
85 site characteristics (climate, age, management) were included.

86 Predictions of stand-based biomass from allometric models of varying levels of
87 generalisation (species-specific, plant functional type) were validated using whole-plot harvest
88 data from 17 contrasting stands (range: 9 to 356 Mg ha⁻¹). Losses in efficiency of prediction were
89 < 1% if generalised models were used in place of species-specific models. Furthermore,
90 application of generalised multi-species models did not introduce significant bias in biomass
91 prediction in 92% of the 53 species tested. Further, overall efficiency of *stand*-level biomass
92 prediction was 99%, with a mean absolute prediction error of only 13%. Hence, for cost-
93 effective prediction of biomass across a wide range of stands, we recommend use of generic
94 allometric models based on plant functional types. Development of new species-specific models
95 is only warranted when gains in accuracy of stand-based predictions are relatively high (e.g.
96 high-value monocultures).

97

98 **Introduction**

99 Vegetation is an important sink within the global carbon budget, with carbon storage
100 facilitated by uptake of atmospheric carbon dioxide through photosynthesis (Le Quéré *et al.*,
101 2015). Ground-based information on the carbon storage in vegetation is critical for calibrating
102 carbon budgets, largely calculated using remote sensing metrics (e.g. Haverd *et al.*, 2013;
103 Mitchard *et al.*, 2013; Chen *et al.*, 2015), or regional carbon accounting models (e.g. Richards &
104 Evans 2004; Paul *et al.*, 2015a,b). In addition, accurate ground-based estimates of biomass are
105 important for the assessment and management of wood and biomass products (e.g. Canadell &
106 Raupach 2008), fire hazard (van der Werf *et al.*, 2010), habitat suitability (e.g. Hatanaka *et al.*,
107 2011), and water yield and quality within catchments (e.g. George *et al.*, 2012).

108 Typically, ground-based estimates of biomass are obtained by applying allometric models
109 to field measurements of biometric data such as stem diameter or plant height (e.g. Picard *et al.*,
110 2012). Two key decisions frame the construction of allometric models to predict total above-
111 ground biomass (AGB_{Indiv}, oven-dry weight of an individual plant). The first is deciding which
112 predictor variable(s) to use. Stem diameter (*D*, typically measured over bark at 130 cm height
113 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 $\text{AGB}_{\text{Indiv}}$ (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 $\text{AGB}_{\text{Indiv}}$ 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 $\text{AGB}_{\text{Indiv}}$ 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 $\text{AGB}_{\text{Indiv}}$ 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 $\text{AGB}_{\text{Indiv}}$ 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 $\text{AGB}_{\text{Indiv}}$ using generalised models.

At the scale of individual plants, allometry-predicted $\text{AGB}_{\text{Indiv}}$ can be validated by independent sampling of new plants. However, it is difficult to ascertain whether sampled plants

148 have been truly selected at random. If specific criteria have been applied for selection (e.g. only
149 healthy trees) the resulting allometric model may be inherently biased. A true test of this possible
150 bias would be a direct validation of stand-based allometric model predictions of above-ground
151 biomass (AGB_{Stand}) against that measured through whole-plot harvesting. Such testing has been
152 undertaken in monoculture hardwood forests (Arthur *et al.*, 2001; Paul *et al.*, 2013b), and in
153 mixed-species vegetation (Búrquez & Martínez-Yrizar, 2011; Paul *et al.*, 2013a), but not using
154 generic allometric models.

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

164 For this project, an AGB_{Indiv} dataset of unprecedented size was compiled, composed of
165 15,054 destructively-measured individuals from both managed (i.e. planted) and natural
166 ecosystems across Australia. This dataset was used to assess whether diameter-based allometric
167 models of biomass were improved: (i) by the inclusion of other plant variables (e.g. height, wood
168 density); (ii) by the inclusion of site characteristics (e.g. climate, age, management); and (iii)
169 when based on species rather than broader categories like plant functional groups. Our objectives
170 were first, to recommend the most appropriate allometric model(s) for estimating AGB_{Indiv} in
171 Australian ecosystems, and secondly, to quantify bias of the recommended model(s) when tested
172 against direct measurements of AGB_{Stand} obtained using whole-plot harvesting across a range of
173 contrasting sites.

174 175 **Materials and methods**

176 ***Dataset***

177 Datasets of AGB_{Indiv} were obtained from destructive harvesting of 15,054 individual
178 trees and shrubs. Data represented a range of managed and natural woody ecosystems across 826
179 sites in various ecoregions of Australia (Fig. 1), and obtained from numerous published and
180 unpublished sources (Table S1; Paul *et al.*, 2015c). They included 274 species, 53 of which had
181 $N > 50$ individuals, sufficient for developing species-specific models that provide a reasonable

approximation of AGB_{Indiv} given population level variability (Roxburgh *et al.*, 2015). To 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_{Shrub}); (ii) multi-stemmed 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 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 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 the three categories of trees of relatively high wood density (F_{Multi} , F_{Euc} and $F_{Other-H}$), 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_{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 $F_{Other-H}$ 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 dataset 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 dataset, this category was also largely found in these two ecoregions. In contrast, F_{Shrub} and $F_{Other-H}$ comprised 16% and 3% of the

216 dataset, respectively, but were sourced from a wide range of ecoregions.

217

218 *Explanatory variables*

219 The primary set of collated data included three explanatory variables for AGB_{Indiv} : stem
220 diameter (D , over bark, cm), height (H , m) and, as described below, measured, estimated or
221 derived basic density of stem wood (ρ , g cm⁻³, typically measured as oven-dry mass per green
222 volume of stem at a standard height of 130 cm, Table 1). Secondary data relating to the site from
223 which an individual was sampled were also collated (Table 1). These included whether the site
224 was ‘natural’ (i.e. naturally regenerated shrubland, woodland, or forest) or managed (i.e. human-
225 induced establishment via either nursery stock, direct seeding or human-induced natural
226 regeneration). If the stand was managed, it was also recorded whether or not the stand was
227 relatively young, defined as < 20 years since establishment. Climatic data were collated (BoM,
228 2015; mean data based on 30-year period 1961-1990, resolution of approximately 2.5 km) and
229 included long-term mean annual precipitation (MAP, mm yr⁻¹) and mean annual temperature
230 (MAT, °C).

