1   **Testing the generality of above-ground biomass allometry across plant**

2   **functional types at the continent scale**

3

4   Keryn I. Paul[1,*], Stephen H. Roxburgh[1], Jerome Chave[2], Jacqueline R. England[3], Ayalsew

5   Zerihun[4], Alison Specht[5,6], Tom Lewis[7], Lauren T. Bennett[8], Thomas G. Baker[8], Mark A.

6   Adams[9], Dan Huxtable[10], Kelvin D. Montagu[11], Daniel S. Falster[12], Mike Feller[13], Stan

7   Sochacki[14], Peter Ritson[15], Gary Bastin[16], John Bartle[17], Dan Wildy[18], Trevor Hobbs[19], John

8   Larmour[1], Rob Waterworth[20], Hugh T.L. Stewart[21], Justin Jonson[22,23], David I. Forrester[24],

9   Grahame Applegate[25], Daniel Mendham[26], Matt Bradford[27], Anthony O'Grady[26], Daryl Green[28],

10   Rob Sudmeyer[29], Stan J. Rance[30], John Turner[31], Craig Barton[32], Elizabeth H. Wenk[12], Tim

11   Grove[30], Peter M. Attiwill[33], Elizabeth Pinkard[26], Don Butler[34], Kim Brooksbank[35], Beren

12   Spencer[17], Peter Snowdon[1], Nick O'Brien[36], Michael Battaglia[26], David M Cameron[37], Steve

13   Hamilton[38], Geoff McAuthur[39], Jenny Sinclair[40]

14

15   *[1]CSIRO Agriculture and CSIRO Land and Water, GPO Box 1700, ACT 2601, Australia;*

16   *[2]UMR 5174 Laboratoire Evolution et Diversité Biologique, CNRS & Université Paul Sabatier, Toulouse 31062, France;*

17   *[3]CSIRO Agriculture and CSIRO Land and Water, Private Bag 10, Clayton South, VIC 3169, Australia;*

18   *[4]Centre for Crop and Disease Management, Department of Environment and Agriculture, Curtin University, Perth, WA 6845, Australia;*

19   *[5]School of Geography Planning and Environmental Management, University of Queensland, St Lucia QLD 4072, Australia;*

20   *[6]CESAB, Fondation pour la Recherche sur la Biodiversité, Immeuble Henri Poincaré, 2ème étage Domaine du Petit Arbois, Avenue Louis*

21   *Philibert, 13100 Aix-en-Provence, France*

22   *[7]Department of Agriculture and Fisheries, University of the Sunshine Coast, Sippy Downs, QLD 4556, Australia*

23   *[8]School of Ecosystem and Forest Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC 3363 and 500 Yarra Boulevard,*

24   *Richmond, VIC 3121, Australia;*

25   *[9]Centre for Carbon Water and Food, Faculty of Agriculture and Environment, University of Sydney, Werombi Road, Camden NSW*

26   *[10]Equinox Environmental Pty Ltd., 6 Craigie Cres, Manning, WA 6152*

27   *[11]School of Environment and Agriculture, The University of Western Sydney, Parramatta NSW 2150, Australia.*

28   *[12]Biological Sciences, Macquarie University NSW 2109, Australia*

29   *[13]Department of Forest and Conservation Sciences, University of British Columbia, 3041-2424 Main Mall, Vancouver, B.C., Canada, V6T 1Z4*

30   *[14]School of Environmental Science, Murdoch University, 90 South St, Murdoch WA 6150, Australia;*

31   *[15]FarmWoods, 3/104 South Street, Fremantle WA 6160, Australia;*

32   [16]*Department of Land Resource Management, PO Box 1120, Alice Springs NT 0871*

33   [17]*Science Division, Department of Parks and Wildlife, Locked Bag 104 Bentley Delivery Centre WA 6983, Australia;*

34   [18]*Fares Rural Pty Ltd, PO Box 526, Wembley, WA 6913, Australia;*

35   [19]*Department of Environment, Water and Natural Resources, GPO Box 1047, SA 5001, Australia;*

36   [20]*Mullion Group, 2a Fitzroy Rd, Forrest ACT 2603, Australia;*

37   [21]*Hugh Stewart Consulting, 8 Upland Road, Strathmore, Victoria 3041, Australia*

