

# 1 **Testing the generality of below-ground biomass allometry** 2 **across plant functional types at the continental scale**

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35 plant functional types

36

### 37 **Abstract**

38 Accurate quantification of below-ground biomass (BGB) of woody vegetation is critical to  
39 understanding ecosystem function and potential for climate change mitigation from sequestration  
40 of biomass carbon. We compiled 2 054 measurements of individual tree and shrub biomass from  
41 across a broad range of ecoregions (arid shrublands to tropical rainforests) to develop allometric  
42 models for prediction of BGB. We found that the relationship between BGB and stem diameter  
43 was generic, with a simple power-law model having a BGB prediction efficiency of 72–93% for  
44 four broad plant functional types: (i) shrubs and *Acacia* trees, (ii) multi-stemmed mallee eucalypts,  
45 (iii) other trees of relatively high wood density, and; (iv) a species of relatively low wood density,  
46 *Pinus radiata*. There was little improvement in accuracy of model prediction by including  
47 variables (e.g. climatic characteristics, stand age or management) in addition to stem diameter  
48 alone. We further assessed the generality of the plant functional type models across 11 contrasting  
49 stands where data from whole-plot excavation of BGB were available. The efficiency of model  
50 prediction of stand-based BGB was 93%, with a mean absolute prediction error of only 6.5%, and  
51 with no improvements in validation results when species-specific models were applied. Given the  
52 high prediction performance of the generalised models, we suggest that additional costs associated  
53 with the development of new species-specific models for estimating BGB are only warranted when  
54 gains in accuracy of stand-based predictions are justifiable, such as for a high-biomass stand  
55 comprising only one or two dominant species. However, generic models based on plant functional  
56 type should not be applied where stands are dominated by species that are unusual in their  
57 morphology and unlikely to conform to the generalised plant functional group models.

58

59

## 60 **Introduction**

61 Both above-ground biomass (AGB) and below-ground biomass (BGB) contribute to the  
62 woody vegetation sink within the global carbon budget (Le Quéré *et al.*, 2015). Climate change  
63 may result in shifts in the ratio of tree BGB to AGB (e.g. via changes in water deficit that affect  
64 partitioning or the size distribution of trees), with far-reaching consequences for the global carbon  
65 budget (Ledo *et al.* 2018). However, BGB cannot be quantified using remote sensing metrics as  
66 has been done for the AGB component (Haverd *et al.*, 2013; Mitchard *et al.*, 2013; Chen *et al.*,  
67 2015). Therefore, the development of models to explain BGB is critical to informing predictions  
68 of biomass yields or biomass carbon stocks (Richards & Evans 2004).

69 BGB can be estimated from AGB at either an individual- or stand-level through the use of  
70 root-to-shoot ratios (BGB:AGB, Ledo *et al.*, 2018), and this approach has merit when broad-scale  
71 AGB estimates are obtained via remote sensing products rather than via field-based assessments.  
72 However, this approach has limitations. Estimating BGB based on predictions of AGB are subject  
73 to relatively high uncertainties; for example, mean absolute prediction error of AGB was 15–39%  
74 and 13% at the individual- and stand-level, respectively, for plant functional types across the  
75 Australian continent (Paul *et al.*, 2016). In contrast, if BGB of an individual is predicted by  
76 applying verified allometric models to field measurement of stem diameter ( $D$ ), the uncertainty is  
77 likely to be much lower because errors in  $D$  estimation are relatively small (e.g. 2–7%, Paul *et al.*,  
78 2017a). Moreover, BGB:AGB defaults obtained from the average of multiple stands of a given  
79 ecosystem (Mokany *et al.*, 2006) do not explicitly account for variations in stand density and the  
80 mix of species; both of which influence BGB (Westman & Rogers, 1977; Bernardo *et al.*, 1998;  
81 Ritson & Sochacki, 2003; Xue *et al.*, 2011; Gonzalez *et al.*, 2013). Stand-based estimates of BGB,  
82 resulting from application of allometric models with  $D$  as a predictor variable to each individual  
83 within a stand, may inherently account for stand density and species-mix.

84 When developing allometric models for prediction of BGB of woody plants, it is unclear  
85 to what extent data should be pooled or separated according to their morphological, phylogenetic

86 and/or phenological characteristics; variation often encapsulated by classification of species into  
87 plant functional types. It is also unclear whether the inclusion of stand characteristics or bioclimatic  
88 variables improves the performance of BGB allometric models above that attained when using *D*  
89 alone. A true test of the accuracy of such models is a direct validation at the stand-level by  
90 comparing allometry-predicted BGB against that measured through whole-plot excavation.  
91 Although such stand-level validation has been undertaken previously by Paul *et al.* (2014) for  
92 young plantings in southern Australia, no such validation has been undertaken for more broadly-  
93 applicable BGB allometric models derived from root data sampled from both planted and natural  
94 systems, and across a range of stand ages and ecosystem types.

95         Australia provides a good case study for testing generalised allometric models given its  
96 long history of research contributions to BGB data sets (e.g. Forrest, 1969; Baldwin & Stewart,  
97 1987; Applegate, 1982) spanning a broad range of ecoregions (i.e. arid shrublands to tropical  
98 rainforests) with plant functional types ranging from shrubs and short multi-stemmed trees to some  
99 of the largest trees in the world (Sillett *et al.*, 2015; Specht & Specht, 2002, Specht & Specht,  
100 2013). Improving the assessment of Australia's vegetation carbon sink is of global importance as  
101 the high inter-annual variability that is characteristic of the global vegetation sink is in large part  
102 due to variability in the carbon capture of the semi-arid ecosystems of Australia (Houghton *et al.*,  
103 2012; Poulter *et al.*, 2014; Ballantyne *et al.*, 2015).

104         Here we collated destructively-measured BGB datasets from individual trees and shrubs  
105 sampled from a broad range of stands from differing climatic regions of Australia, including those  
106 in natural ecosystems or otherwise established through human intervention (i.e. planted). We then  
107 analysed this data set to assess whether *D*-based allometric models of BGB were improved: (i)  
108 when based on species rather than broader categories such as plant functional groups; and (ii) by  
109 the inclusion of stand characteristics (age and management) or climatic variables. Our objectives  
110 were firstly to recommend the most appropriate allometric model(s) for estimating BGB in  
111 ecosystems across the Australian continent, and secondly to quantify the accuracy of the

112 recommended model(s) when tested against direct measurements of stand-level BGB obtained  
113 using whole-plot excavation across a range of contrasting sites. The recommended models for  
114 predicting BGB were applied together with those previously recommended for prediction of AGB  
115 (Paul *et al.*, 2016) to provide estimates of BGB:AGB ratios for plant functional types of differing  
116 allometry.

117

## 118 **Methods**

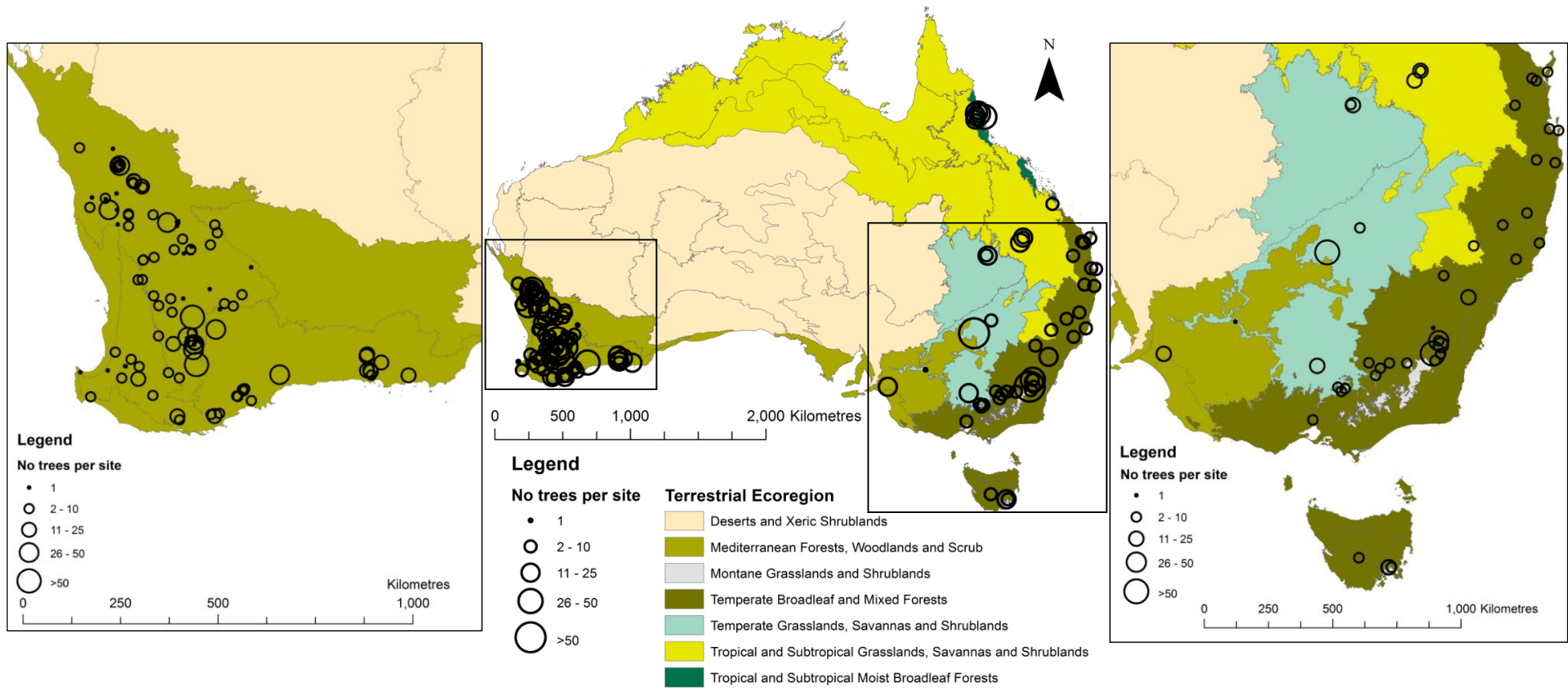
### 119 *Data set*

#### 120 *Data compilation*

121 Data sets of BGB from destructive harvesting of 2 054 individual trees and shrubs were  
122 obtained from 38 published and unpublished sources (Paul *et al.*, 2017b). These were from a range  
123 of managed and natural woody ecosystems across 210 sites in various Australian ecoregions (Fig.  
124 1).

125 BGB was defined here as tree and shrub roots of >2 mm in diameter extracted from a soil  
126 depth of 2–3 m, including stem biomass to a height of 10 cm above ground (i.e. the ‘stump’). This  
127 method of root extraction ensured the majority of root biomass was captured because: (i) fine roots  
128 (< 2 mm) of woody plants only comprise 8–14% of the total root biomass, depending on the AGB  
129 (Applegate, 1982; Misra *et al.*, 1998; Li *et al.*, 2003; Mokany *et al.*, 2006), and (ii) typically 95%  
130 of all roots are found within 2 m of the ground surface (Schenk and Jackson, 2002). The stump  
131 was included in the calculation of BGB because 10 cm is a common height targeted in operational  
132 harvesting, and hence, remains together with the roots as part of the unharvested biomass.

133 When sampling for BGB, sub-samples (0.5–25 kg each, depending on the size of the  
134 individual) were used for percentage moisture content determination, with the lignotuber and/or  
135 root stump sampled separately from other coarse roots. These sub-samples were oven-dried at  
136 70°C to constant weight, with the estimates of moisture content of components used to calculate  
137 the total dry weight of BGB (kg dry matter (DM) of an individual plant).



138

139 **Fig1** Location of trees or shrubs sampled for biomass by terrestrial ecoregion across Australia (DSWPC, 2015).

140 Each tree or shrub excavated for BGB sampling also had a measure of stem diameter ( $D$ ,  
141 measured over bark). For single-stemmed trees,  $D$  was measured at 130 cm height above ground  
142 level ( $D_{130}$ ); the most common international standard (e.g. Picard *et al.*, 2012). However, for  
143 species of shrubs and small multi-stemmed trees where  $D_{130}$  measurements introduced errors due  
144 to the presence of multiple stems at this height, or where the individual was too small to have a  
145 measurable  $D_{130}$ , the  $D$  of each stem was typically measured at 10 cm height above the ground  
146 ( $D_{10}$ ). For multi-stemmed individuals, a single, pooled  $D$  estimate was obtained from the diameter  
147 equivalent representing the sum of the cross-sectional areas of each of the individual stems.

148

#### 149 *Functional groups*

150 The data set included 128 species. Only seven species (*Eucalyptus polybractea*, *E.*  
151 *loxophleba*, *E. kochii*, *E. globulus*, *E. occidentalis*, *Pinus pinaster* and *P. radiata*) were sampled  
152 in sufficient numbers ( $N > 100$  individuals) to have confidence in developing species-specific  
153 models that are likely to reflect the true population (i.e. targeted coefficient of variation in  
154 predicted BGB being ca 5%; Roxburgh *et al.*, 2015). This relatively high sample size requirement  
155 was based on the assumption that, due to measurement errors being relatively high when extracting  
156 roots from the soil, species-specific BGB allometric models are likely to have a relatively high  
157 inter-sample variability, with residual standard deviations being in the order of about 0.50.