231

232 *Measurements and data cleaning*

233 Conventionally, tree diameter is measured at 130 cm (D_{130}) height above ground level to
234 avoid marked stem buttress swelling or exposed lignotubers in some species, and thus better
235 represents the diameter of a log above the stump. Consequently, most trees (F_{Euc} , $F_{Other-H}$ and
236 $F_{Other-L}$) had D_{130} measurements. For species of F_{Shrub} and F_{Multi} , where D_{130} measurements
237 introduced errors due to the presence of multiple stems at this height, or where the individual
238 was too small to have a measurable D_{130} , D was typically measured at 10 cm height above the
239 ground (D_{10}). For such multi-stemmed individuals, a single, pooled D estimate was obtained
240 from the quadratic mean - representing the sum of the cross sectional areas of individual stems
241 (Chojnacky & Milton, 2008).

242 For many individuals in the dataset, D was measured at multiple heights, allowing
243 derivation of generic relationships for prediction of D at a given height based on D measured at
244 another height (Table S2). These relationships were used to ‘gap-fill’ D estimates where
245 required, with D_{10} and D_{130} estimated for 33% and 14% of the 15,054 individuals, respectively.
246 Similarly, generic relationships were derived to ‘gap-fill’ H estimates of an individual through
247 the development of generic relationships between H and either D_{10} or D_{130} (Table S2). In this
248 way, H was estimated for 15% of the individuals in the database. The wood specific gravity ρ
249 was measured (or estimated based on local data) in only 8% (or 4%) of individuals in the dataset.
250 For individuals where ρ 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. $D_{10} < 0.3$ 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 of fresh weights.

Statistical analysis

A simple power-law allometric model was used to predict AGB_{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 (ε ; which becomes a multiplicative error in the power model, ε' , Picard *et al.* (2012)).

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

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

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

285 individuals that have a D that is appreciably larger or smaller than the mean D used to develop
286 the allometric model. But in this study the MM and Baskerville CF 's were consistent, at less two
287 decimal places, due to our sample sizes. Therefore, although the MM CF is recommended, we
288 also report the Baskerville CF for reference.

289 To confirm the validity of tested models, we checked: (i) that there was no
290 heteroscedasticity by confirming standardised residuals were not correlated with the
291 $\ln(AGB_{Indiv})$, and (ii) for influential points (i.e. data points having a Cook's D value > 1 ; Cook,
292 1979). Then, performance of valid models was quantified using five fit statistics: (i) standard
293 errors of the coefficients $\ln(a)$ and b , (ii) residual standard error of Eq. 2, $RMSE$, (iii) adjusted
294 coefficient of determination, R^2 , (iv) 95% confidence interval of the slope and intercept of the
295 line of best fit to the plot of observed versus predicted back-transformed AGB_{Indiv} , and (v)
296 average bias, or mean of the residuals expressed in absolute terms and provided as a proportion
297 (%) of the observed value (i.e. mean absolute prediction error ' $MAPE$ ', using back-transformed
298 AGB_{Indiv} predictions) (Sileshi 2014).

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

306 307 *Testing compound predictor variables including height and wood density*

308 To explore whether accuracy of AGB_{Indiv} prediction could be improved by using a
309 compound predictor variable *cf.* D -alone, we tested three alternatives of X : (i) D alone, based on
310 a simple geometrical argument that should hold across forests (Chave *et al.*, 2005), (ii) the
311 compound stem volume index D^2H , and (iii) the compound stem mass index $D^2H\rho$. We
312 calculated for each dataset, the change in fit statistics ($RSME$, R^2 and AIC) between D -alone
313 based model and each of the two alternative compound predictor variables, i.e.: D^2H , and $D^2H\rho$.
314 For example, for the F_{Euc} model, changes in fit statistics were assessed for (F_{Euc} using D -alone) –
315 (F_{Euc} using D^2H), and for (F_{Euc} using D -alone) – (F_{Euc} using $D^2H\rho$). To examine uncertainties
316 associated with the inclusion of estimates, rather than direct measured, of H and ρ (Sileshi *et al.*,
317 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 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 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_{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 $\ln(AGB_{Indiv})$ 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 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 $All_{Universal}$ 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 generalisation in allometric models. We calculated for each species dataset, the change in fit statistics ($RSME$, R^2 and AIC) between the $All_{universal}$ 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 $(F_{Euc}) - (All_{universal})$, and for $(Species-specific\ model\ for\ E.\ wandoo) - (All_{universal})$.

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 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 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 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 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 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 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

384 generalised models provided reasonable accuracy across the datasets, explaining 84-96% of
385 variation in AGB_{Indiv} (Fig. 4), with a $MAPE$ range of 15-41% (Table 3).

386 There was some evidence that the simple power-law allometric model was not
387 appropriate for $F_{Other-L}$ plant functional types, with under-prediction of AGB_{Indiv} in larger trees
388 and over-prediction of AGB_{Indiv} in smaller trees. However, if small saplings ($D_{130} < 10$ cm) were
389 excluded, the performance of the power-law model was satisfactory, with the $RMSE$ of
390 $\ln(AGB_{Indiv})$ prediction decreasing from 0.273 (data not shown) to 0.189 (Fig. 3).

391 392 ***Compound predictor variables including height and wood density***

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

399 400 ***Inclusion of site-factor predictor variables***

401 Since the addition of H and/or ρ in a compound predictor did not markedly influence
402 performance of the D -based model in predicting $\ln(AGB_{Indiv})$, only models based on D were
403 used to test the benefits of including site-factor predictor variables. When compared to using D -
404 alone, accounting for site-factors resulted in negligible model improvements, with the increase in
405 explained variation of $\ln(AGB_{Indiv})$ being consistently $< 0.4\%$ (Table 5). For example,
406 accounting for whether or not the individual was from a young (< 20 years old) stand, or whether
407 or not the individual was from a stand that was managed, resulted in $RMSE$ and AIC decreases of
408 < 0.03 and $< 5\%$, respectively. Furthermore, these site factors had negligible influence across all
409 models based on plant functional types where a majority of the individuals were from young
410 planted stands (e.g. F_{Multi} , $F_{Other-H}$, $F_{Other-L}$). Accounting for ecoregion reduced $RMSE$ by $<$
411 0.03% and AIC by $< 8\%$. If ecoregion was added as supplementary variable, C_p was sometimes
412 greater than the number of explanatory variables used, suggesting a poor model fit. Inclusion of
413 numerical variables of MAT or MAP led to even less improvement in predictions, with $RMSE$
414 reduced by $< 0.01\%$, AIC reduced by $< 3\%$.