38   [22]*Threshold Environmental Pty Ltd, PO Box 1124, Albany, WA 6331, Australia*

39   [23]*Centre of Excellence in Natural Resource Management, The University of Western Australia, 1 Foreshore House, Albany, WA 6330, Australia*

40   [24]*Chair of Silviculture, Faculty of Environment and Natural Resources, Freiburg University, Tennenbacherstr. 4, 79108 Freiburg, Germany.*

41   [25]*University of the Sunshine Coast, Sippy Downs, QLD 4556, Australia*

42   [26]*CSIRO Agriculture CSIRO Land and Water, Private Bag 12, Hobart, TAS 7001, Australia;*

43   [27]*CSIRO Land and Water, PO Box 780, Atherton QLD 4883, Australia;*

44   [28]*PO Box 1683, Dubbo NSW 2830, Australia;*

45   [29]*Department of Agriculture and Food, Western Australia, Private Mail Bag 50, Esperance WA 6450, Australia;*

46   [30]*CSIRO Land and Water, 4Private Bag 5, Wembley, WA 6913, Australia;*

47   [31]*Forsci Pty Ltd., Ste 4.05/ 32 Delhi Rd, North Ryde NSW 2113, Australia;*

48   [32]*Western Sydney University, Hawkesbury Institute for the Environment, Locked Bag 1797, Penrith 2751 NSW, Australia;*

49   [33]*School of Biological Sciences, The University of Melbourne, VIC 3010, Australia;*

50   [34]*Queensland Department of Science, Information Technology, Innovation and the Arts (DSITIA), Mt Coot-tha Road, Toowong QLD 4066;*

51   *Australia;*

52   [35]*Department of Agriculture and Food, Western Australia (DAFWA), 444 Albany Hwy, Albany WA 6330, Australia;*

53   [36]*New Forests Asset Management Pty Ltd., PO Box 434, North Sydney NSW 2059, Australia;*

54   [37]*School of Environment, Science and Engineering, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia;*

55   [38]*Hamilton Environmental Services, 2345 Benalla-Tatong Road, Tatong VIC 3673, Australia;*

56   [39]*AusCarbon Pty Ltd., PO Box 395, Nedlands, WA 6909, Australia;*

57   [40]*Green Collar Group, Level 1, 37 George St, Sydney, NSW 2000, Australia;*

59   [*]Author for correspondence: Keryn.Paul@csiro.au, +61 2 6246 4227

61   *Keywords*: aboveground; density; destructive; diameter; *Eucalyptus;* height; multi-stemmed;

62   shrubs

Generic allometrics 2

66   **Abstract**

67   Accurate ground-based estimation of the carbon stored in terrestrial ecosystems is critical

68   to quantifying the global carbon budget. Allometric models provide cost-effective methods for

69   biomass prediction. But do such models vary with ecoregion or plant functional type? We

70   compiled 15,054 measurements of individual tree or shrub biomass from across Australia to

71   examine the generality of allometric models for prediction above-ground biomass. This provided

72   a robust case study because Australia includes ecoregions ranging from arid shrublands to

73   tropical rainforests, and has a rich history of biomass research, particularly in planted forests.

74   Regardless of ecoregion, for five broad categories of plant functional type (shrubs; multi-

75   stemmed trees; trees of the genus *Eucalyptus* and closely related genera; other trees of high wood

76   density; and other trees of low wood density), relationships between biomass and stem diameter

77   were generic. Simple power-law models explained 84-95% of the variation in biomass, with little

78   improvement in model performance when other plant variables (height, bole wood density), or

79   site characteristics (climate, age, management) were included.

80   Predictions of stand-based biomass from allometric models of varying levels of

81   generalisation (species-specific, plant functional type) were validated using whole-plot harvest

82   data from 17 contrasting stands (range: 9 to 356 Mg ha^{-1}). Losses in efficiency of prediction were

83   < 1% if generalised models were used in place of species-specific models. Furthermore,

84   application of generalised multi-species models did not introduce significant bias in biomass

85   prediction in 92% of the 53 species tested. Further, overall efficiency of *stand*-level biomass

86   prediction was 99%, with a mean absolute prediction error of only 13%. Hence, for cost-

87   effective prediction of biomass across a wide range of stands, we recommend use of generic

88   allometric models based on plant functional types. Development of new species-specific models

89   is only warranted when gains in accuracy of stand-based predictions are relatively high (e.g.