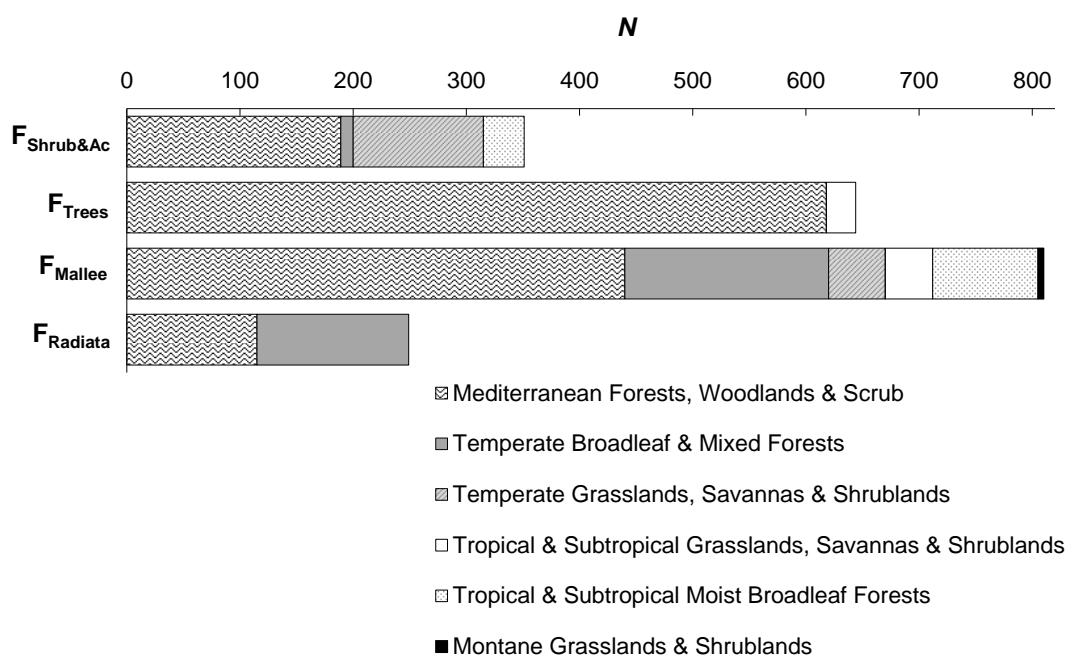
158 Because the sample size of most (95%) species was insufficient to assess the allometry of  
159 BGB at a species-specific level, we categorised all species in the data set into plant functional  
160 types of unique physiognomic growth form (Gitay & Noble, 1997), i.e. groupings of plant species  
161 with distinctive branch architecture and/or stem wood density. There is evidence that such an  
162 approach negates the need to explicitly account for stem wood density in allometric models of  
163 biomass (Paul *et al.* 2016). The groups used were:

- 164 i. *F<sub>Shrub&Ac</sub>*. Shrubs and small multi-stemmed trees. This group included the common  
165 Australian genus of *Acacia* (36% of the *F<sub>Shrub&Ac</sub>* data set), which comprised both shrub  
166 (31%, e.g. *A. hemiteles*, *A. murrayana* and *A. victoriae*) and small tree (69%, e.g. *A.*  
167 *saligna*, *A. acuminata* and *A. aneura*) forms. The group also included another 18 genera of  
168 shrubs (generally < 2 m height), with the most common genera being *Eremophila*,  
169 *Dodonaea* and *Melaleuca*.
- 170 ii. *F<sub>Mallee</sub>*. Multi-stemmed (mallee) trees from the genus *Eucalyptus*, and which commonly  
171 have a lignotuber and relatively high wood density: mean  $0.88 \pm 0.08 \text{ g cm}^{-3}$  standard  
172 deviation, largely (93%) based on estimates from global stem density database (Chave *et*  
173 *al.*, 2009; Zanne *et al.*, 2009), with the remainder being directly measured. This group  
174 included 17 species, with the most common being those typically established in  
175 monoculture plantings, such as *E. loxophleba* subsp. *lissophloia* (41%), *E. polybractea*  
176 (24%) and *E. kochii* subsp. *plenissima* and subsp. *borealis* (18%). Other species that were  
177 commonly sampled included *E. loxophleba* that were not subsp. *lissophloia*, *E. porosa*,  
178 and *E. platypus*.
- 179 iii. *F<sub>Tree</sub>*. Typically single-stemmed trees of relatively high wood density: mean  $0.69 \pm 0.16 \text{ g}$   
180  $\text{cm}^{-3}$  standard deviation, largely (80%) based on estimates from the global stem density  
181 database, with the remainder being directly measured. This group included 35 genera, most  
182 commonly *Eucalyptus* (or the closely-related *Corymbia*) (77%) from either hardwood  
183 plantations or native forests or woodlands. Other well-sampled species included the  
184 introduced *Pinus pinaster* (14%), which is a common low-rainfall plantation species in  
185 Australia. There was a large diversity of genera sampled from the tropical ecoregion, with  
186 the most common being species from the genera *Argyrodendron*.
- 187 iv. *F<sub>Radiata</sub>*. An introduced tree species *Pinus radiata*, of relatively low stem woody density:  
188 mean  $0.40 \pm 0.04 \text{ g cm}^{-3}$  standard deviation, largely (86%) based on estimates from the



189 global stem density database, with the remainder being directly measured. This species is  
 190 the most common species in softwood plantations within high rainfall regions of temperate  
 191 Australia.

192 The  $F_{Shrub\&Ac}$ ,  $F_{Mallee}$ ,  $F_{Tree}$ , and  $F_{Radiata}$  groupings comprise about 20, 30, 40 and 10% of the  
 193 data set respectively. The geographical extent of the Australian terrestrial ecoregions is shown in  
 194 Fig. 1, and the representation of these ecoregions in the sampling for each plant functional type is  
 195 shown in Fig. 2. The ‘Mediterranean forests, woodlands and scrub’ was the most well represented  
 196 ecoregion (66%).



197  
 198 **Fig 2** Number of individuals ( $N$ ) sampled of each of the four plant functional types by ecoregion (defined in Fig. 1).

199  
 200 *Harmonisation of BGB data estimates*

201 Because measurement of BGB is resource-intensive and challenging, among the 38 studies  
 202 used to build the data set (Paul *et al.*, 2017b), various protocols were utilised, based on the  
 203 resources available and the type of ecosystem sampled. The most common protocol used (51% of  
 204 the data obtained) was to include the stump in the BGB sampling, and to excavate the area around  
 205 the individual to the mid-point boundaries with neighbouring trees, termed ‘Voronoi polygons’

206 (Wildy & Pate, 2002; Saint-Andre *et al.*, 2005). Three other protocols were used for the remaining  
207 49% of the data set. For 20% of the data set, the stump was included with the AGB. In these cases,  
208 stump biomass was estimated using empirical data as described by Paul *et al.* (2014), and added  
209 to the BGB. For 15% of the data set, BGB was excavated in a set area (generally 4 m<sup>2</sup> around a  
210 tree base). Based on empirical evidence described by Paul *et al.* (2014), it was assumed that only  
211 70.2% of BGB was excavated and so an additional 29.8% was added to the mass sampled. Finally,  
212 for 14% of the data set, excavation of the BGB of an individual tree or shrub was not possible due  
213 to the close spatial association of the target individual with nearby individuals (known as  
214 ‘clustering’). In such instances, relatively large areas (50–200 m<sup>2</sup>) were excavated and the BGB  
215 of the entire vegetation ‘cluster’ was provided. Although root stumps belonging to each individual  
216 could be identified, the remaining coarse roots were allocated to each individual within the  
217 ‘cluster’ in accordance with its proportional contribution to the total AGB measured for that  
218 ‘cluster’.

219 As quantified by Paul *et al.* (2014), uncertainties in allometry-predicted BGB result from  
220 assumptions required to harmonise the BGB data sets derived from alternative protocols. These  
221 uncertainties may be reduced as additional data becomes available to inform the adjustment factors  
222 applied, e.g. varying the adjustment factor for set area excavation based on the size of the tree  
223 and/or the stand density.

224

#### 225 *Ancillary stand and site data*

226 Data about the stand and site from which an individual was sampled were also collated  
227 (Table 1). Stand variables included whether the site was ‘natural’ (i.e. naturally-regenerated  
228 shrubland, woodland or forest) or managed (i.e. human-induced establishment from planting of  
229 nursery stock, direct seeding or human-induced natural regeneration). It was noted if a stand was  
230 younger than 20 years. There was insufficient replication, and/or confidence in exact ages, to  
231 facilitate further age-class groupings. Site factors included long-term mean annual rainfall (MAR,

232 mm yr<sup>-1</sup>) and mean annual temperature (MAT, °C) (BoM, 2015; 1970–2015, 2.5 km resolution).

233

#### 234 *Standardising diameter estimates, and outlier checking*

235 For many individuals in the data set,  $D$  was measured at multiple heights, thereby allowing  
236 derivation of generic relationships for prediction of  $D$  at a given height based on  $D$  measured at  
237 another height (see Table S2 of Paul *et al.*, 2016). These relationships were used to ‘gap-fill’  $D$   
238 estimates where required, with  $D_{130}$  or  $D_{10}$  being estimated for 28% of the 2 054 individuals within  
239 the data set.

240 Very small individuals ( $D_{10} < 0.6$  cm and  $D_{130} < 1.1$  cm) were not included in the database  
241 because they were considered unlikely to conform to biomass scaling laws typical of woody plants  
242 as they had relatively little secondary thickening (Niklas, 2004; Enquist *et al.*, 2007). Data for a  
243 further 38 individuals from 10 sites (and six sources) were also excluded as outliers. Here,  
244 individuals were defined as outliers if their measured BGB fell outside the 99.9% confidence  
245 interval of prediction of the appropriate plant functional type model. Although the BGB of these  
246 outliers were assumed to come from a normally-distributed population and had no major influence  
247 on model fit, they were nonetheless removed on the basis that they were highly unlikely values of  
248 BGB for the measured dimensions, and were most likely due to errors in data entry.

249 **Table 1** Characteristics collated for the entire data set (*AllUniversal*), or for each of the four categories of plant functional types (*FShrub&Ac*, *FMallee*, *FTree*, and *FRadiata*) Abbreviations as follows: 'N', total  
 250 number of individuals; '*D*<sub>10</sub>' and '*D*<sub>130</sub>', mean stem diameter measured over bark at 10 cm and 130 cm respectively; 'N stand', number of stands from which the trees or shrubs were harvested; '*N* spp.',  
 251 number of species that were sampled; '%Age<20 yrs', percentage of individuals from stands where age was known to be <20 years old; '%Managed', percentage of individuals from stands that were  
 252 managed rather than naturally regenerated without human intervention; 'MAT', long-term mean annual temperature, averaged across sites from which individuals were sampled; and 'MAR', long-  
 253 term mean annual rainfall, averaged across sites from which individuals were sampled. Where relevant, standard deviations (and for *D*<sub>10</sub> and *D*<sub>130</sub>, the range in values) are provided in parentheses.

Type	N	<i>D</i> <sub>10</sub> (cm)	<i>D</i> <sub>130</sub> (cm)	<i>N</i> stands	<i>N</i> spp.	%Age < 20 years	%Managed	MAT (°C)	MAR (mm yr <sup>-1</sup> )
<i>AllUniversal</i>	2 054	17.0 (19.6; 0.6–177.0)	NA	210	128	72.0	77.4	16.9 (2.5)	591 (510)
<i>FShrub&amp;Ac</i>	351	11.8 (10.6; 0.6–98.4)	NA	45	33	41.0	43.0	18.8 (2.0)	532 (496)
<i>FMallee</i>	644	11.8 (10.0; 1.0–81.1)	NA	100	17	88.8	97.2	17.0 (1.5)	393 (75)
<i>FTree</i>	810	24.4 (27.1; 2.1–177.0)	18.9 (21.2; 1.1–138.8)	72	77	65.8	69.5	16.7 (2.9)	781 (683)
<i>FRadiata</i>	249	13.8 (8.8; 3.6–49.6)	9.8 (7.8; 1.4–41.4)	4	1	92.4	100.0	14.6 (1.8)	569 (211)

254

255 *Allometric model*

256 There are alternative approaches for developing statistical models of the allometric scaling  
257 relationships of biomass. Traditionally, logarithmic transformations have been used in order to  
258 apply linear regression, with back-transformation required. An alternative is the application of  
259 nonlinear statistical procedures. There is a lack of consensus in the literature over the preferred  
260 approach (e.g. Packard et al. 2009 *cf.* Kerkhoff and Enquist 2009). We elected to use the traditional  
261 approach given: (i) critical reviews or tests of different approaches support the validity of this  
262 approach (e.g. Xiao et al. 2011; Ballantyne 2013; Sileshi 2014), and; (ii) it provides consistency  
263 with a complementary study (based on similar datasets) of AGB allometry (Paul et al. 2017).  
264 Bayesian approaches to parameter estimation have also been successfully applied and they offer  
265 great promise, particularly for combining predictions from multiple alternative allometric models  
266 (e.g. Mavouroulou et al. 2014), and for including prior information when constructing or updating  
267 existing allometric models with new data (Zianis et al 2016). Nonetheless, for large samples sizes  
268 as used in our work, the least squares regression and the Bayesian approaches yield the identical  
269 results (Table 2 of Sileshi 2014; Fig 5 of Zapata et al. 2012).