415 416 ***Levels of generalisation***

417 Addition of plant functional type as a categorical explanatory variable improved
 418 performance of the All_{Universal} model ($RMSE$ reduced by 0.04, R^2 increased by 0.01%, and
 419 negative changes in AIC , Table 6). As further evidence of improvements in prediction accuracy
 420 by reducing level of generalisation, there was a consistent increase in fit statistics when, for each
 421 plant functional type, the relevant plant functional type model was applied in place of the
 422 All_{Universal} model. When generalising at the level of plant functional type there was a decrease in
 423 the $RMSE$ of 0.01-0.25, with R^2 increasing by 0.00-0.05% (Table 6). Gains in accuracy when
 424 generalising at the plant functional type level were particularly pronounced for $F_{Other-L}$ (or F_{Multi})
 425 where increases in $RMSE$ were 0.25 (or 0.05), compared to < 0.02 for the other categories of
 426 plant functional type. When considering the reduced dataset for $F_{Other-L}$ (i.e. excluding saplings
 427 with $D_{130} < 10$ cm, $N=455$), gains in accuracy were similarly larger when using a model specific
 428 for that dataset than when applying the All_{Universal} model (i.e. $\Delta RMSE$ of -0.162, ΔR^2 of 0.150,
 429 data not shown).

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

434 As expected, when applied to datasets restricted to focal species, the greatest accuracy of
 435 prediction in $\ln(AGB_{Indiv})$ was attained using the least generalised model – i.e. models specific to
 436 a given species. Compared to the All_{Universal} model, plant functional type models yielded some
 437 modest improvements, but were still not as good as species-specific models (Table 7). Gains in
 438 accuracy of $\ln(AGB_{Indiv})$ predictions could be made by reducing the level of generalisation from
 439 functional type to species, especially for F_{Shrub} and F_{Euc} .

441 **Model performance**

442 Fig. 5 illustrates the overlap of the 95% confidence interval of generalised model
 443 prediction with that attained using the species-specific model for predicting $\ln(AGB_{Indiv})$ under
 444 the scenarios of assuming an observed D_{10} of 10, 50 and 100 cm. On average, 74% (SD 14%) of
 445 the confidence interval of prediction obtained using the models generalised at the level of plant
 446 functional type overlapped with that attained using the species-specific model. Tested against the
 447 All_{Universal} model, this figure decreased to 67% (SD 13%), largely because two key species of
 448 $F_{Other-L}$ were relatively poorly represented by the All_{Universal} model. However for most tested
 449 species, results were similar (with mean $\pm 8\%$, SD 5%) when comparisons were made between
 450 the confidence intervals of species-specific models and two alternative, more generalised

451 models.

452 Of the 53 species tested, only four (or 8%) had < 55% overlap in confidence intervals of
453 prediction obtained using generalised and species-specific models. These four species were
454 *Eucalyptus vegrandis*, *Acacia calamifolia*, *E. pilularis* and *E. muelleriana*. For *Acacia*
455 *calamifolia*, this was partly attributable to the relatively low *RMSE* of prediction of the species-
456 specific model resulting in relatively small confidence intervals of prediction relative to the more
457 generalised models. However, generalised multi-species models poorly represented the allometry
458 of all four of these species, indicating potential for significant bias in up to 8% of the tested
459 species generalised models were applied.

460 When allometry-predicted AGB_{Stand} was compared to that observed by direct whole-plot
461 harvesting across 17 contrasting stands (Table 2), prediction quality was not affected by
462 increasing the level of generalisation of models. Differences in efficiency of prediction of
463 AGB_{Stand} were < 1% between scenarios, while differences in *MAPE* were < 5.61% between
464 scenarios (Fig. 6).

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

470

471 Discussion

472 Allometric models

473 Results obtained here confirmed that a simple power-law model largely encapsulated
474 scaling laws common to most woody plants (e.g. Niklas, 2004). There may be bias in AGB_{Indiv}
475 prediction for any given individual tree or shrub. But across a wide range of individuals,
476 AGB_{Indiv} may be predicted using generalised allometric models with reasonable accuracy (i.e.
477 *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
478 explanatory variable. Despite these models being based on AGB_{Indiv} datasets that were larger,
479 and from a broader range of vegetation types than previously collated for Australia, the fit
480 statistics obtained were comparable to generalised allometric models for AGB_{Indiv} previously
481 developed for much smaller datasets (e.g. Williams *et al.*, 2005; Montagu *et al.*, 2005; Jonson &
482 Freudenberger 2011; Paul *et al.*, 2013a,b).

483 Our results suggest that increasing the domain of application of generalised allometric
484 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_{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 non-linear 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).

519 This finding supports the conclusions of others (e.g. Molto *et al.*, 2013; Sileshi, 2014; Kuyah &
520 Rosenstock, 2015) that using D alone is an appropriate predictor of AGB_{Indiv} as it minimises
521 costs associated with these additional biometric measurements, and also the uncertainty resulting
522 from measurement and prediction errors of H and/or ρ .

523 The fact that H is often correlated with D (e.g. Pérez-Cruzado & Rodríguez-Soalleiro,
524 2011; Mugasha *et al.*, 2013; Ishihara *et al.*, 2015) may largely explain why inclusion of H as an
525 additional predictor did not markedly influence the performance of the D -based models. Indeed
526 scaling theory of larger woody plants predicts that H scales with diameter to the $2/3$ power
527 (Niklas & Spatz, 2004). Nonetheless, although the inclusion of H may not be necessary to
528 accurately predict AGB_{Indiv} , there is evidence that it may be beneficial to include in allometric
529 models of foliage biomass, which tends to be influenced by plant architecture (e.g. Picard *et al.*,
530 2015).

531 We make two suggestions as to why inclusion of ρ did not improve the predictive ability
532 of the D -based model. The first is possible measurement errors. For example, ρ varies with
533 height (e.g. Pérez-Cruzado & Rodríguez-Soalleiro, 2011; Wiemann & Williamson, 2014), and
534 with stand age or rates of growth (e.g. Ilic *et al.*, 2000). Hence database-derived ρ values may
535 have been erroneous due to the height and/or age at which ρ was measured (e.g. Molto *et al.*,
536 2013). Second, most of our dataset was obtained from temperate regions, where ρ is typically
537 less variable than, for example, among tropical trees (Swenson & Enquist, 2007). This is
538 consistent with ρ having greater predictive potential in AGB_{Indiv} models for tropical trees (Chave
539 *et al.*, 2014) than was found in this study.