90   high-value monocultures).

91

92   **Introduction**

93   Vegetation is an important sink within the global carbon budget, with carbon storage

94   facilitated by uptake of atmospheric carbon dioxide through photosynthesis (Le Quéré *et al*.,

95   2015). Ground-based information on the carbon storage in vegetation is critical for calibrating

96   carbon budgets, largely calculated using remote sensing metrics (e.g. Haverd *et al*., 2013;

97   Mitchard *et al*., 2013; Chen *et al*., 2015), or regional carbon accounting models (e.g. Richards &

98   Evans 2004; Paul *et al*., 2015a,b). In addition, accurate ground-based estimates of biomass are

99   important for the assessment and management of wood and biomass products (e.g. Canadell &

100   Raupach 2008), fire hazard (van der Werf *et al*., 2010), habitat suitability (e.g. Hatanaka *et al*.,

101   2011), and water yield and quality within catchments (e.g. George *et al*., 2012).

102   Typically, ground-based estimates of biomass are obtained by applying allometric models

103   to field measurements of biometric data such as stem diameter or plant height (e.g. Picard *et al*.,

104   2012). Two key decisions frame the construction of allometric models to predict total above-

105   ground biomass (AGB_{Indiv}, oven-dry weight of an individual plant). The first is deciding which

106   predictor variable(s) to use. Stem diameter (*D*, typically measured over bark at 130 cm height

107   above the ground) is commonly used because it can be easily measured with high accuracy

108   (Husch *et al*., 2003, but see Clark, 2002 for issues in some tropical forests). Plant height (*H*) and

109   bole wood density (ρ) are also often considered, since $D^2H\rho$ is expected to strongly correlate

110   with AGB_{Indiv} (e.g. Chave *et al*., 2005). The second decision relates to the level of generalisation

111   to be used. Most allometric models are based on relatively small species-specific datasets

112   obtained from local areas, and often ignore variation across both species and sites (Henry *et al*.,

113   2011; de Miranda *et al*., 2014).

114   Localised species-specific models provide the most accurate estimates of AGB_{Indiv} for the

115   domain for which they were developed (e.g. Wirth *et al*., 2004; Williams *et al*., 2005; Basuki *et*

116   *al*., 2009; Paul *et al*., 2013a,b; Ngomanda *et al*., 2014), but can generate substantial uncertainty

117   when applied outside the range of calibration, with potential for significant biases (20-200%, e.g.

118   Ketterings *et al.*, 2001; Wirth *et al.*, 2004; Chave *et al.*, 2014; Ishihara *et al.*, 2015). The

119   development of new models for new local area-by-species combinations is costly, particularly

120   for woody ecosystems where there are numerous species.

121   Generalised allometric models can greatly simplify AGB_{Indiv} estimation by assuming that

122   all individuals, irrespective of species or site, are represented by one allometric relationship.

123   Data from large numbers (100s to 1000s) of destructively-sampled plants can then be used to re-

124   parameterise new broadly applicable models (e.g., Brown *et al.*, 1989; Jenkins *et al.*, 2003;

125   Moore 2010; Paul *et al.*, 2013a,b; Chave *et al.*, 2005, 2014; Gonzalez-Benecke *et al.*, 2014;

126   Ishihara *et al.*, 2015). Models developed with such relatively large sample sizes have the added

127   advantage of greatly reducing uncertainty in parameter estimates (Chave *et al.*, 2004; van

128   Breugel *et al.*, 2011; Roxburgh *et al.*, 2015) when compared to most (~75%) localised species-

129   specific models that are developed with $N < 50$ trees (e.g. Zianis *et al.*, 2005; Genet *et al.*, 2011).

130   Because it is physically difficult to collect and assemble AGB_{Indiv} data, many questions

131   about the usefulness of generic approaches and models remain unanswered. For example, it is

132   unclear to what extent data should be pooled or separated according to their physical,

133   phylogenetic and/or phenological characteristics; often defined as plant functional types (e.g.