270 Once the data set was ‘cleaned’ as described, the simple power-law allometric model was  
271 used to predict BGB of an individual tree or shrub based on the explanatory variable,  $X$  (Eqn. 1).  
272 Eqn. 1 was linearized by logarithmic transformation (Eqn. 2) so that coefficients ( $a$  and  $b$ ) could  
273 be estimated using ordinary least squares linear regression analyses, with data corrected for  
274 heteroscedasticity, such that residual errors were normally distributed on the logarithmic scale ( $\epsilon$ ;  
275 which becomes a multiplicative error in the power model,  $\epsilon'$ , Picard *et al.* (2012)):

276 
$$\text{BGB} = a \times X^b \times \epsilon'$$
 (1)

277 
$$\ln\text{BGB} = \ln a + b \times \ln X + \epsilon$$
 (2)

278 Eqn. 2 was applied to model the entire dataset (universal model,  $All_{Universal}$ ), and to the data sets of  
279 the four plant functional types:  $F_{Shrub\&Ac}$ ,  $F_{Mallee}$ ,  $F_{Tree}$  and  $F_{Radiata}$ . The simplest form of Eqn. 2 had

280  $X = D$ , where  $D$  is  $D_{10}$  or  $D_{130}$  for  $F_{Tree}$  and  $F_{Radiata}$ , and by necessity,  $D_{10}$  for  $F_{Shrub\&Ac}$  and  $F_{Mallee}$ ,  
281 and hence, *AllUniversal*.

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

292

### 293 *Statistical analysis*

#### 294 *Model checking and selection criteria*

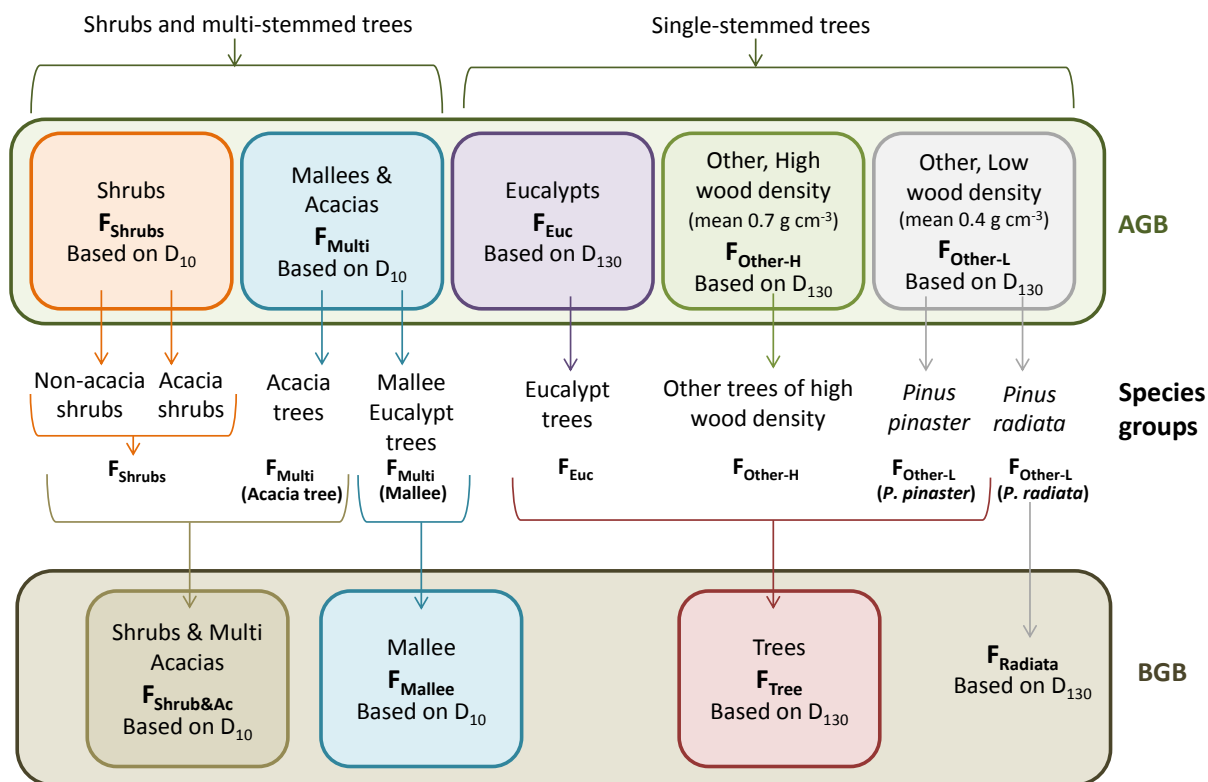
295 To confirm the validity of tested models, we checked that there was no heteroscedasticity  
296 through examination of probability and quantile plots of the residuals. Then, the performance of  
297 valid models of lnBGB (Eqn. 2) was quantified using four fit statistics: (i) standard errors of the  
298 coefficients  $\ln a$  and  $b$ , (ii) residual mean square error, *RMSE*, (iii) adjusted coefficient of  
299 determination,  $R^2$ , (iv) Akaike's information criterion (*AIC*, Burnham & Anderson, 2004), where  
300 the lowest *AIC* indicated the most parsimonious model, and to further aid comparisons among  
301 alternative models of differing numbers of parameters, (v) the Mallows'  $C_p$  statistics (Mallows,  
302 1973) were calculated, where a  $C_p$  higher than the number of explanatory variables indicates poor  
303 model fit.

304 Using back-transformed BGB predictions, the predictive performance was quantified by:  
305 (i) model efficiency, expressed as a proportion (*EF*, Soares *et al.*, 1995), where a model efficiency

306 of 1.0 indicates perfect fit, and a value of 0.0 indicates the predictions are no better than simply  
307 using the mean of the observations, and (ii) average bias, or mean of the residuals expressed in  
308 absolute terms and provided as a proportion (%) of the observed value (i.e. mean absolute  
309 prediction error, 'MAPE', using back-transformed BGB predictions) (Sileshi, 2014).

### 310 311 *Alignment of plant functional groupings for BGB and AGB allometries*

312 To facilitate the application of allometric models of both AGB and BGB to various stands  
313 across Australia, the sub-categories of plant functional groupings used for BGB were consistent  
314 with those applied for allometric models of AGB (Paul *et al.*, 2016, see Fig. S1). The eight species  
315 groups identified by Paul *et al.* (2016), and shown in Fig. 3, were only pooled together when their  
316 allometries for BGB did not statistically differ. General linear modelling (GLM) was used to assess  
317 whether  $\ln\text{BGB}$  prediction from  $\ln D$  was significantly influenced by species group, and if so,  
318 which species groupings had statistically ( $P < 0.05$ ) unique BGB allometry. Although alternative  
319 statistical approaches are available for testing whether species or groups of species have  
320 statistically-significant allometry, these provided results consistent with GLM (Paul *et al.* 2018).  
321 For practical reasons, plant species typically measured at  $D_{10}$  (shrubs and multi-stemmed trees)  
322 required separate allometric models to those typically measured at  $D_{130}$  (single-stemmed trees).  
323 Hence, the analysis of unique functional sub-categories was undertaken for both of these broad  
324 groups of species. As indicated in Fig. 3, from the eight species groups, four categories of plant  
325 functional types were required for BGB allometric models ( $F_{\text{Shrub\&Ac}}$ ,  $F_{\text{Mallee}}$ ,  $F_{\text{Tree}}$  and  $F_{\text{Radiata}}$ ).



326

327 **Fig 3** Groupings of plant species into plant functional types as applied in AGB generic allometric models (Paul *et al.*, 2016), and  
 328 how these relate to the grouping of plant species into the plant functional types used here for BGB generic allometric models.

329

330 *Effect of level of generalisation on BGB prediction accuracy*

331 The impact of the level of generalisation of allometric models on the accuracy of BGB  
 332 prediction was also explored. Data from the seven tree species with  $N > 100$  (*E. polybractea*, *E.*  
 333 *loxophleba*, and *E. kochii*, *E. globulus*, *E. occidentalis*, *P. pinaster* and *P. radiata*) were used to  
 334 assess the improvement in fit in BGB predictions as specificity in the allometric models increased  
 335 (i.e. *Alluniversal* model *cf.* functional-type model *cf.* species-specific model). Large samples sizes  
 336 were required to target a 5% coefficient of variation prediction of biomass when applying  
 337 allometric models of relatively high variability, as anticipated for BGB (i.e. residual standard  
 338 deviations 0.47–0.50; Roxburgh *et al.*, 2015). Although the shrub species *Dodonaea viscosa* subsp.  
 339 *angustissima* and *Eremophila sturtii* were not as well sampled as the seven tree species (i.e.  $N=49$ –  
 340 51, thereby indicating a coefficient of variation of prediction of about 7%, Roxburgh *et al.*, 2015),  
 341 data for these species were used to explore whether the application of the generalised multi-species



342  $F_{Shrub\&Ac}$  model generates significant bias in prediction of BGB when compared to a species-  
343 specific model.

344

#### 345 *Effect of stand and site factors on BGB allometry*

346 General linear modelling was used to assess whether accounting for stand or site factors  
347 improved the performance of Eqn. 2, as indicated by an improvement in the fit statistics. The stand  
348 and site factors tested included: (i) stand age (<20 years or  $\geq$ 20 years), (ii) management (natural  
349 or managed vegetation), (iii) ecoregion (as per Fig. 2), (iv) MAT, and (v) MAR. Interactions of  
350 these site-factors with lnD were included in the model only where these were significant.

351 Within our data set (Table1), the single-stemmed tree species *Eucalyptus populnea* was the  
352 most suitable for comparison between ecoregions: (i) ‘Temperate Grasslands, Savannas and  
353 Shrublands’, where MAR was 400–460 mm ( $N=20$ , collated from two stands), and (ii) ‘Tropical  
354 and Subtropical Grasslands, Savannas and Shrublands’ where MAR was 600–1 070 mm ( $N=36$ ,  
355 collated from three stands). This was because the sample sizes of 20–36 for this species indicated  
356 a coefficient of variation of allometry-predicted biomass of only 8–11% (Roxburgh *et al.*, 2015).  
357 These data provided a case study that enabled us to test the effect of ecoregion on the  $F_{Tree}$  model.

358

#### 359 *Model validation using whole plot root excavation*

360 To test the accuracy of allometric models, we utilised data from 11 stands of varying  
361 structure and contrasting environments (Table 2) where whole plots were excavated to obtain  
362 ‘true’ and direct measurements of stand-scale BGB as described by Paul *et al.* (2014). The generic  
363  $F_{Shrub\&Ac}$ ,  $F_{Mallee}$  and  $F_{Tree}$  models of best fit we identified (Eqn. 2, using  $D$  as the predictor variable)  
364 were applied to inventories of  $D$  obtained from each of these 11 stands. The allometry-predicted  
365 BGB of all individuals within the stand was then summed to provide a predicted BGB at the stand-  
366 level. We calculated the resulting prediction quality statistics of  $EF$ ,  $MAPE$  and  $RMSE$ . To  
367 determine whether there was any improvement in model performance when less generalised

368 models are applied, this analysis was repeated with the use of species-specific models when they  
 369 were available (Table S1).

370

371 **Table 2** Summary of the main characteristics of 11 contrasting stands where whole-plot BGB excavation was used to test the  
 372 accuracy of generalised allometric models based on plant functional type. Modified from Paul *et al.* (2014). Abbreviations as  
 373 follows: ‘MAR’, long-term mean annual rainfall; ‘Tree *N*’, number of live trees or shrubs measured; ‘Type of stand’, where A  
 374 refers to ‘Belt monoculture planting of the mallee eucalypt species *E. loxophleba* subsp. *lissophloia*’, B refers to ‘Block  
 375 monoculture planting of the mallee eucalypt species *E. loxophleba* subsp. *lissophloia*’, C refers to ‘Belt planting of mixed-species’,  
 376 and D refers to ‘Block planting of mixed-species’.

Site	Location (decimal degrees)	MAR (mm yr <sup>-1</sup> )	Age (year)	Tree <i>N</i>	Stand-scale AGB (Mg DM ha <sup>-1</sup> )	Stand-scale BGB (Mg DM ha <sup>-1</sup> )	Type of stand
Strathearn	-35.0485 S, 149.2325 E	637	15	371	38.9	25.30	C
Moir <sup>^</sup>	-34.2809 S, 118.1820 E	439	20	346	42.4	17.07	C
Jenharwill	-36.3958 S, 144.4304 E	406	12	163	69.1	21.34	D
Gumbinnen	-36.2447 S, 141.8148 E	347	10	305	19.1	4.48	C
McFall	-33.7290 S, 117.3217 E	438	15-24	313	189.6	76.00	D
Leos	-37.8381 S, 147.7582 E	626	16	96	113.6	44.94	D
Pepal <sup>#</sup>	-33.4865 S, 117.7912 E	406	11	77	20.87	14.77	B
Bird <sup>#</sup>	-32.8515 S, 117.5892 E	376	11	41	37.68	18.27	B
Quicke <sup>#</sup>	-32.6736 S, 118.2361 E	339	14	29	77.63	37.79	B
Temby <sup>#</sup>	-33.1457 S, 117.7187 E	353	16	44	22.61	12.32	A
Angel <sup>#</sup>	-30.1970 S, 117.1160 E	297	16	34	9.93	9.78	A

377 <sup>#</sup> Species-specific allometric model for *Eucalyptus loxophleba* (Table S1) was applied as an alternative to the *F<sub>Mallee</sub>* model.