540

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

542 Our study indicated that including site-related factors such as characteristics of the stand
543 (stand age and management), and climatic characteristics (e.g. MAP, MAT), did not markedly
544 improve the predictive ability of D -based models (increased R^2 of <1%, Table 5). These results
545 provided support to findings that while the allocation of AGB_{Indiv} and plant architecture (i.e. the
546 D - H relationship) may vary with site factors as individuals optimize their growth strategies, the
547 impact on total AGB_{Indiv} allometry appears to be negligible (e.g., António *et al.*, 2007; Peichl &
548 Arain, 2007; Feldpausch *et al.*, 2011, 2012; Banin *et al.*, 2012; de Miguel *et al.*, 2014; Gonzalez-
549 Benecke *et al.*, 2014; Moncrieff *et al.*, 2014; Hulshof *et al.*, 2015). This may be due to the
550 compensatory relationship between stem and canopy mass resulting in similar AGB_{Indiv} for trees
551 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_{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_{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 generalisation

Compared to the most generalized model (All_{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).

It is often suggested that plant functional attributes (e.g. ρ , 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 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

586 & 7) and by others (e.g. Chojnacky *et al.*, 2014; Hulshof *et al.*, 2015). Lower average values of ρ
587 for species of $F_{\text{Other-L}}$ (Table 1) explain why, for a given D , the $\text{AGB}_{\text{Indiv}}$ was relatively low when
588 compared to most other tree species, particularly F_{Euc} (Fig. 3). Although less evident from ρ
589 measurement and estimates collated due to the high uncertainties in these datasets, such
590 differences in stem anatomy may also be one of the reasons why species of F_{Euc} (average ρ 0.77
591 g cm^{-3} , Table 1) of large size (e.g. $D_{10} > 50$ cm) had relatively high $\text{AGB}_{\text{Indiv}}$ for a given D when
592 compared to species of $F_{\text{Other-H}}$ (average ρ 0.67 g cm^{-3} , Table 1) (Fig. 3).

593 There is evidence that ρ varies greatly among species in Australia (e.g. Onoda *et al.*,
594 2010). Further refinement and consistency in protocols used to measure ρ is required to confirm
595 whether, as observed by others (e.g. van Breugel *et al.*, 2011; Fayolle *et al.*, 2013; Chojnacky *et*
596 *al.*, 2014), ρ may be more similar within than between different plant functional types, resulting
597 in each having a unique $\text{AGB}_{\text{Indiv}}$ allometry. Hence, although ρ was found not to impact the
598 model directly via a compound predictor variable, it may nonetheless have an indirect impact via
599 influencing categories (i.e. groups of species, or plant functional types) upon which generalised
600 models are developed.

601

602 **Model performance**

603 Species datasets for which we had confidence in prediction of $\text{AGB}_{\text{Indiv}}$ using species-
604 specific models (i.e. 53 species where $N > 50$) provided a test for bias in predictions with the
605 application of more generalised models. Most (92%) demonstrated no significant bias, with the
606 95% confidence interval of prediction obtained using generalised allometry overlapping with that
607 attained using the species-specific model in 55-85% of the cases (Fig. 5). In contrast, species-
608 specific models appeared to avoid risks of significant bias in $\text{AGB}_{\text{Indiv}}$ in about 8% of the species
609 studied. Thus, to minimise the potential for significant bias when accurate predictions are
610 required at the *individual* level, representative species-specific models (i.e. $N > 50$, Roxburgh *et*
611 *al.*, 2015) should be used when these are available (e.g. Table S3). However because allometry-
612 predicted $\text{AGB}_{\text{Indiv}}$ are generally used to derive $\text{AGB}_{\text{Stand}}$, user decision on whether the
613 additional costs associated with developing new species-specific models is justified should be
614 based on the extent to which these more specific models improve accuracy (and particularly,
615 reduce bias) at the *stand* level.

616 Stand-level validation of allometric models showed that there was relatively little added
617 benefit (EF of $\text{AGB}_{\text{Stand}}$ prediction increasing by $<1\%$, and $RMSE$ and $MAPE$ decreasing by $<$
618 3.2 Mg ha^{-1} and $< 5.6\%$, respectively) of using species-specific models when compared to more
619 generalised models (Fig. 6). The stand of Leos (observed $\text{AGB}_{\text{Stand}}$ of 113.6 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_{Indiv} in about 8% of the species tested, results obtained from validation of allometric models against 17 stands that had AGB_{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_{Stand} prediction when applying multiple species-specific models when compared to a generalised multi-species model.

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

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

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

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

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

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

666 There are two exceptions to the recommendation of application of Eq. 4. First, where the
667 trade-off between accuracy and cost effectiveness is relatively high, such as when estimating
668 AGB_{Stand} for a given high carbon stand comprising only one or two dominant species. In such
669 circumstances, additional costs associated with obtaining species-specific models may warrant
670 the improved accuracy of AGB_{Stand} prediction. Second, where AGB_{Stand} is required for stands
671 dominated by species suspected of not conforming to the generalised plant functional groups
672 models. Another line of enquiry to pursue is to build improved species-specific models to expand
673 the testing done here that found 8% of species did not conform to generalised plant functional
674 type models.

675 As with all allometric models, to avoid bias in AGB_{Indiv} predictions, recommended
676 models in this study should only be applied within their valid diameter range as indicated by the
677 maximum D sampled (e.g. Table 3, Table S3). Further sampling is required to extend the D
678 range of allometric models to both increase the replication (and confidence) of prediction of
679 larger sized trees ($D_{130} > 50$ cm), and to account for some of the variation in AGB_{Indiv} due to
680 hollows or piping of larger over-mature trees or trees affected by termites (e.g. Rayner *et al.*,
681 2014; Monda *et al.*, 2015).

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- 980

981 List of Figures

982

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

985

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

987

988 **Fig 3** Generic allometric equations for prediction of total above-ground biomass ($\ln(\text{AGB}_{\text{Indiv}})$)
989 from stem diameter ($\ln(D)$, at 10 cm, D_{10} , or at 130 cm, D_{130}) of: (a) all individuals $\text{All}_{\text{Universal}}$;
990 (b) shrubs and small trees (F_{Shrub}); (c) multi-stemmed trees (F_{Multi}); (d) single-stemmed eucalypt
991 trees (F_{Euc}); (e) single-stemmed other hardwood trees ($F_{\text{Other-H}}$); and (f) softwood trees ($F_{\text{Other-L}}$).
992 Black solid lines represent the model of best fit, and dotted lines the 95% prediction interval.
993 Different symbols for the scatter points represent the different categories of plant functional
994 types (in (a)) or sub-categories of plant functional types (b-g) as defined in Fig. S1. Grey dashed
995 lines in plots b-g represent predictions obtained using the $\text{All}_{\text{Universal}}$ model based on D_{10} .
996 Datasets with $D_{130} < 10$ cm were not used in the $F_{\text{Other-L}}$ model.