134   trees *vs*. shrubs (Paul *et al.*, 2013a), multi-stemmed *vs*. single-stemmed trees (Paul *et al.*,

135   2013a,b), angiosperms *vs*. gymnosperms (Chojnacky *et al.*, 2014)). Similarly, we need to

136   quantify the extent to which the use of multi-species allometric models introduces bias to

137   AGB_{Indiv} predictions for some species relative to others. Finally, we need guidance as to which

138   types and combinations of predictor variables (plant dimensions, bioclimatic variables, and stand

139   characteristics) will best predict AGB_{Indiv} using generalised models.

140   At the scale of individual plants, allometry-predicted AGB_{Indiv} can be validated by

141   independent sampling of new plants. However, it is difficult to ascertain whether sampled plants

142   have been truly selected at random. If specific criteria have been applied for selection (e.g. only

143   healthy trees) the resulting allometric model may be inherently biased. A true test of this possible

144 bias would be a direct validation of stand-based allometric model predictions of above-ground

145 biomass (AGB$_{Stand}$) against that measured through whole-plot harvesting. Such testing has been

146 undertaken in monoculture hardwood forests (Arthur *et al.*, 2001; Paul *et al.*, 2013b), and in

147 mixed-species vegetation (Búrquez & Martínez-Yrízar, 2011; Paul *et al.*, 2013a), but not using

148 generic allometric models.

149   Australia provides a good case study for testing generalised allometric models given it

150 has both a long history of research contributing to AGB$_{Indiv}$ datasets (e.g. Holland, 1969; Forrest

151 & Ovington, 1970; Attiwill, 1979), and spans a broad range of ecoregions, ranging from arid

152 shrublands to tropical rainforests, with plant functional types varying from shrubs and short

153 multi-stemmed trees through to some of the largest trees in the world (e.g. Sillett *et al.*, 2015;

154 Specht & Specht, 2002, Specht & Specht, 2013). Improving methods for quantifying biomass

155 and its carbon content in Australia is also of global significance given high inter-annual

156 variability in biomass carbon globally (Houghton *et al.*, 2012; Ballantyne *et al.*, 2015), with

157 semi-arid ecosystems in Australia playing a significant role (Poulter *et al.*, 2014).

158   For this project, an AGB$_{Indiv}$ dataset of unprecedented size was compiled, composed of

159 15,054 destructively-measured individuals from both managed (i.e. planted) and natural

160 ecosystems across Australia. This dataset was used to assess whether diameter-based allometric

161 models of biomass were improved: (i) by the inclusion of other plant variables (e.g. height, wood

162 density); (ii) by the inclusion of site characteristics (e.g. climate, age, management); and (iii)

163 when based on species rather than broader categories like plant functional groups. Our objectives

164 were first, to recommend the most appropriate allometric model(s) for estimating AGB$_{Indiv}$ in

165 Australian ecosystems, and secondly, to quantify bias of the recommended model(s) when tested

166 against direct measurements of AGB$_{Stand}$ obtained using whole-plot harvesting across a range of

167 contrasting sites.

168

169 **Materials and methods**

170 *Dataset*

171   Datasets of AGB_{Indiv} were obtained from destructive harvesting of 15,054 individual trees

172 and shrubs. Data represented a range of managed and natural woody ecosystems across 826 sites

173 in various ecoregions of Australia (Fig. 1), and obtained from numerous published and

174 unpublished sources (Table S1; Paul *et al*., 2015c). They included 274 species, 53 of which had

175 *N* > 50 individuals, sufficient for developing species-specific models that provide a reasonable

176 approximation of AGB_{Indiv} given population level variability (Roxburgh *et al*., 2015). To utilise

177 the wider dataset, we categorised all species into plant functional types as described below.