378 <sup>^</sup> Species-specific allometric model for *E. occidentalis* (Table S1) was applied as an alternative to the *F<sub>Tree</sub>* model for this species,  
 379 although within this mixed-species stand, *E. occidentalis* only comprised 6% of the individuals sampled, or 16 individuals out of  
 380 the 275 individual trees or shrubs excavated for direct measurement of stand-level BGB.

381

### 382 **BGB:AGB**

383 The allometric models developed for BGB, and those developed by Paul *et al.* (2016) for  
 384 AGB, were applied to predict the BGB:AGB ratio for the different sub-categories of plant  
 385 functional types (Fig. 3). A comparison of this predicted BGB:AGB ratio with that observed was  
 386 possible for the 1 990 individuals in the data set where both AGB and BGB were measured. We  
 387 then compared the average ( $\pm$  standard deviation) allometry-predicted BGB:AGB between the  
 388 different species groups. We also explored the relationship between allometry-predicted

389 BGB:AGB and the  $D$  of an individual tree or shrub.

390

## 391 **Results**

### 392 *Allometric models*

393 The model (Eqn. 2) predicted BGB with good accuracy for four categories of plant  
394 functional types:  $F_{Shrub\&Ac}$ ,  $F_{Mallee}$ ,  $F_{Tree}$ , and  $F_{Radiata}$  (Fig. 4a, d, g, j). The amount of variation in  
395  $\ln$ BGB explained by these models was 90–97%, with errors ( $RMSE$ ) of 0.26–0.55 (Table 4). When  
396  $\ln$ BGB was back-transformed and bias corrected, there was a relatively high uncertainty in the  
397 prediction of BGB for any given tree or shrub for a given  $D$  (see 95% confidence intervals of  
398 prediction, Fig. 4b, e, h, k). However, these individual errors tend to cancel out when predictions  
399 are made across a large number of individuals. The generalised models provided reasonable  
400 accuracy across the data sets, giving an efficiency of prediction of BGB of 72–93%, with a  $MAPE$   
401 range of 21–55% (Fig. 4c, f, i, l; Table 3).

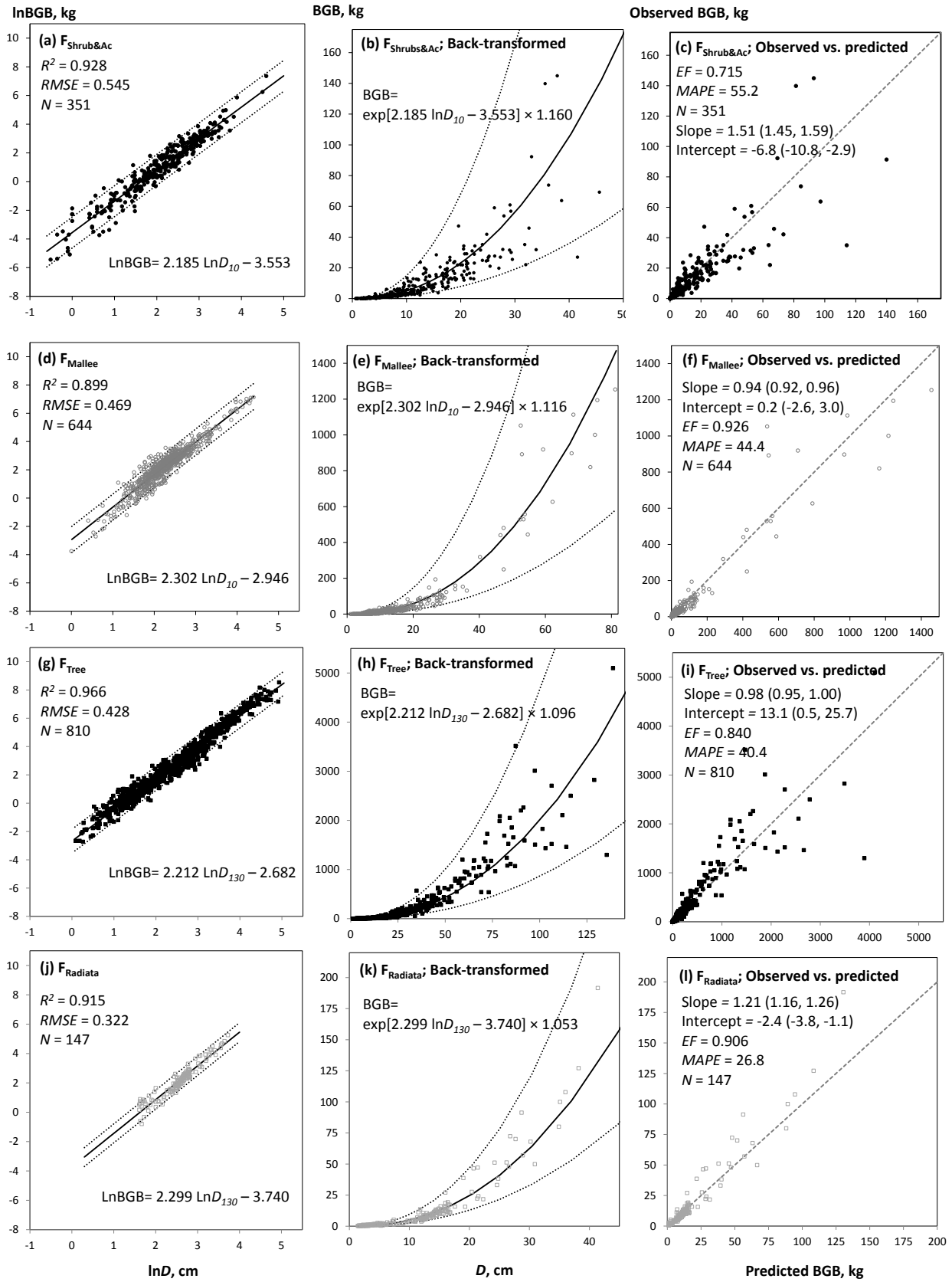
402 **Table 3** The fitted coefficient (and their standard errors) and fit statistics of generalised allometric models for BGB of the form given in Eqn. 2, and using a predictor of D measured at 10 cm height  
 403 ( $D_{10}$ ) or 130 cm height ( $D_{130}$ ). Here  $RMSE$ ,  $R^2$ ,  $CF$ ,  $EF$ ,  $MAPE$ , and  $N$  refer to the standard error of the linear regression, adjusted coefficient of determination, bias correction factor, model efficiency  
 404 (based on back-transformed BGB predictions), mean absolute percentage error (based on back-transformed BGB predictions), and sample size, respectively. All models fitted were highly significant  
 405 ( $P < 0.001$ ). The diameter range relevant to each model is indicated in brackets (assuming a minimum  $D_{10}$  of 0.6 cm, and a minimum  $D_{130}$  of 1.1 cm). Parameters and performance of the species-specific  
 406 allometric models are provided in the Table S1.

Model	$\ln(a)$	$b$	MM CF*	Baskerville CF†	$RMSE$	$R^2$	$EF$	$MAPE$	$N$
<i>AllUniversal</i> ( $D_{10} < 177$ cm)	-3.524 (0.045)	2.295 (0.017)	1.2373–1.2421	1.2426	0.659	0.896	0.735	78.9	2 054
<i>FShrub&amp;Ac</i> ( $D_{10} < 98$ cm)	-3.553 (0.075)	2.185 (0.033)	1.0782–1.1508	1.1601	0.545	0.928	0.715	55.2	351
<i>FMaltee</i> ( $D_{10} < 81$ cm)	-2.946 (0.071)	2.302 (0.031)	1.1047–1.1154	1.1160	0.469	0.899	0.926	44.4	644
<i>FTree</i> ( $D_{10} < 177$ cm)	-3.854 (0.046)	2.389 (0.016)	1.0913–1.0955	1.0959	0.428	0.965	0.703	40.5	810
<i>FTree</i> ( $D_{130} < 139$ cm)	-2.682 (0.039)	2.212 (0.015)	1.0923–1.0953	1.0958	0.428	0.966	0.840	40.4	810
<i>FRadiata</i> ( $D_{10} < 50$ cm)	-4.858 (0.067)	2.463 (0.027)	1.0259–1.0331	1.0575	0.257	0.972	0.902	21.3	249
<i>FRadiata</i> ( $D_{130} < 41$ cm)	-3.740 (0.152)	2.299 (0.058)	1.0272–1.0522	1.0534	0.322	0.915	0.906	26.8	147‡

407 \*Recommended Minimize mean Square Error (MM) correction factor (CF).

408 †Simpler Baskerville correction factor (CF) for reference.

409 ‡102 data sets with  $D_{130} < 5$  cm excluded in this model.



411

412

413

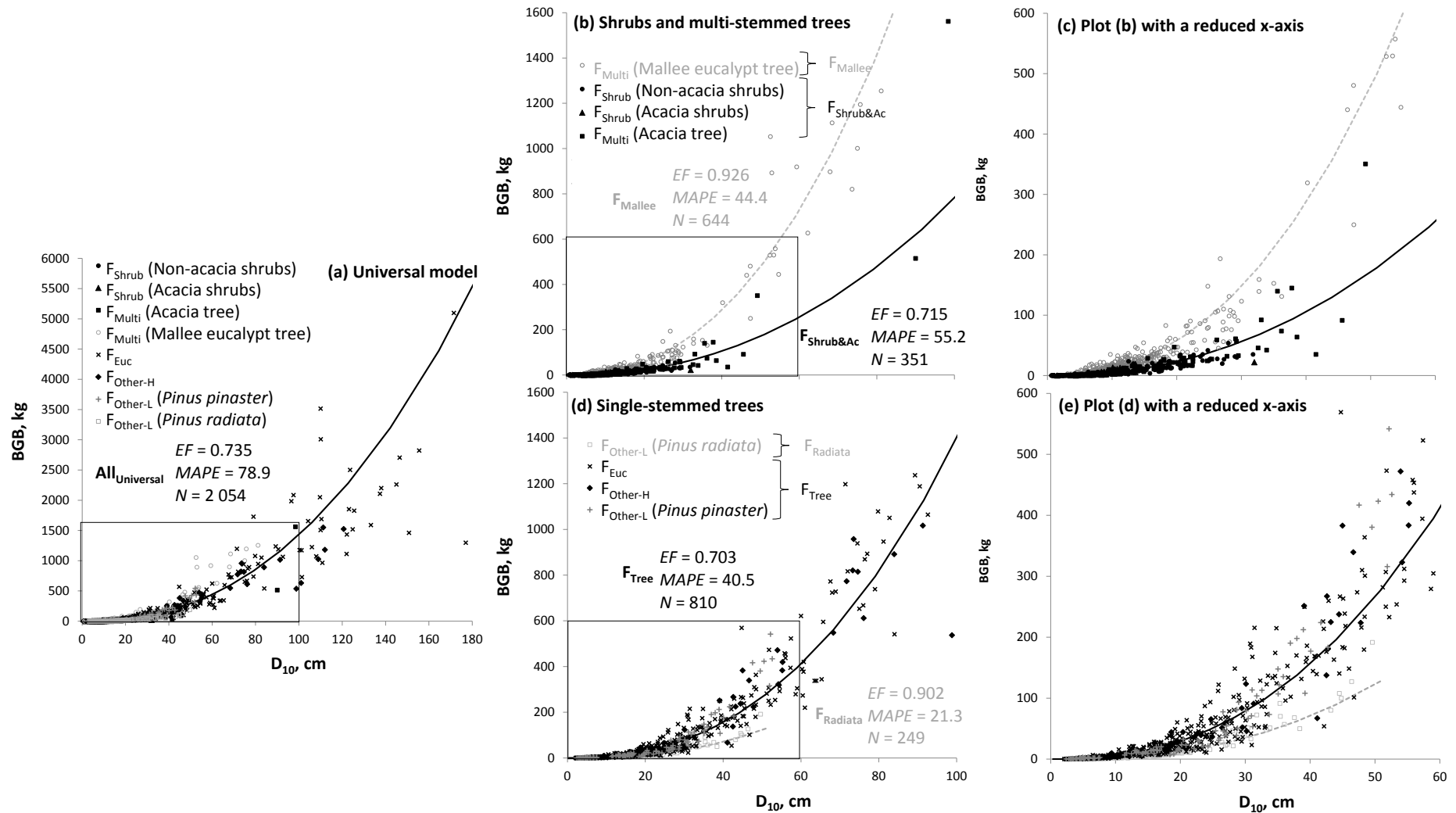
**Fig 4** Generic allometric equations for prediction of BGB from stem diameter (D cm) of (a, b, c) shrubs and acacia trees ( $F_{Shrub\&Ac}$ , where D was at 10 cm,  $D_{10}$ ), (d, e, f) multi-stemmed mallee eucalypt trees ( $F_{Mallee}$  where D was at 10 cm,  $D_{10}$ ), (g, h, i) single-

414 stemmed trees ( $F_{Tree}$ , where  $D$  was at 130 cm,  $D_{130}$ ), and (j, k, l) *Pinus radiata* tree species ( $F_{Radiata}$ , where  $D$  was at 130 cm,  $D_{130}$ ).  
415 There were three plots for each plant functional type: (a, d, g, j) indicating Eqn. 2 fitted to the lnBGB data set, (b, e, h, k) indicating  
416 accuracy of the back-transformed and biased corrected model, and (c, f, i, l) indicating observed *vs.* predicted BGB. Black solid  
417 lines represent the model of best fit, dotted lines the 95% prediction interval, and dashed lines the 1:1 line. Values in parentheses  
418 are the 95% prediction interval of the slope and intercept. NB: To improve the clarity of the figure, panels (b) and (c) excluded  
419 three observations of the relatively large ( $D_{10}$  of 49–98 cm, and height of 17–20 m) *Acacia* trees sampled from the wet tropics.