997

998 **Fig 4** Generic allometric equations for prediction of total above-ground biomass ($\text{AGB}_{\text{Indiv}}$) from
999 stem diameter (D at 10 cm, D_{10} , or at 130 cm, D_{130}) of: (a) all individuals $\text{All}_{\text{Universal}}$; (b) shrubs
1000 and small trees (F_{Shrub}); (c) multi-stemmed trees (F_{Multi}); (d) single-stemmed eucalypt trees
1001 (F_{Euc}); (e) single-stemmed other hardwood trees ($F_{\text{Other-H}}$); and (f) softwood trees ($F_{\text{Other-L}}$).
1002 Back-transformed predictions were derived by applying the MM correction factor (CF), with
1003 superscripts a, b, c, d, e and f indicating CF ranges of 1.1042-1.1046, 1.268-1.1279, 1.0775-
1004 1.078, 1.0664-1.0668, 1.0407-1.0433, 1.0366-1.0378, respectively. Black solid lines represent
1005 the model of best fit, dotted lines represent the 95% confidence interval of fitting the model, and
1006 dashed lines represent the 95% confidence interval of prediction when applying the model.
1007 Different symbols for the scatter points represent the different categories of plant functional
1008 types (in (a)) or sub-categories of plant functional types (b-f) as defined in Fig. S1. Datasets with
1009 $D_{130} < 10$ cm were not used in the $F_{\text{Other-L}}$ model. R^2 and RMSE refer to the linear regression of
1010 predicted vs. observed AGB.

1011

1012 **Fig 5** Box plots describing the Proportion of the 95% confidence interval (CI) of generalised
1013 allometry prediction overlapped by the 95% CI of species-specific allometry prediction when the
1014 level of generalisation was; (a) plant functional type, or (b) universal, $\text{All}_{\text{Universal}}$. These results

1015 are for prediction of $\ln(\text{AGB}_{\text{Indiv}})$ using models (Eq. 2) across 53 species and a total of 92
1016 scenarios where D_{10} was assumed to be 10 cm ($N = 53$), 50 cm ($N = 28$), or 100 cm ($N = 11$).
1017 Note, species presented here are those reported in Table S3, each of which had an $N > 50$. Only
1018 species sampled to these larger sizes were represented in scenario of D_{10} of 50 and 100 cm.

1019
1020 **Fig 6** Relationship between total above-ground biomass ($\text{AGB}_{\text{Stand}}$) from whole-plot harvesting
1021 at 17 contrasting stands (Table 2) and that predicted for those stands through the application of
1022 three scenarios of increasing generalisation of allometric models applied: (a) information on
1023 species identity of each individual at each of the test sites was utilised, and for species that were
1024 represented by the 53 available species-specific models, these were applied (Eq. 2 using
1025 parameters given in Table S3), while for all other species, the appropriate plant functional type
1026 model was applied (Eq. 2 using parameters given for F_{Shrub} , F_{Multi} , F_{Euc} , $F_{\text{Other-H}}$ and $F_{\text{Other-L}}$ in
1027 Table 3), (b) species identification and/or species-specific models were assumed to be
1028 unavailable, and so plant functional type models were applied (Eq. 2 using parameters given for
1029 F_{Shrub} , F_{Multi} , F_{Euc} , $F_{\text{Other-H}}$ and $F_{\text{Other-L}}$ in Table 3), and (c) species identification, species-specific
1030 models and plant functional type models were assumed to be unavailable, and so the universal
1031 model ($\text{All}_{\text{Universal}}$) was applied (Eq. 2 using parameters given for $\text{All}_{\text{Universal}}$ in Table 3). In all
1032 scenarios, the MM correction factor was applied when back-transforming predictions. Grey
1033 dashed line represents the 1:1 line. EF indicates model efficiency. Black solid line represents the
1034 line of best fit, with slope, intercept and fit statistics as shown. Values in parentheses are the 95%
1035 prediction interval of the slope and intercept.

1036 **Supplementary material**

1037 **Table S1** Number of individuals obtained for each plant functional type from various sources.

1038 *Indicates sources where data were sourced directly from the publication. References for
1039 published data sources are listed below.

Sources	F _{Shrub}	F _{Multi}	F _{Euc}	F _{Other-H}	F _{Other-L}	Total N
Paul <i>et al.</i> , (2013a)	600	973	1760	155	9	3,497
Peck <i>et al.</i> , (2012)	~	994	~	~	~	994
Spencer B, pers. com.	~	647	201	74	~	922
Paul KI, pers. com.	41	191	560	6	~	798
McAthur G, pers. com.	229	469	~	4	~	702
Bastin, (2014)	617	6	~	~	~	623
Sinclair J, pers. com.	312	64	69	119	~	564
Waterworth <i>et al.</i> , (2016); Ximenes <i>et al.</i> , (2006)	~	24	482	~	~	506
Hobbs <i>et al.</i> , (2013)	35	231	115	18	~	399
Wildy D, pers. com.	~	372	~	~	~	372
Falster <i>et al.</i> , (2015)	330	~	~	~	~	330
Sochacki <i>et al.</i> , (2007)	~	~	208	~	115	323
Rance <i>et al.</i> , (2012)	~	~	302	~	~	302
Huxtable D., pers. com.	~	297	~	~	~	297
O'Connell <i>et al.</i> , (1999)	~	~	263	~	~	263
Snowdon P., pers. com.	~	~	~	~	213	213
Green, (2013)	73	62	37	26	~	198
Williams <i>et al.</i> , (2005)	~	~	171	21	~	192
Ritson <i>et al.</i> , (2015)	~	78	97	10	~	185
Brooksbank & Goodwin, (2012)	~	181	1	~	~	182
O'Brien N., pers. com.	~	~	86	~	74	160
Bi <i>et al.</i> , (2015)*	~	~	150	~	~	150
Ritson P, pers. com.	~	150	~	~	~	150
Barton & Parekh, (2006)	~	~	145	~	~	145
Cromer & Williams, (1982)	~	~	141	~	~	141
Grove <i>et al.</i> , (2007)	~	139	~	~	~	139
Bartle <i>et al.</i> , (2012)	~	124	~	~	~	124
Paul <i>et al.</i> , (2010)	42	24	41	14	~	121
Ritson & Sochacki, (2003)	~	~	~	~	114	114
Paul <i>et al.</i> , (2013b)	~	107	~	~	~	107
Forrest, (1969)	~	~	~	~	99	99
Hawkins <i>et al.</i> , (2010)	60	29	~	4	~	93
Montagu <i>et al.</i> , (2005)	~	~	88	~	~	88
England <i>et al.</i> , (2007)	12	35	35	~	~	82
Jonson & Freudenberger, (2011)	~	58	14	10	~	82
Forrester <i>et al.</i> , (2012)	~	~	59	~	~	59
Turner & Lambert, (1986); Turner <i>et al.</i> , (1992)	~	~	57	~	~	57
Lambert, (1979); Turner & Lambert, pers. com.	~	~	56	~	~	56
Brand (1999)	~	~	55	~	~	55
Attiwill P, pers. com.	~	~	32	~	16	48
Turner & Lambert, (1986, 2014)	~	~	46	~	~	46
Ximenes (2014)	~	~	44	~	~	44
Sudmeyer <i>et al.</i> , (2008)	~	20	20	~	~	40