178

179 *Plant functional types*

180   Five categories of plant functional types of unique physiognomic growth form (Gitay and

181 Noble 1997) were included: (i) shrubs or small trees characterised by being relatively short

182 (generally < 2 m height) and typically multi-stemmed or highly branched, with a relatively small

183 (< 7 cm) stem diameter (F_{Shrub}); (ii) multi-stemmed hardwood (angiosperm) trees, including

184 mallees from the genus *Eucalyptus*, and trees from the genus *Acacia* (F_{Multi}); (iii) typically

185 single-stemmed hardwood trees from the genus *Eucalyptus* and closely-related genera of

186 *Corymbia* and *Angophora* (F_{Euc}); (iv) other tree species that typically have single stems and

187 relatively high wood density (mean 0.67 g cm^{-3}) ($F_{Other-H}$); and (v) other trees, namely conifers

188 from the genera of *Pinus, Araucaria* and *Agathis*, that typically have single stems and relatively

189 low stem wood density (mean 0.40 g cm^{-3}) ($F_{Other-L}$). Each of these five plant functional types

190 could also be further sub-categorised as indicated in Fig. S1.

191   Most of these plant functional types include plant species with distinctive branch

192 architecture and/or stem wood density. A highly branched architecture is a unique characteristic

193 of species within F_{Shrub}, while a unique characteristic of conifer species within $F_{Other-L}$ is a

194 relatively low wood density. By comparison, such distinctions were less obvious between the

195   three categories of trees of relatively high wood density (F_{Multi}, F_{Euc} and $F_{Other-H}$), with their

196   categorisation based on two issues of practicality. The first related to the height at which stem

197   diameter was typically measured in multi- and single-stemmed trees, resulting in the F_{Multi}

198   category having different predictor variables to that of the other two hardwood tree categories.

199   When compared to single-stemmed trees, multi-stemmed mallee eucalypts and shrubs have stem

200   diameter measurements taken closer to the ground (usually 10 cm height) below the point at

201   which the stem forks (e.g. Paul *et al*., 2013a,b). Second, for practicality, the relatively

202   heterogeneous category of $F_{Other-H}$ was segregated from the much more widely sampled F_{Euc}

203   category that solely represented typically single-stemmed *Eucalyptus* trees of relatively high

204   wood densities (Ilic *et al*., 2000).

205   The majority of the 15,054-tree dataset comprised two categories of plant functional

206   types, namely F_{Euc} (40%) and F_{Multi} (36%), largely representing the ecoregions that supported

207   either 'Mediterranean forests, woodlands and scrub', or 'Temperate broadleaf and mixed forests'

208   (Fig. 2). Although $F_{Other-L}$ represented only 5% of the dataset, this category was also largely

209   found in these two ecoregions. In contrast, F_{Shrub} and $F_{Other-H}$ comprised 16% and 3% of the

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

211

212   *Explanatory variables*

213   The primary set of collated data included three explanatory variables for AGB_{Indiv}: stem

214   diameter (*D*, over bark, cm), height (*H*, m) and, as described below, measured, estimated or

215   derived basic density of stem wood (ρ, g cm^{-3}, typically measured as oven-dry mass per green

216   volume of stem at a standard height of 130 cm, Table 1). Secondary data relating to the site from

217   which an individual was sampled were also collated (Table 1). These included whether the site

218   was 'natural' (i.e. naturally regenerated shrubland, woodland, or forest) or managed (i.e. human-

219   induced establishment via either nursery stock, direct seeding or human-induced natural

220   regeneration). If the stand was managed, it was also recorded whether or not the stand was

221   relatively young, defined as < 20 years since establishment. Climatic data were collated (BoM,

222   2015; mean data based on 30-year period 1961-1990, resolution of approximately 2.5 km) and

223   included long-term mean annual precipitation (MAP, mm yr^{-1}) and mean annual temperature

224   (MAT, °C).

225

226   *Measurements and data cleaning*

227   Conventionally, tree diameter is measured at 130 cm (D_{130}) height above ground level to

228   avoid marked stem buttress swelling or exposed lignotubers in some species, and thus better

229   represents the diameter of a log above the stump. Consequently, most trees (F_{Euc}, $F_{Other-H}$ and

230    $F_{Other-L}$) had D_{130} measurements. For species of F_{Shrub} and F_{Multi}, where D_{130} measurements

231   introduced errors due to the presence of multiple stems at this height, or where the individual

232   was too small to have a measurable D_{130}, D was typically measured at 10 cm height above the

233   ground ($D10$). For such multi-stemmed individuals, a single, pooled D estimate was obtained

234   from the quadratic mean - representing the sum of the cross sectional areas of individual stems

235   (Chojnacky & Milton, 2008).