420

421 For  $F_{Tree}$  and  $F_{Radiata}$  models, there was no consistent difference in fit statistics when the  
422 model (Eqn. 2) used the explanatory variable  $D_{10}$  instead of  $D_{130}$  (Table 3). However, for  $F_{Radiata}$   
423 models using  $\ln D_{130}$ , it was necessary to exclude trees with  $D_{130} < 5.0$  cm to avoid positive bias in  
424 predictions of larger ( $D_{130} > 30$  cm) trees.

425 The performance of the *AllUniversal* model was relatively poor (efficiency of prediction of  
426 BGB only 74%, Fig. 5a) because it generalises across plant functional types with substantially  
427 different BGB allometry (Fig. 5b, c). General linear modelling demonstrated that allometry of  
428 mallee eucalypts were significantly different ( $p < 0.001$ ) to that of shrubs and other multi-stemmed  
429 trees (e.g. *Acacia* species) (Fig. 5c,d), while allometry of *Pinus radiata* was significantly different  
430 ( $p < 0.001$ ) to that of other single-stemmed trees (Fig. 5d,e). These results justify splitting the  
431 universal model into four plant functional type models (Table 3, Fig. 4).



432

433 **Fig 5** Back-transformed and bias-corrected generic allometric relationships (Eqn. 2) for prediction of BGB from stem diameter ( $D$  at 10 cm,  $D_{10}$ ) of: (a) all individuals ( $All_{Universal}$ ), and at a reduced x-  
 434 axis, the statistically different (b, c)  $F_{Shrub\&Ac}$  and  $F_{Mallee}$  models representing shrub and multi-stemmed tree species groupings, and (d, e)  $F_{Tree}$  and  $F_{Radiata}$  models representing groups of single-stemmed  
 435 trees. The second plot in the panel (c, e) shows the first plot (b, d) with the x-axis further reduced to increase clarity. Black solid and grey dashed line represent the statistically different models.

436 The application of alternative models to the seven species that were adequately sampled  
 437 ( $N > 100$ ) showed that the predictive performance generally increased with increasing model  
 438 specificity: universal *cf.* plant functional type *cf.* species-specific. When compared to the  
 439 application of the universal model, the application of more specific models generally increased the  
 440 efficiency of prediction of BGB by up to 15–17%, while *MAPE* decreased by up to 16–50% (Table  
 441 4). There were some exceptions, with the application of the *AllUniversal* model to *P. radiata*, or the  
 442 application of *F<sub>Mallee</sub>* to *E. kochii*, resulting in substantial bias as indicted by an *MAPE* of 100–  
 443 226% (Table 4). The investigation of BGB allometry of the two shrub species shown in Fig. 6 also  
 444 demonstrated the need for caution when applying generic models. One species had a slight bias in  
 445 prediction of BGB when the generic *F<sub>Shrub&Ac</sub>* model was applied (mean bias +2.3 kg for *D. viscosa*  
 446 subsp. *angustissima*), but with bias being negligible for the other species ( $< 0.5$  kg, *E. sturtii*) (Fig.  
 447 6a, b). Indeed when the *F<sub>Shrub&Ac</sub>* model was applied to predict BGB of *D. viscosa* subsp.  
 448 *angustissima*, the prediction efficiency was only 13% while *MAPE* was 73%. The performance of  
 449 the *F<sub>Shrub&Ac</sub>* was much better for the second shrub species, with an efficiency of prediction of 90%  
 450 and a *MAPE* of only 33%.

451

452 **Table 4** For the seven species that were well sampled ( $N > 100$ ), comparison of prediction performance of lnBGB (*RMSE*,  $R^2$ ,  
 453 *AIC*), and of BGB when back-transformed (*EF* and *MAPE*), following the application of *AllUniversal* and the less generalised plant  
 454 functional type (Table 3) and species-specific models (Table S1). All models applied had, by necessity,  $D_{10}$  as the explanatory  
 455 variable. *N* indicates the number of individuals to which the models were applied. Note *AIC* can only be compared across categories  
 456 where *N* is the same.

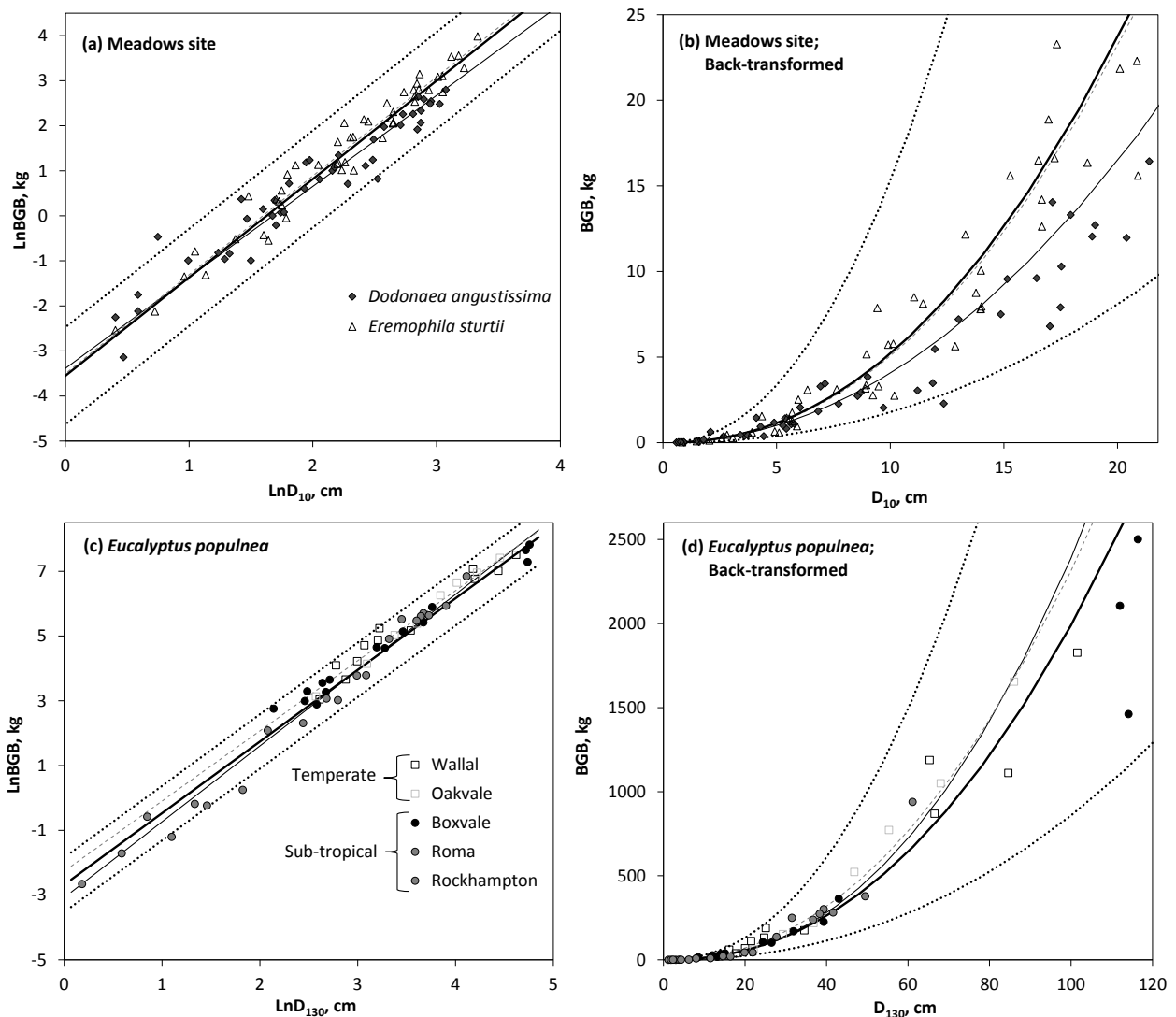
Species	Model	<i>N</i>	<i>RMSE</i>	$R^2$	<i>AIC</i>	<i>EF</i>	<i>MAPE</i>
<i>E. polybractea</i>	<i>AllUniversal</i>	154	0.36	0.56	-114.5	0.59	30.3
	<i>F<sub>Mallee</sub></i>	154	0.36	0.87	-304.3	0.57	35.1
	<i>E. polybractea</i>	154	0.36	0.88	-309.2	0.74	30.5
<i>E. loxophleba</i>	<i>AllUniversal</i>	312	0.39	0.65	-101.7	0.80	40.1
	<i>F<sub>Mallee</sub></i>	312	0.39	0.91	-532.6	0.93	30.2
	<i>E. loxophleba</i>	312	0.39	0.92	-581.9	0.93	34.5
<i>E. kochii</i>	<i>AllUniversal</i>	114	0.51	0.88	-134.2	0.78	43.8
	<i>F<sub>Mallee</sub></i> <sup>#</sup>	114	0.51	0.82	-83.3	-0.15	100.9
	<i>E. kochii</i>	114	0.51	0.90	-147.3	0.58	47.1
	<i>AllUniversal</i>	221	0.33	0.94	-359.4	0.96	76.2



<i>E. globulus</i>	$F_{Tree}$	221	0.32	0.96	-450.6	0.98	41.4
	<i>E. globulus</i>	221	0.32	0.97	-502.5	0.99	25.8
<i>E. occidentalis</i>	$AllUniversal$	114	0.32	0.90	-235.2	0.97	28.9
	$F_{Tree}$	114	0.32	0.85	-191.0	0.94	26.0
	<i>E. occidentalis</i>	114	0.32	0.91	-251.2	0.99	26.1
<i>P. pinaster</i>	$AllUniversal$	114	0.41	0.96	-194.7	0.87	51.6
	$F_{Tree}$	114	0.42	0.96	-187.6	0.84	36.9
	<i>P. pinaster</i>	114	0.41	0.96	-195.7	0.79	38.3
<i>P. radiata</i>	$AllUniversal$	249	0.28	0.60	-8.72	-0.45	226.0
	$F_{Radiata}$	249	0.26	0.97	-668.8	0.90	21.3

457 # $F_{Mallee}$  model developed for 0.6–81 cm mallee eucalypt trees over-predicted BGB for the 114 relatively small *E. kochii* trees ( $D_{10}$   
458 of 1–28 cm);  $F_{Mallee}$  application is not recommended for this species until further model validation is possible.

459



460

461

462

463

**Fig 6** Application of generic plant functional-type allometric equations for prediction of BGB from stem diameter ( $D$ , cm) of (a,  
of 1–28 cm);  $F_{Mallee}$  application is not recommended for this species until further model validation is possible.

464 plots (b) and (d) indicate the accuracy of the back-transformed and biased corrected model. Thick black solid lines represent the  
 465 generic model of best fit, and dotted lines, the 95% prediction interval. The thin black and grey dashed lines represent the model  
 466 of best fit for the individual species (a, b), or ecoregions (c, d).

467

### 468 *Inclusion of stand and site-factor predictor variables*

469 When compared to using  $D$  alone, including stand-factors (age and management) resulted  
 470 in only minor model improvements, with the increase in explained variation of  $\ln\text{BGB}$  being  
 471 consistently  $< 2\%$  (Table 5). Furthermore, for categories of plant functional types where a majority  
 472 of the individuals were from planted stands (e.g.  $F_{Mallee}$  and  $F_{Radiata}$ ), there were insufficient data  
 473 sets from natural stands to statistically ascertain any impact of management on BGB allometry.  
 474 Accounting for ecoregion, MAT or MAR also resulted in relatively small model improvements,  
 475 with the increase in explained variation being  $< 3\%$  (Table 5). These findings were reinforced by  
 476 the observation that there was negligible difference in BGB allometry for the one species ( $E.$   
 477  $populnea$ ) that was reasonably well sampled from two contrasting climates and ecoregions (Fig.  
 478 6c, d).

479

480 **Table 5** Fit statistics from general linear model analysis for assessing whether the allometric model represented by Eqn. 2 was  
 481 improved by the inclusion of site-factors (and their interactions with  $\ln D$ ) as supplementary predictor variables. Factors tested  
 482 included: (i) binary categorical variable [1,0] of stand age ( $\text{Age}<20_{[1,0]}$ : relatively young at  $<20$  yrs, or older), (ii) binary categorical  
 483 variable [1,0] of stand management ( $\text{Managed}_{[1,0]}$ : managed or ‘natural’), (iii) categorical variable ecoregion (see Fig. 1), (iv)  
 484 numerical variable of mean annual temperature (MAT), and (v) numerical variable of mean annual rainfall (MAR). Interactions of  
 485 these site-factors with  $\ln D$  were included in the model only where they were significant. Numbers in parentheses are the number  
 486 of parameters in the model ( $C_p$  values greater than this number indicate models of poor fit). Here, ‘NA’ refers to not applicable,  
 487 and ‘n.s.’ refers to not statistically significant, with  $P<0.05$ . Note;  $AIC$  can only be compared across categories where  $N$  is the same.