Turner & Lambert, (1983, 2008); Turner, (1986)	~	~	39	~	~	39
O'Grady <i>et al.</i> , (2000)	~	~	31	6	~	37
Forrest & Ovington (1970)	~	~	~	~	36	36
Theiveyanathan S, pers. com.	~	~	36	~	~	36
O'Grady <i>et al.</i> , (2006)	~	~	33	~	~	33
Jonson, (2010)	~	10	22	~	~	32
Stewart <i>et al.</i> , (1979)	~	~	31	~	~	31
Zerihun, <i>et al.</i> , (2006)	~	~	31	~	~	31
Groves, (1987)*	15	~	17	~	~	32
Snowdon <i>et al.</i> , (2000)	~	~	29	~	~	29
Birk & Turner, (1992)	~	4	24	~	~	28
Hingston & Galbraith, (1998)	~	~	26	~	~	26
Bennett <i>et al.</i> , (2014)	~	25	~	~	~	25
Bi <i>et al.</i> , (2001) *	~	11	14	~	~	25
Dargavel, (1970)	~	~	~	~	25	25
Feller, (1980)	~	3	22	~	~	25
Bennett <i>et al.</i> , (1997)*	~	~	24	~	~	24
Paul <i>et al.</i> , (2008)	~	~	24	~	~	24
Specht & West, (2003)	~	~	12	6	6	24
Hingston <i>et al.</i> (1990)	~	~	22	~	~	22
Lewis T, pers. com.	~	~	12	~	10	22
Montagu K, pers. com.	14	~	8	~	~	22
Pinkard L, pers. com.	~	~	22	~	~	22
Applegate, (1982)	~	~	21	~	~	21
Sudmeyer & Daniels, (2010)	~	21	~	~	~	21
Cromer <i>et al.</i> , (1993)	~	~	20	~	~	20
Turner <i>et al.</i> , (1989)	~	~	~	19	~	19
Holland, (1969)*	~	19	~	~	~	19
Zerihun & Montagu, (2004)	~	~	~	~	19	19
Carter & White, (2009)	~	18	~	~	~	18
Hamilton <i>et al.</i> , (2005)	~	~	18	~	~	18
Barton & Montagu, (2006)	~	~	16	~	~	16
Resh <i>et al.</i> , (2003)	~	~	16	~	~	16
Birk & Turner, pers. com.	~	~	15	~	~	15
Adams & Attiwill, (1988)	~	~	13	~	~	13
Bradford M, pers. com.	~	2	~	10	~	12
Adams M, pers. com.	~	~	11	~	~	11
Ashton, (1976)*	~	~	11	~	~	11
Baker, (1982)	~	~	11	~	~	11
Baker <i>et al.</i> , (1984)	~	~	~	~	11	11
Specht, (2000)	~	~	11	~	~	11
Guo <i>et al.</i> , (2008)	~	~	~	~	10	10
Stewart <i>et al.</i> , (1981)	~	~	~	~	10	10
Forrester <i>et al.</i> , (2004)	~	8	~	~	~	8
Turner <i>et al.</i> , (1986); Turner & Lambert, (2014)	~	~	6	~	~	6
Grove, (1988)	~	~	6	~	~	6
Rose B, pers. com.	3	1	2	~	~	6
Lewis, (1978)	~	~	5	~	~	5
Keith <i>et al.</i> , (2003)*	~	~	5	~	~	5
Westman & Rogers, (1977)	~	~	2	1	~	3

Baldwin & Stewart, (1987)	~	~	1	~	~	1
<i>Total</i>	<i>2,383</i>	<i>5,397</i>	<i>6,004</i>	<i>503</i>	<i>767</i>	<i>15,054</i>

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1240

1241 Table S2 Empirical relationships used to ‘gap fill’ missing D and H measurements using the
 1242 equation $Y = c + d X$, where X may be D (cm) or H (m). All relationships were highly
 1243 significant ($P < 0.0001$), with no log-transformations required.

<i>Y</i>	<i>X</i>	<i>c</i>	<i>d</i>	<i>RMSE</i>	<i>R</i> ²	<i>N</i>
<i>D</i> ₁₀	<i>D</i> ₀	0.445 (0.081)	0.879 (0.004)	2.584	0.973	1,540
	<i>D</i> ₃₀	0.155 (0.047)	1.077 (0.003)	1.663	0.984	2,918
	<i>D</i> ₅₀	0.395 (0.050)	1.122 (0.003)	2.007	0.972	4,353
	<i>D</i> ₁₃₀	1.488 (0.074)	1.195 (0.004)	2.690	0.953	3,760
	<i>H</i>	1.201 (0.121)	2.099 (0.020)	6.671	0.574	8,283
<i>D</i> ₁₃₀	<i>D</i> ₀	0.414 (0.181)	0.683 (0.006)	3.577	0.930	991
	<i>D</i> ₁₀	-0.577 (0.061)	0.798 (0.003)	2.198	0.953	3,760
	<i>D</i> ₃₀	-0.397 (0.050)	0.854 (0.003)	1.849	0.970	3,366
	<i>D</i> ₅₀	-0.494 (0.036)	0.912 (0.002)	1.516	0.976	4,686
	<i>H</i>	-2.834 (0.208)	1.924 (0.016)	11.297	0.683	7,003

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1 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
2 which species-specific allometric models for AGB_{Indiv} of the form given in Eq. 2 could be developed. Here RMSE, R^2 , CF, MAPE, and N refer to
3 the standard error of the linear regression, adjusted coefficient of determination, bias correction factor, mean absolute percentage error (based on
4 back-transformed AGB_{Indiv} predictions), and sample size, respectively. All equations fitted were highly significant ($P < 0.001$). The diameter range
5 relevant to each model is indicated in brackets (assuming a minimum diameter (D_{10}) of 0.3 cm). Note: All species-specific models tested in Table 8
6 were based on D_{10} (out of necessity to allow comparison with the $All_{Universal}$ model), but coefficients and provided here for species of F_{Euc} , $E_{Other-H}$
7 and $E_{Other-L}$ were based on the recommended (for single-stemmed trees) D_{130} .