236   For many individuals in the dataset, *D* was measured at multiple heights, allowing

237   derivation of generic relationships for prediction of *D* at a given height based on *D* measured at

238   another height (Table S2). These relationships were used to 'gap-fill' *D* estimates where

239   required, with D_{10} and D_{130} estimated for 33% and 14% of the 15,054 individuals, respectively.

240   Similarly, generic relationships were derived to 'gap-fill' *H* estimates of an individual through

241   the development of generic relationships between *H* and either D_{10} or D_{130} (Table S2). In this

242   way, *H* was estimated for 15% of the individuals in the database. The wood specific gravity ρ

243   was measured (or estimated based on local data) in only 8% (or 4%) of individuals in the dataset.

244   For individuals where ρ was not measured, estimates were derived based on the species (49% of

245   the dataset), or if unavailable, the genus (39% of the dataset) using the global wood density

246   database (Chave *et al*., 2009; Zanne *et al*., 2009).

247   Very small individuals (i.e. *D10* < 0.3 cm) were not included in the database. Such

248   individuals are unlikely to conform to biomass scaling laws typical of woody plants given

249   relatively little secondary thickening (e.g. Niklas, 2004; Enquist *et al.*, 2007). Data for a further

250   72 individuals from 51 sites (and 24 sources) were also excluded as outliers. Here, individuals

251   were defined as outliers if their measured AGB_{Indiv} fell outside the 99.9% confidence interval of

252   prediction of the appropriate plant functional type model. Although the AGB_{Indiv} of these outliers

253   were assumed to come from a normally-distributed population and had no major influence on

254   model fit, they were nonetheless removed on the basis that they were highly unlikely values of

255   AGB_{Indiv} for the measured dimensions, and were most likely due to errors in data entry of field

256   measurements of fresh weights.

257

258   ***Statistical analysis***

259   A simple power-law allometric model was used to predict AGB_{Indiv} based on the

260   explanatory variable, *X* (Eq. 1). Eq. 1 is linearized by logarithmic transformation (Eq. 2) so that

261   coefficients (*a* and *b*) may be estimated using ordinary least squares linear regression analyses,

262   with data corrected for heteroscedasticity, such that residual errors were normally distributed on

263   the logarithmic scale (ε; which becomes a multiplicative error in the power model, ε', Picard et

264   al. (2012)).

265         $AGB_{Indiv} = a\,X^{b} + ε'$ (1)

266         $\ln(AGB_{Indiv}) = \ln(a) + b\,\ln(X) + ε$ (2)

267   Xiao *et al.* (2011) found that Eq. 2 produced more accurate estimates of biomass than

268   alternative nonlinear fitting. Eq. 2 was applied to the entire dataset (universal model, $All_{Universal}$),

269   and to the datasets for each of the five plant functional types: F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$

270     $_L$. The simplest versions of the models depicted by Eq. 2 had $X = D$, where D was D_{130} (or D_{10})

271   for F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$, and by necessity, D_{10} for F_{Shrub}, F_{Multi}, and hence, $All_{Universal}$.

272   When back-transforming from logarithmic to natural scales (i.e. to obtain the estimate of

273   AGB_{Indiv}), a correction factor (CF) is required to remove bias. Nine different CFs were reviewed

274   by Clifford *et al*. (2013), and the MM CF (Minimise Mean Square Error CF, Shen and Zhu

275   2008) was recommended for predicting biomass of new trees or shrubs as it gave relatively low

276   prediction bias. Because the value of the MM CF varies with D, a range of MM CF values are

277   reported here. The more commonly used Baskerville CF (Baskerville 1972, which assumes the

278   variability is constant across D) may lead to biased AGB_{Indiv} estimates, particularly for

279   individuals that have a D that is appreciably larger or smaller than the mean D used to develop

280   the allometric model. But in this study the MM and Baskerville CF's were consistent, at less two

281   decimal places, due to our sample sizes. Therefore, although the MM CF is recommended, we

282   also report the Baskerville CF for reference.