Model	Variables	RMSE	$R^2$	$C_p$	AIC
$F_{Shrub\&Ac}$ $N=351$	$\ln D_{10}$ alone	0.547	0.928	2.00 (2)	-422
	+ $\text{Age}<20_{[1,0]}$	0.503	0.939	4.00 (4)	-478
	+ $\text{Managed}_{[1,0]}$	0.505	0.939	4.00 (4)	-475
	+ Ecoregion	0.492	0.943	8.00 (8)	-490
	+ MAT	0.537	0.931	4.00 (4)	-431
	+ MAR	0.511	0.937	4.00 (4)	-467
$F_{Mallee}$	$\ln D_{10}$ alone	0.469	0.899	2.00 (2)	-972

N=644	+ Age<20 <sub>[1,0]</sub>	0.466	0.900	3.00 (3)	-980
	+ Managed <sub>[1,0]</sub>	n.s.	n.s.	n.s.	n.s.
	+ Ecoregion	n.s.	n.s.	n.s.	n.s.
	+ MAT	0.442	0.911	4.00 (4)	-1049
	+ MAR	n.s.	n.s.	n.s.	n.s.
<b><i>F<sub>Tree</sub></i></b>	<b>lnD<sub>130</sub> alone</b>	<b>0.428</b>	<b>0.965</b>	<b>2.00 (2)</b>	<b>-1372</b>
N=810	+ Age<20 <sub>[1,0]</sub>	0.407	0.969	4.00 (4)	-1451
	+ Managed <sub>[1,0]</sub>	0.412	0.968	4.00 (4)	-1433
	+ Ecoregion	0.408	0.969	12.00	-1423
	+ MAT	0.421	0.967	4.00 (4)	-1399
	+ MAR	0.424	0.966	4.00 (4)	-1386
<b><i>F<sub>Radiata</sub></i></b>	<b>lnD<sub>130</sub> alone</b>	<b>0.325</b>	<b>0.915</b>	<b>2.00 (2)</b>	<b>-329</b>
N=147	+ Age<20 <sub>[1,0]</sub>	0.275	0.939	3.00 (3)	-377
	+ Managed <sub>[1,0]</sub>	NA	NA	NA	NA
	+ Ecoregion	0.266	0.943	4.00 (4)	-385
	+ MAT	0.257	0.947	4.00 (4)	-395
	+ MAR	0.282	0.936	4.00 (4)	-368

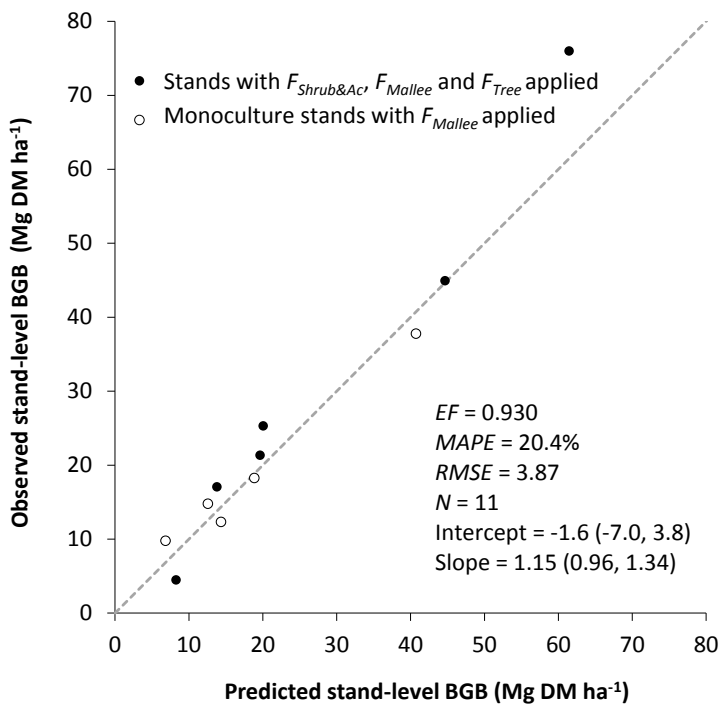
488

#### 489 ***Model validation using whole-plot root excavation***

490 Comparison of allometry-predicted BGB to observed BGB from direct whole-plot  
491 excavation across 11 contrasting stands (Table 2), showed prediction of stand-level BGB was good  
492 overall. The efficiency of prediction was 93%, and the *MAPE* was 20.4% (Fig. 7). When this  
493 validation was repeated with application of species-specific models (where available), there was a  
494 negligible difference in the accuracy of stand-level BGB prediction, with efficiency of prediction  
495 and *MAPE* both changing by less than one percent (Fig. S1 *cf.* Fig. 7).

496

497



498

499 **Fig 7** Relationship between stand-level BGB from whole-plot harvesting at 11 contrasting stands (Table 2) and that predicted for  
500 those stands through the application of the generic plant functional type allometric models (Table 3). Values in parentheses are the  
501 95% prediction interval of the slope and intercept. Grey dashed line represents the 1:1 line.

502

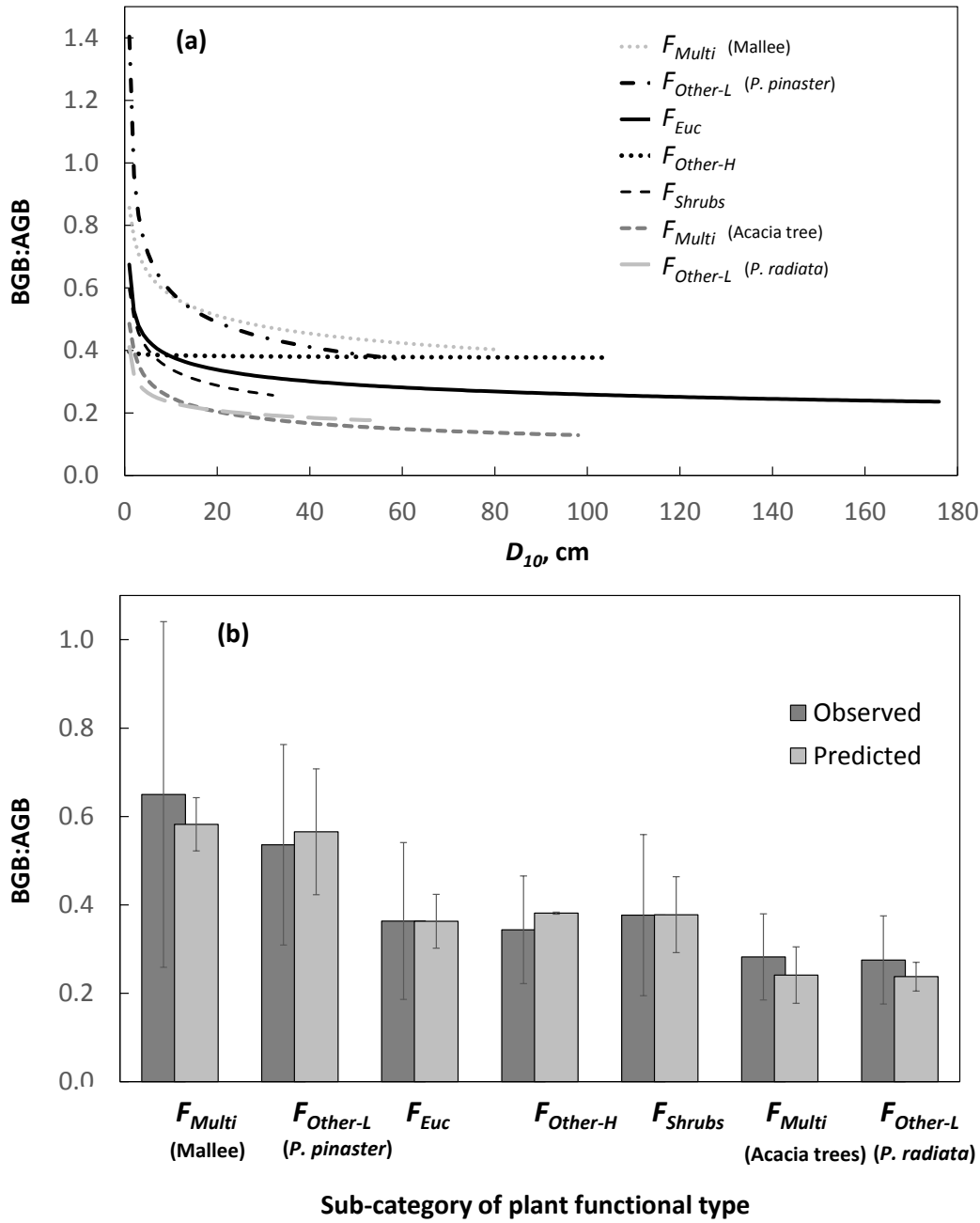
### 503 **BGB:AGB**

504 The ratio of BGB:AGB was predicted to differ between the seven unique plant functional  
505 types, with the highest values for other low wood density trees and mallee trees and the lowest  
506 values for multi-stemmed acacias (Fig. 8). With the exception of other high wood density trees  
507 ( $F_{\text{Other-H}}$ ), BGB:AGB was predicted to rapidly decline with increasing size of the individual, with  
508 equilibrium values attained at  $D_{10} > 50$  cm (Fig. 8a, Fig. S2).

509 The size distribution of individuals sampled will influence the average observed  
510 BGB:AGB ratios. For the samples here, Mallee eucalypts tended to have relatively high  
511 BGB:AGB, while the softwood species *Pinus radiata* had relatively low BGB:AGB (Fig. 8b).  
512 Comparison of the observed and predicted mean ( $\pm$  standard deviation) BGB:AGB no consistent  
513 significant bias in predicted BGB:AGB (Fig. 8b). This may have been partly attribute to the high  
514 variability in observed BGB:AGB within each category of plant functional type. Due to the high

515 accuracy of the generic allometric models derived for AGB and BGB, predicted BGB:AGB ratios  
 516 were in agreement (by within  $\pm 0.07$ ) with those observed (Fig. 8b).

517



518

519 **Fig 8** Predicted BGB:AGB from application of generic allometric equations of BGB and AGB (Paul *et al.*, 2016), in relation to:  
 520 (a) the size of the individual ( $D_{10}$ ) for contrasting sub-categories of plant functional types, and (b) the average BGB:AGB observed  
 521 among contrasting sub-categories of plant functional types. Error bars represent standard deviations.

522

523

## 524 Discussion

### 525 *Allometric models*

526 Results confirmed that across a wide range of individuals, BGB can be predicted using  
527 generalised plant functional type allometric models with reasonable accuracy and efficiencies of  
528 72–93% (Fig. 4). Significantly, this is achieved using the easily measured predictor variable of  $D$ .

529 Although the BGB allometric models here were based on datasets covering a broader range  
530 of vegetation types and site characteristics than have previously been collated for Australia  
531 (including the previously under-represented tropical ecoregions), the fit statistics obtained were  
532 comparable to those for generalised allometric models previously developed for much smaller  
533 datasets covering smaller stem diameters (Paul *et al.*, 2014). Hence, increasing the domain of  
534 application of generalised allometric models does not substantially reduce their prediction  
535 accuracy. For example, considering single-stemmed trees of  $D_{130}$  30–45 cm, the average ( $\pm$   
536 standard deviation) BGB of  $265 \pm 89$  kg for trees of various genera from tropical moist broadleaf  
537 forests (ca 2 000 mm yr<sup>-1</sup> MAR,  $N = 17$ , Fig. S3a) was similar to the  $266 \pm 118$  kg found for  
538 eucalypt trees from the Mediterranean ecoregion (ca 430 mm yr<sup>-1</sup> MAR,  $N = 14$ , Fig. S3b).  
539 Interestingly, although BGB was similar among these individuals of similar size, the area occupied  
540 by the root architecture could vary substantially between ecoregions and/or soil types. In our  
541 example above, the BGB densities differed between ecoregions (from 3–7 kg to 16–27 kg m<sup>-3</sup> soil,  
542 respectively for tropical moist broadleaf forests and the sparse stands from Mediterranean  
543 ecoregions).

544 Of the plant functional type models developed here, the model for relatively small multi-  
545 stemmed plants ( $F_{Shrub\&Ac}$ ) was the least precise, with a relatively high  $RMSE$  of 0.545 (Table 3).  
546 Measurement of  $D$  for such small multi-stemmed individuals is prone to relatively high  
547 measurement errors (Paul *et al.*, 2017a). Further research is currently underway to explore if  
548 alternative predictor variables can improve the precision of BGB prediction of such individuals.

549 The data set used here was a sub-set of that utilised by Paul *et al.* (2016) to assess

550 generalised allometry for AGB of trees and shrubs. Performance of the BGB *AllUniversal* model was  
551 much poorer than the AGB *AllUniversal* model provided by Paul *et al.* (2016), with the *MAPE* being  
552 78.9% *cf.* 40.7%. The *AllUniversal* model is therefore relatively inaccurate for BGB prediction, with  
553 a higher influence of plant functional type on allometry for BGB than for AGB.