Form	Species	$\ln(a)$	b	RMSE	R^2	CF	MAPE	N
F_{Shrub}	<i>Acacia calamifolia</i> ($D_{10} < 16$ cm)	-2.228 (0.094)	2.398 (0.055)	0.353	0.939	1.0520-1.0618	30.6	127
	<i>Acacia hakeoides</i> ($D_{10} < 21$ cm)	-2.255 (0.095)	2.181 (0.051)	0.341	0.944	1.0463-1.0572	28.4	111
	<i>Acacia hemiteles</i> ($D_{10} < 9$ cm)	-2.920 (0.107)	2.393 (0.077)	0.293	0.948	1.0273-1.0398	22.8	55
	<i>Acacia kempeana</i> ($D_{10} < 26$ cm)	-3.169 (0.042)	2.492 (0.025)	0.376	0.960	1.0689-1.0723	32.8	419
	<i>Eremophila mitchellii</i> ($D_{10} < 37$ cm)	-2.716 (0.143)	2.261 (0.056)	0.370	0.933	1.0580-1.0679	32.6	119
	<i>Eremophila sturtii</i> ($D_{10} < 35$ cm)	-2.848 (0.153)	2.194 (0.063)	0.482	0.926	1.0946-1.1165	46.0	98
	<i>Geijera parviflora</i> ($D_{10} < 50$ cm)	-2.515 (0.192)	2.312 (0.069)	0.452	0.917	1.0743-1.1028	43.4	105
	<i>Senna artemisioides</i> ($D_{10} < 14$ cm)	-2.790 (0.057)	2.144 (0.053)	0.495	0.908	1.1124-1.1262	50.4	167
F_{Multi}	<i>Acacia acuminata</i> ($D_{10} < 34$ cm)	-3.003 (0.073)	2.516 (0.037)	0.373	0.960	1.0636-1.0701	33.8	193
	<i>Acacia aneura</i> ($D_{10} < 49$ cm)	-2.561 (0.126)	2.402 (0.045)	0.373	0.954	1.0577-1.0693	33.7	138
	<i>Acacia harpophylla</i> ($D_{10} < 47$ cm)	-2.789 (0.102)	2.570 (0.035)	0.262	0.982	1.0281-1.0332	21.3	102
	<i>Acacia mearnsii</i> ($D_{10} < 38$ cm)	-2.381 (0.152)	2.348 (0.056)	0.296	0.964	1.0268-1.0416	25.0	67
	<i>Acacia melanoxylon</i> ($D_{10} < 27$ cm)	-2.928 (0.112)	2.478 (0.051)	0.245	0.979	1.0205-1.0277	21.2	53
	<i>Acacia pycnantha</i> ($D_{10} < 26$ cm)	-2.502 (0.118)	2.394 (0.063)	0.433	0.925	1.0781-1.0939	41.6	121
	<i>Acacia saligna</i> ($D_{10} < 46$ cm)	-3.075 (0.145)	2.424 (0.065)	0.420	0.899	1.0746-1.0891	41.0	159
	<i>Eucalyptus incrassata</i> ($D_{10} < 27$ cm)	-3.123 (0.203)	2.488 (0.088)	0.409	0.933	1.0686-1.0796	39.0	59
	<i>Eucalyptus kochii</i> ($D_{10} < 28$ cm)	-2.887 (0.049)	2.439 (0.021)	0.345	0.955	1.0553-1.0609	30.5	631
	<i>Eucalyptus loxophleba</i> ($D_{10} < 37$ cm)	-2.760 (0.037)	2.526 (0.017)	0.361	0.920	1.0651-1.0672	32.3	1,873
	<i>Eucalyptus platypus</i> ($D_{10} < 31$ cm)	-1.851 (0.193)	2.194 (0.079)	0.301	0.942	1.0327-1.0416	23.6	49*
	<i>Eucalyptus polybractea</i> ($D_{10} < 35$ cm)	-2.736 (0.042)	2.483 (0.018)	0.340	0.941	1.0570-1.0593	29.3	1,140
F_{Euc}	<i>Corymbia citriodora</i> ($D_{130} < 34$ cm)	-2.863 (0.053)	2.687 (0.053)	0.214	0.979	1.0169-1.0212	17.8	58