554 Application of more specific models generally increased the efficiency of prediction of  
555 BGB by up to 15–17% (Table 4). This is largely consistent with previous work showing that  
556 application of generic multi-species models (i.e. based on plant functional type) does not generally  
557 result in loss of accuracy in allometry-predicted biomass compared to species-specific models  
558 (Feller 1992; Williams *et al.*, 2005; Montagu *et al.*, 2005; Mugasha *et al.*, 2013; Mbow *et al.*,  
559 2014; Ali *et al.*, 2015; Ishihara *et al.*, 2015; Paul *et al.*, 2016). However, there are exceptions, with  
560 biased estimates of BGB for some non-conforming species, which is of concern when applying  
561 generalised allometric models to stands dominated by such species. For example, if a woodland is  
562 composed of predominately *E. kochii* of moderate size ( $D_{10}$  10–20 cm), and the generic *F<sub>Mallee</sub>*  
563 model is applied, stand-level BGB estimates are likely to be over-estimated, with bias averaging  
564 +6.4 kg per tree (Table 4). Similarly, if a shrubland is composed of predominately *D. viscosa*  
565 subsp. *angustissima* of moderate size ( $D_{10}$  10–20 cm), and the generic *F<sub>Shrub&Ac</sub>* model is applied,  
566 stand-level BGB estimates are likely to be over-estimated, with bias averaging +2.3 kg per tree  
567 (Fig. 6b).

568 Further research is required to increase the sample size of different species represented by  
569 each plant functional type, and thereby, quantify which species are non-conforming (Paul *et al.*  
570 2018). Only seven species were sampled sufficiently to develop species-specific models, with most  
571 of these being relatively small trees sampled from managed monocultures. There is relatively large  
572 inherent variability in the species-specific models for BGB ( $RMSE = 0.32–0.51$ , Table S1). Given  
573 this, and based on the findings of Roxburgh *et al.* (2015), an  $N$  of ca 50–110 individuals will be  
574 required to develop accurate species-specific models of BGB, i.e. to achieve a coefficient of  
575 variation of BGB prediction of 5%. Even assuming consistency in the protocols used to excavate

576 roots, a larger inherent variability (and hence, larger required sample size) of BGB *cf.* AGB  
577 allometry is to be expected. Due to the difficulty in sampling BGB, measurement errors are likely  
578 to be relatively high. Furthermore, BGB allometry may be influenced by factors such as the  
579 presence of substantial root suckering, and the degree of senescence in response to recent  
580 disturbance, e.g. fire, grazing. In the example shown in Fig. 6b, BGB allometry of *E. sturtii* may  
581 be related to this species' ability to form extensive colonies via root suckers, whereas BGB  
582 allometry of the relatively fire- and grazing-sensitive *D. viscosa* subsp. *angustissima* may be  
583 influenced by disturbance-induced cycles of senescence and re-shooting (NSW LLS, 2014).

584

#### 585 ***Inclusion of stand- or site-factor predictor variables***

586 Including site-related factors such as stand characteristics (e.g. age, management), and  
587 climatic variables (e.g. MAR, MAT), even where statistically significant, did not markedly  
588 improve the predictive ability of *D*-based models, with increases in  $R^2$  of  $< 3\%$  (Table 5). Indeed,  
589 even when the same species was reasonably-well sampled across contrasting ecoregions,  
590 negligible differences in BGB allometry were observed (Fig. 6d). For a given species and size  
591 range, within-site variation is often as great as between-site variation in BGB. Thus there is only  
592 a minor trade-off in accuracy from application of simple power-law models based on *D*-alone  
593 relative to more complex models that include multiple explanatory variables (Sileshi, 2014; Picard  
594 *et al.*, 2015; Paul *et al.*, 2016).

595 Recent analysis of a global biomass data set which combined our data set (Table 1) with  
596 similar data sets from other continents (Ledo *et al.*, 2018), showed that after *D*, the next most  
597 important factor influencing allometry (in this case, of BGB:AGB) was the deficit between  
598 monthly rainfall and potential evapotranspiration. BGB:AGB increased with increasing moisture  
599 deficit, which accounted for 17% of the variance in BGB:AGB. Although BGB:AGB differed  
600 between different vegetation types, due to a correlation between vegetation type and climate, when



601 the moisture deficit was accounted for, the vegetation type ceased to be an important explanatory  
602 variable (Ledo *et al.*, 2018).

603 In the present study, climate factors appeared to be inherently accounted for in the grouping  
604 of species into plant functional types. The inclusion of plant functional types greatly improved the  
605 performance of the *AllUniversal* models for Australian trees and shrubs (Fig. 5, Table 4), yet the  
606 inclusion of climate factors had marginal impact (Table 5). Clearly, plant functional attributes  
607 often reflect coordinated adaptations to environmental factors (Onoda *et al.*, 2010; van Gelder *et*  
608 *al.*, 2006; Banin *et al.*, 2012; Pfautsch *et al.*, 2016), and such convergence probably also accounts  
609 for differences in allometry between plant functional types.

610 Despite plant functional types inherently accounting for some climate-related factors, for  
611 each of the four plant functional types, the inclusion of ecoregion, MAR and/or MAT as  
612 explanatory variables resulted in some (although minor) improvement to predictive performance,  
613 with this being greater for BGB (Table 5) than for AGB (Paul *et al.*, 2016). It remains unclear  
614 whether the effect of such climate variables would have been greater on BGB allometry of plant  
615 functional types had our data set encompassed an even greater range of the ecoregions. A next step  
616 is to evaluate the impact of climate, and hence climate change, on BGB allometry through  
617 measurement of more individuals from the relatively under-sampled combinations of various plant  
618 functional types and ecoregions (e.g. tropical and subtropical regions, medium to high rainfall, tall  
619 closed temperate forests, and arid shrublands, Fig. 2).

620 Another caveat was that our assessment of the impacts of stand age and management on  
621 BGB allometry included only broad categories, e.g. managed or unmanaged, and younger or older  
622 than 20 years. This was a necessity given insufficient observations in the data set to explore  
623 whether, across a range of plant functional types and ecoregions, BGB allometry changes with  
624 age, stand structure and management. Although relatively localised and species-specific studies of  
625 BGB have explored some of these factors (e.g. Ritson & Sochacki, 2003), further work is required  
626 to confirm their significance more broadly.

627

628 ***Model validation using whole plot root excavation***

629 Application of allometric models based on plant functional type resulted in high efficiency  
630 of prediction of stand-level BGB across contrasting direct-measurement stands (Fig. 7).  
631 Previously, Paul *et al.* (2014) used these same whole-plot excavation data to validate BGB  
632 allometric models developed using BGB of individuals covering a smaller range of sizes, and  
633 sampled from mixed-species environmental and mallee plantings. Despite the fact that allometric  
634 models developed in this study included a broader range of vegetation types and site characteristics  
635 compared to those developed by Paul *et al.* (2014), the decline in efficiency of BGB prediction  
636 across these 11 direct stands was only 6%. This provides further evidence that increased  
637 applicability of allometric models does not result in significant loss of accuracy.

638 Application of species-specific models resulted in only a modest improvement in the  
639 efficiency of prediction of stand-level BGB compared to the application of more generalised  
640 models based on plant functional types (Fig. S1 *cf.* Fig. 7). Furthermore, it may be that, for mixed-  
641 species stands, due to the smaller sample size and larger overall number of model coefficients to  
642 parameterise, uncertainties associated with the propagation of errors (including measurement,  
643 model-fitting and prediction errors) may be larger following application of multiple species-  
644 specific models compared to a single generalised multi-species model. Additionally, large sample  
645 sizes are required for each species-specific model (Roxburgh *et al.*, 2015), resulting in significant  
646 costs associated with development of models for each new species. These likely higher  
647 uncertainties and costs would negate the small gain in average accuracy of stand-level BGB  
648 prediction when applying multiple species-specific models versus a generalised multi-species  
649 model in mixed-species stands. Hence, models generalised at the level of plant functional group  
650 (Eqn. 3a–d, reported here using the Baskerville CF) are recommended for application in both  
651 Australia, and for validation in similar ecoregions in other continents.

652 BGB (kg) for species of:

653  $F_{Shrub\&Ac} = \exp [-3.553 + 2.185 \ln D_{10}] \times 1.160$  (3a)

654  $F_{Mallee} = \exp [-2.946 + 2.302 \ln D_{10}] \times 1.116$  (3b)

655  $F_{Tree} = \exp [-2.682 + 2.212 \ln D_{130}] \times 1.096$  (3c)

656  $F_{Radiata} = \exp [-3.740 + 2.299 \ln D_{130}] \times 1.053$  (3d)

657

658 As with all allometric models, to avoid bias in BGB predictions, recommended models in  
659 this study should only be applied within their valid diameter range as indicated by the maximum  
660  $D$  sampled (e.g. Table 3, Table S1). There are two exceptions to the recommendation of application  
661 of Eqn. 3 for stand-level prediction. First, where the trade-off between accuracy and cost  
662 effectiveness is relatively high, e.g. for a given high-biomass stand comprising only one or two  
663 dominant species. Here, additional costs associated with obtaining species-specific models may  
664 warrant the improved accuracy. Second, where BGB estimates are required for stands dominated  
665 by species suspected of not conforming to the generalised plant functional groups models (e.g.  
666 poor representation of *E. kochii* by the  $F_{Mallee}$  model, and *D. viscosa* subsp. *angustissima* by the  
667  $F_{Shrub\&Ac}$  model, respectively).

668

### 669 **BGB:AGB**

670 As outlined earlier, estimates of BGB based on  $D$  are preferable to those based on a ratio  
671 to AGB, particularly when estimates of AGB are only available at the stand-level. Indeed,  
672 predictions of BGB:AGB were relatively uncertain as they include the uncertainty in both  
673 allometry-predicted BGB and AGB (Fig. 8b, Fig S2). Nonetheless, the results are of interest in  
674 demonstrating how BGB:AGB of Australian woody plants vary with size and functional type. As  
675 expected, predictions of BGB:AGB decreased with increasing  $D$  (Fig. 8a). This is consistent with  
676 the understanding that saplings invest more biomass below ground for nutrient and water  
677 acquisition to facilitate rapid early growth and survival, and with non-conductive xylem  
678 accumulating in AGB as  $D$  increases (Barton and Montagu, 2006; Poorter *et al.*, 2012). Further,

679 BGB:AGB estimates were relatively high for mallee species that have lignotubers and have  
680 evolved in relatively arid environments (Paul *et al.*, 2014), but relatively small for *P. radiata* trees  
681 that are established in fast-growing and fertilised plantations, with presumably relatively little  
682 investment BGB allocation (Ledo *et al.*, 2018).

683

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696

## 697 **References**

- 698 Applegate GB (1982) Biomass of Blackbutt (*Eucalyptus pilularis* Sm.) forests on Fraser Island. Master of Natural  
699 Resources. University of New England.
- 700 Banin L, Feldpausch TR, Phillips OL *et al.* (2012) What controls tropical forest architecture? Testing environmental,  
701 structural and floristic drivers. *Global Ecology and Biogeography*, **21**, 1179–1190.
- 702 Ballantyne AP, Andres R, Houghton R *et al.* (2015) Audit of the global carbon budget: estimate errors and their impact  
703 on uptake uncertainty. *Biogeosciences*, **12**, 2565–2584.
- 704 Ballantyne F (2013) Evaluating model fit to determine if logarithmic transformations are necessary in allometry: A  
705 comment on the exchange between Packard (2009) and Kerkhoff and Enquist (2009). *Journal of Theoretical*  
706 *Biology*, **317**, 418–4321.
- 707 Baldwin PJ, Stewart HTL (1987) Distribution, length and weight of roots in young plantations of *Eucalyptus grandis*  
708 W. Hill ex. Maiden irrigated with recycled water. *Plant Soil*, **97**, 243–252.