	<i>Corymbia maculata</i> ($D_{130} < 140$ cm)	-2.118 (0.033)	2.433 (0.020)	0.235	0.977	1.0255-1.0275	18.1	353
	<i>Eucalyptus astringens</i> ($D_{130} < 29$ cm)	-1.509 (0.251)	2.346 (0.094)	0.345	0.907	1.0429-1.0564	29.2	65
	<i>Eucalyptus blakeyi</i> ($D_{130} < 71$ cm)	-1.982 (0.091)	2.235 (0.046)	0.265	0.979	1.0210-1.0323	20.4	53
	<i>Eucalyptus camaldulensis</i> ($D_{130} < 63$ cm)	-2.147 (0.087)	2.371 (0.037)	0.332	0.966	1.0477-1.0545	28.7	144
	<i>Eucalyptus cladocalyx</i> ($D_{130} < 52$ cm)	-1.859 (0.144)	2.434 (0.065)	0.339	0.956	1.0405-1.0548	30.3	67
	<i>Eucalyptus crebra</i> ($D_{130} < 50$ cm)	-2.659 (0.090)	2.638 (0.033)	0.301	0.980	1.0376-1.0446	23.8	130
	<i>Eucalyptus globulus</i> ($D_{130} < 64$ cm)	-1.878 (0.024)	2.295 (0.013)	0.308	0.979	1.0466-1.0482	25.5	712
	<i>Eucalyptus grandis</i> ($D_{130} < 40$ cm)	-1.576 (0.036)	2.181 (0.018)	0.318	0.969	1.0485-1.0512	26.4	477
	<i>Eucalyptus largiflorens</i> ($D_{130} < 54$ cm)	-1.474 (0.123)	2.119 (0.052)	0.215	0.964	1.0142-1.0216	17.5	66
	<i>Eucalyptus leucoxylon</i> ($D_{130} < 55$ cm)	-2.394 (0.142)	2.526 (0.049)	0.276	0.981	1.0281-1.0353	23.4	55
	<i>Eucalyptus melanophloia</i> ($D_{130} < 97$ cm)	-3.004 (0.128)	2.699 (0.045)	0.276	0.982	1.0291-1.0362	23.3	71
	<i>Eucalyptus melliodora</i> ($D_{130} < 92$ cm)	-2.139 (0.051)	2.361 (0.020)	0.323	0.978	1.0490-1.0526	26.6	307
	<i>Eucalyptus muelleriana</i> ($D_{130} < 100$ cm)	-2.316 (0.121)	2.457 (0.036)	0.208	0.983	1.0177-1.0205	16.9	80
	<i>Eucalyptus nitens</i> ($D_{130} < 30$ cm)	-1.952 (0.157)	2.240 (0.056)	0.224	0.955	1.0130-1.0239	16.3	78
	<i>Eucalyptus obliqua</i> ($D_{130} < 167$ cm)	-2.866 (0.157)	2.609 (0.042)	0.325	0.968	1.0432-1.0520	28.9	131
	<i>Eucalyptus occidentalis</i> ($D_{130} < 79$ cm)	-2.203 (0.068)	2.517 (0.032)	0.385	0.951	1.0680-1.0757	34.5	329
	<i>Eucalyptus pilularis</i> ($D_{130} < 129$ cm)	-2.633 (0.071)	2.570 (0.023)	0.231	0.988	1.0237-1.0262	17.9	156
	<i>Eucalyptus polyanthemus</i> ($D_{130} < 125$ cm)	-1.907 (0.106)	2.298 (0.040)	0.365	0.980	1.0524-1.0637	32.0	69
	<i>Eucalyptus populnea</i> ($D_{130} < 117$ cm)	-1.799 (0.053)	2.304 (0.017)	0.262	0.986	1.0311-1.0342	22.4	242
	<i>Eucalyptus regnans</i> ($D_{130} < 70$ cm)	-2.576 (0.102)	2.559 (0.040)	0.259	0.987	1.0251-1.0310	22.0	55
	<i>Eucalyptus saligna</i> ($D_{130} < 169$ cm)	-2.131 (0.158)	2.425 (0.051)	0.255	0.975	1.0198-1.0302	21.9	60
	<i>Eucalyptus sideroxylon</i> ($D_{130} < 72$ cm)	-2.167 (0.183)	2.341 (0.064)	0.312	0.951	1.0362-1.0465	26.7	71
	<i>Eucalyptus spathulata</i> ($D_{130} < 42$ cm)	-1.347 (0.048)	2.231 (0.020)	0.209	0.979	1.0207-1.0217	16.7	279
	<i>Eucalyptus tereticornis</i> ($D_{130} < 47$ cm)	-2.368 (0.079)	2.428 (0.033)	0.237	0.975	1.0234-1.0274	18.6	145
	<i>Eucalyptus vegrans</i> ($D_{130} < 15$ cm)	-1.179 (0.212)	2.189 (0.094)	0.216	0.908	1.0144-1.0216	18.0	57
	<i>Eucalyptus viminalis</i> ($D_{130} < 30$ cm)	-2.225 (0.053)	2.316 (0.024)	0.228	0.992	1.0240-1.0259	18.3	373
	<i>Eucalyptus wandoo</i> ($D_{130} < 27$ cm)	-1.807 (0.117)	2.202 (0.055)	0.365	0.957	1.0523-1.0640	29.8	73
F _{Other-H}	<i>Allocasuarina huegeliana</i> ($D_{130} < 29$ cm)	-1.545 (0.114)	2.193 (0.050)	0.256	0.974	1.0242-1.0303	20.5	55
	<i>Callitris glaucophylla</i> ($D_{130} < 69$ cm)	-1.638 (0.066)	2.176 (0.025)	0.276	0.983	1.0333-1.0374	21.4	131
	<i>Casuarina obesa</i> ($D_{130} < 13$ cm)	-1.526 (0.135)	2.181 (0.057)	0.212	0.947	1.0096-1.0214	17.7	84
F _{Other-L}	<i>Pinus radiata</i> ($10 < D_{130} < 49$ cm)	-2.435 (0.087)	2.407 (0.031)	0.189	0.942	1.0162-1.0178	15.3	376
	<i>Pinus pinaster</i> ($10 < D_{130} < 47$ cm)	-2.664 (0.134)	2.484 (0.043)	0.139	0.983	1.0054-1.0121	11.5	61

1 *Included here as N ~ 50.

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Fig S1 Diagram depicting the categorisation of vegetation into five categories of functional type, and how these were further subdivided into sub-categories and species in order to assess four levels of generalisation 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 sub-category (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. $N > 50$). Definition of functional type sub-categories were as follows; F_{Shrub_A} (61%): 40 different genera of shrubs or small trees, with the three most common genera of shrubs being *Eremophila*, *Melaleuca* and *Senna*; F_{Shrub_B} (39%): Shrubs or small trees from the genus *Acacia*; F_{Multi_A} (76%): Mallee eucalypts. There were 32 species of mallee eucalypts, although the three most common species were *E. loxophleba*, *E. polybractea* and *E. kochii*; F_{Multi_B} (24%): *Acacia* trees; F_{Euc_A} (91%): *Eucalyptus* genus; F_{Euc_B} (9%): Genera of *Corymbia* or *Angophora*; F_{Other-H_A} (68%): pine-like (in that they have foliage that resembles pine needles) genera of trees, including *Casuarina*, *Allocasuarina*, *Callitris* and *Grevillea*. [Note: *Callitris* is a gymnosperm (softwood), but was included in this category given its very dense wood which is similar to hardwood species]; F_{Other-H_B} (23%): 20 different rainforest tree genera of angiosperms; F_{Other-H_C} (9%): genera of *Abrophyllum*, *Banksia*, *Erythrophleum*, *Lophostemon*, *Pittosporum* and *Terminalia*; F_{Other-L_A} (83%): *Pinus radiata* (the most commonly established softwood plantation species in high rainfall regions of temperate Australia); F_{Other-L_B} (15%): *Pinus pinaster* (the most commonly established softwood plantation species in low rainfall regions of

1 Mediterranean Western Australia); F_{Other-L_C} (2%): other species of softwood trees (e.g. species from the genera of either
2 *Araucaria*, *Agathis* or *Pinus*).

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