- 709 Barton CVM, Montagu KD (2006) Effect of spacing and water availability on root:shoot ratio in *Eucalyptus*  
710 *camaldulensis*. *Forest Ecology and Management*, **221**, 52-62.
- 711 Baskerville G (1972) Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forest*  
712 *Research*, **2**, 49–53.
- 713 Bernardo AL, Reis MGF, Reis GG, Harrison RB, Firme DJ (1998) Effect of spacing on growth and biomass  
714 distribution in *Eucalyptus camaldulensis*, *E. pellita* and *E. urophylla* plantations in southeastern Brazil.  
715 *Forest Ecology and Management*, **104**, 1–13.
- 716 BoM (2015) Bureau of Meteorology Gridded climatological data. Climate Data Services, Melbourne 3001, Australia.
- 717 Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in Model Selection,  
718 *Sociological Methods & Research*, **33**, 261–304.
- 719 Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics  
720 spectrum. *Ecology Letters*, **12**, 351–366.
- 721 Chen Q, Laurin GV, Valentini R (2015) Uncertainty of remotely sensed aboveground biomass over an African tropical  
722 forest: Propagating errors from trees to plots to pixels. *Remote Sensing of Environment*, **160**, 134–143
- 723 Clifford D Cressie N, England JR, Roxburgh SH, Paul KI (2013) Correction factors for unbiased, efficient estimation  
724 and prediction of biomass from log-log allometric models. *Forest Ecology and Management*, **310**, 375–381.
- 725 DSWPC (2015) Australia's ecoregions map. Department of Sustainability, Environment, Water, Populations and  
726 Communities (adapted from World Wildlife Fund, WWF). Last accessed 5 September 2017. Commonwealth  
727 of Australia, Canberra. [https://www.environment.gov.au/system/files/pages/1716eb1c-939c-49a0-9c0e-  
728 8f412f04e410/files/ecoregions\\_1.pdf](https://www.environment.gov.au/system/files/pages/1716eb1c-939c-49a0-9c0e-8f412f04e410/files/ecoregions_1.pdf)
- 729 Enquist BJ, Kerhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA (2007) A general integrative model for  
730 scaling plant growth, carbon flux, and functional trait spectra. *Nature Letters*, **449**, 218-222.
- 731 Feller M (1992) Generalized versus site-specific biomass regression equations for *Pseudotsuga menziesii* var.  
732 *menziesii* and *Thuja plicata* in coastal British Columbia. *Bioresource Technology*, **39**, 9-16.
- 733 Forrest WG (1969) Variations in the accumulation, distribution and movement of mineral nutrients in radiata pine  
734 plantations. Ph.D. Thesis. Australian National University, Canberra.
- 735 Gardiner B, Peltola H, Kellomaki S (2000) Comparison of two models for predicting the critical wind speeds required  
736 to damage coniferous trees. *Ecological Modelling*, **129**, 1-23
- 737 Gonzalez-Benecke CA, Gezan SA, Albaugh TJ *et al.* (2014) Local and general above-stump biomass functions for  
738 loblolly pine and slash pine trees. *Forest Ecology and Management*, **334**, 254-276.
- 739 Gitay H, Noble IR (1997) What are functional types and how should we see them? In: Smith, T.M., Shugart, H.H. &  
740 Woodward, F.I. (eds.) Plant functional types: their relevance to ecosystem properties and global change, pp.  
741 3-19. Cambridge University Press, Cambridge.
- 742 Haverd V, Raupach MR, Briggs PR *et al.* (2013) The Australian terrestrial carbon budget. *Biogeosciences*, **10**, 851-  
743 869.
- 744 Houghton RA, House JI, Pongratz J *et al.* (2012) Carbon emissions from land use and land-cover change.  
745 *Biogeosciences*, **9**, 5125–5142.
- 746 Ishihara MI, Utsugi H, Tanouchi H *et al.* (2015) Efficacy of generic allometric equations for estimating biomass: a  
747 test in Japanese natural forests. *Ecological Applications*, **25**, 1433–1446.
- 748 Kerkhoff AJ, Enquist BJ (2009) Multiplicative by nature: Why logarithmic transformation is necessary in allometry.  
749 *Journal of Theoretical Biology*, **257**, 519–521.

- 750 Ledo, A, Paul, KI, Burslem, D. *et al.* (2018). Tree size and climatic water deficit control root to shoot ratio in individual  
751 trees globally. *New Phytologist*, **217**, 8-11.
- 752 Le Quéré C, Moriarty R, Andrew RM *et al.* (2015) Global carbon budget. *Earth System Science Data*, **7**, 47–85.
- 753 Mallows CL (1973) Some Comments on CP. *Technometrics*, **15**, 661–675.
- 754 Mavouroulou QM., Ngomanda A, Obiang NLE, Lebamba J, Gomat H, Mankou GS, Loumeto J, Iponga DM, Ditsouga  
755 FK, Koumba RZ, Bobe KHB, Lepengue N, Mbatchi B, Picard N (2014) How to improve allometric equations  
756 to estimate forest biomass stocks? Some hints from a central African forest. *Canadian Journal of Forest  
757 Research*, **44**, 685-691
- 758 Mbow C, Verstraete MM, Sambou B, Diaw AT Neufeldt H (2014) Allometric models for aboveground biomass in  
759 dry savanna trees of the Sudan and Sudan–Guinean ecosystems of Southern Senegal. *Journal of Forest  
760 Research*, **19**, 340–347.
- 761 Mitchard ETA, Saatchi SS, Baccini A *et al.* (2013) Uncertainty in the spatial distribution of tropical forest biomass: a  
762 comparison of pan-tropical maps. *Carbon Balance and Management*, **8**, 10.
- 763 Mokany K, Raison J, Prokushkin AS (2006). Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change  
764 Biology*, **12**, 84–96.
- 765 Montagu K, Düttmer K, Barton C, Cowie A (2005) Developing general allometric relationships for regional estimates  
766 of carbon sequestration—an example using *Eucalyptus pilularis* from seven contrasting sites. *Forest Ecology  
767 and Management*, **204**, 115-129.
- 768 Mugasha WA, Eid T, Bollandsås OM, Malimbwi RE, Chamshama SAO, Zahabu E, Katani JZ (2013) Allometric  
769 models for prediction of above- and belowground biomass of trees in the miombo woodlands of Tanzania.  
770 *Forest Ecology and Management*, **310**, 87-101.
- 771 NSW LLS (2014) Managing invasive native scrub to rehabilitate native pastures and open woodlands: A Best  
772 Management Practice Guide for the Central West and Western Regions. New South Wales Local Land  
773 Services (NSW LLS), Cobar and Dubbo, NSW.
- 774 Nicoll BC, Ray D (1996) Adaptive growth of tree root systems in response to wind action and site conditions. *Tree  
775 Physiology*, **16**, 891-898.
- 776 Niklas KJ (2004) Plant allometry: is there a grand unifying theory? *Biological Review*, **79**, 871-889.
- 777 Onoda Y, Richards AE, Westoby M (2010) The relationship between stem biomechanics and wood density is modified  
778 by rainfall in 32 Australian woody plant species. *New Phytologist*, **185**, 493-501.
- 779 Packard, G.C. (2000). On the use of logarithmic transformations in allometric analyses. *Journal of Theoretical  
780 Biology*, **257**, 515-518.
- 781 Paul KI., Roxburgh SH, England JR *et al.* (2014). Root biomass of carbon plantings in agricultural landscapes of  
782 southern Australia: Development and testing of allometrics. *Forest Ecology and Management*, **318**, 216-227.
- 783 Paul KI, Roxburgh SH, Chave, J. *et al.* (2016) Testing the generality of above-ground biomass allometry across plant  
784 functional types at the continent scale. *Global Change Biology*, **22**, 2106-2124.
- 785 Paul KI, Larmour JS, Roxburgh SH, England JR, Davies MJ, Luck H (2017a) Measurements of stem diameter:  
786 implications for individual- and stand-level errors. *Environmental Monitoring and Assessment*, **189**, 416, 1-  
787 14.
- 788 Paul KI, Larmour, J., Zerihun, A., *et al.* (2017b) Australian Individual Tree Biomass Library, Version 3.  
789 10.4227/05/566629ADA95DA. <http://www.aekos.org.au/dataset/223706>. Obtained from Australian  
790 Ecological Knowledge and Observation System Data Portal (ÆKOS, <http://www.portal.aekos.org.au/>), ,

- 791 made available by Commonwealth Scientific and Industrial Research Organisation, Australian Government  
792 Department of Agriculture and Food, Western Australian Department of Parks and Wildlife, South Australian  
793 Department of Environment, Water and Natural Resources, Victorian Department of Primary Industries,  
794 Queensland Department of Science, Information Technology, Innovation and the Arts, Southern Cross  
795 University (accessed August 2017). *In review*.
- 796 Paul, K.I., Radtke, P.J., Roxburgh, S.H., Larmour, J., Waterworth, R., Butler, D., Brooksbank, K, Ximenes, F. (2018).  
797 Validation of allometric biomass models: How to have confidence in the application of existing models.  
798 *Forest Ecology and Management*, 412, 70–79
- 799 Picard N, Saint-André L, Henry M (2012) Manual for building tree volume and biomass allometric equations: from  
800 field measurement to prediction. Food and Agricultural Organization of the United Nations, Rome, and  
801 Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, 215  
802 pp.
- 803 Picard N, Rutishauser E, Ploton P, Ngomanda A, Henry M (2015) Should tree biomass allometry be restricted to  
804 power models? *Forest Ecology and Management*, **353**, 156-163.
- 805 Pfautsch S., Harbusch M, Wesolowski A, Smith R, Macfarlane C, Tjoelker MG, Reich PB, Adams MA (2016).  
806 Climate determines vascular traits in the ecologically diverse genus *Eucalyptus*. *Ecology Letters*, 1-9.
- 807 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots:  
808 meta-analyses of interspecific variation and environmental control. *New Phytologist*, **193**, 30–50.
- 809 Poulter B, Frank D, Ciais P *et al.* (2014) Contribution of semi-arid ecosystems to interannual variability of the global  
810 carbon cycle. *Nature*, **509**, 600-603.
- 811 Richards GP, Evans DMW (2004) Development of a carbon accounting model (FullCAM Vers. 1.0) for the Australian  
812 continent. *Australian Forestry*, **67**, 277-283.
- 813 Ritson P, Sochacki S (2003) Measurement and prediction of biomass and carbon content of *Pinus pinaster* trees in  
814 farm forestry plantations, south-western Australia. *Forest Ecology and Management*, **175**, 103-117.
- 815 Roxburgh SH, Paul KI, Clifford D, England JR, Raison RJ (2015) Guidelines for constructing allometric models for  
816 the prediction of woody biomass: how many individuals to harvest? *Ecosphere*, **6**, 1-27.
- 817 Ryan CM, Williams M, Grace J (2011) Above-and belowground carbon stocks in a miombo woodland landscape of  
818 Mozambique. *Biotropica*, **43**, 423-432.
- 819 Saint-André L, M'Bou AT, Mabila A *et al.* (2005) Age related equation for above and below ground biomass of a  
820 *Eucalyptus* in Congo. *Forest Ecology and Management*, **205**, 199–214.
- 821 Schenk HJ, Jackson BR (2002) The global biogeography of roots. *Ecological Monographs*, **72**, 311–328.
- 822 Shen H, Zhu Z (2008) Efficient mean estimation in log-normal linear models. *Journal of Statistical Planning and*  
823 *Inference*, **138**, 552–567.
- 824 Sileshi GW (2014) A critical review of forest biomass estimation models, common mistakes and corrective measures.  
825 *Forest Ecology and Management*, **329**, 237-264.
- 826 Sillett SC, van Pelt R, Kramer RD, Carroll AL, Koch GW (2015) Biomass and growth potential of *Eucalyptus regnans*  
827 up to 100 m tall. *Forest Ecology and Management*, **348**, 78–91
- 828 Soares P, Tome M, Skovsgaard JP, Vanclay JK (1995) Evaluating a growth model for forest management using  
829 continuous forest inventory data. *Forest Ecology and Management*, **71**, 251-265.
- 830 Specht RL, Specht A (2002) Structure, Growth and Biodiversity of Australian Plant Communities. 2nd edition. Oxford  
831 University Press. 500pp.

- 832 Specht A, Specht RL (2013) Australia: Biodiversity of Ecosystems. *In*, The Encyclopedia of Biodiversity Vol. 1 (ed.  
833 B. Levin, *et al.*) pp 291-306. Waltham, MA: Academic Press.
- 834 Van Gelder HA, Poorter L, Sterck FJ (2006) Wood mechanics, allometry, and life-history variation in a tropical rain  
835 forest tree community. *New Phytologist*, **171**, 367-78.
- 836 Westman, WE, Rogers RW (1977) Biomass and structure of a subtropical eucalypt forest, north Stradbroke Island.  
837 *Australian Journal of Botany*, **25**, 171-191.
- 838 Wildy DT, Pate JS (2002) Quantifying above- and below-ground growth responses of the Western Australian oil  
839 mallee, *Eucalyptus kochii* subsp. *plenissima*, to contrasting decapitation regimes. *Annals of Botany*, **90**, 185–  
840 197.
- 841 Williams R, Zerihun A, Montagu K, Hoffman M, Hutley L, Chen X (2005) Allometry for estimating aboveground  
842 tree biomass in tropical and subtropical eucalypt woodlands: towards general predictive equations. *Australian*  
843 *Journal of Botany*, **53**, 607-619.
- 844 Xiao X, White EP, Hooten MB, Durham SL (2011) On the use of log-transformation vs. nonlinear regression for  
845 analyzing biological power laws. *Ecology*, **92**, 1887–1894.
- 846 Xue L, Pan L, Zhang R, Xu P (2011) Density effects on the growth of self-thinning *Eucalyptus urophylla* stands.  
847 *Trees*, **25**, 1021–1031.
- 848 Zapata-Cuartas M, Sierra AC, Alleman L (2012) Probabiloity distribution of allometric coefficients and Bayesian  
849 estimation of aboveground tree biomass. *Forest Ecology and Management*, **277**, 173-179.
- 850 Zanne AE, Lopez-Gonzalez G, Coomes DA *et al.* (2009) Global wood density database. Dryad. Available at:  
851 <http://datadryad.org/handle/10255/dryad.235> (accessed 5 September 2017).
- 852 Zianis D, Spyroglou G, Tiakas E, Radoglou KM (2016) Bayesian and classical models to predict aboveground tree  
853 biomass allometry. *Forest Science*, **62**, 247–259.
- 854