283   To confirm the validity of tested models, we checked: (i) that there was no

284   heteroscedasticity by confirming standardised residuals were not correlated with the

285    $\ln(AGB_{Indiv})$, and (ii) for influential points (i.e. data points having a Cook's D value > 1; Cook,

286   1979). Then, performance of valid models was quantified using five fit statistics: (i) standard

287   errors of the coefficients $\ln(a)$ and b, (ii) residual standard error of Eq. 2, *RMSE*, (iii) adjusted

288   coefficient of determination, R^2, (iv) 95% confidence interval of the slope and intercept of the

289   line of best fit to the plot of observed versus predicted back-transformed AGB_{Indiv}, and (v)

290   average bias, or mean of the residuals expressed in absolute terms and provided as a proportion

291   (%) of the observed value (i.e. mean absolute prediction error '*MAPE*', using back-transformed

292   AGB_{Indiv} predictions) (Sileshi 2014).

293   Additional measures of accuracy were used to aid comparisons among alternative models

294   with differing numbers of variables. These included Mallows' *Cp* statistics (Mallows, 1973) and

295   Akaike's information criterion (*AIC*, Burnham & Anderson, 2004). Models of poor fit have *Cp*

296   values greater than the number of model parameters (including the intercept), while the lowest

297   *AIC* indicates the most parsimonious model. The Bayesian information criterion (*BIC*) was also

Generic allometrics 11

298   assessed (Burnham & Anderson, 2004), but not reported as it provided very similar indications

299   to *AIC*.

300

301   *Testing compound predictor variables including height and wood density*

302   To explore whether accuracy of AGB_{Indiv} prediction could be improved by using a

303   compound predictor variable *cf. D*-alone, we tested three alternatives of *X*: (i) *D* alone, based on

304   a simple geometrical argument that should hold across forests (Chave *et al.*, 2005), (ii) the

305   compound stem volume index D^2H, and (iii) the compound stem mass index $D^2H\rho$. We

306   calculated for each dataset, the change in fit statistics (*RSME*, R^2 and *AIC*) between *D*-alone

307   based model and each of the two alternative compound predictor variables, i.e.: D^2H, and $D^2H\rho$.

308   For example, for the F_{Euc} model, changes in fit statistics were assessed for (F_{Euc} using *D*-alone) –

309   (F_{Euc} using D^2H), and for (F_{Euc} using *D*-alone) – (F_{Euc} using $D^2H\rho$). To examine uncertainties

310   associated with the inclusion of estimates, rather than direct measured, of *H* and *ρ* (Sileshi *et al.*,

311   2014), these analyses were repeated using sub-sets of data that only included individuals for

312   which *H* was measured (when testing the D^2H predictor variable), or that only included

313   individuals for which both H and *ρ* were measured (when testing the $D^2H\rho$ predictor variable).

314

315   *Testing inclusion of site-factor predictor variables*

316   General linear model analyses were used to assess whether accounting for site factors

317   improved the performance of Eq. 2, as indicated by an improvement in the fit statistics of *RSME*,

318   R^2 and *AIC*. The site factors tested included: (i) stand age (<20 yrs, or >20 yrs), (ii) management

319   (natural or managed vegetation), (iii) ecoregion (Fig. 1), (iv) MAT, and (v) MAP. Interactions of

320   these site-factors with ln(D) were included in the model only where they were significant.

321

322   *Testing levels of generalisation*

323   Three approaches were used to determine the impact of the level of generalisation of

324   allometric models (Eq. 2) on accuracy of AGB_{Indiv} prediction. First, using the entire dataset,

325   general linear model analysis was used to assess whether the fit statistics (*RSME*, R^2 and *AIC*) of

326     $ln(AGB_{Indiv})$ prediction from $ln(D)$ could be enhanced by accounting for the supplementary

327   categorical variable of plant functional type in the $All_{Universal}$ model. Second, using each dataset

328   of the five plant functional types, increases in such fit statistics were assessed when using the

329   less generalised plant functional type model rather than the $All_{Universal}$ model. Third, the 53

330   species that had $N > 50$ (and which thus provided reasonable prediction of AGB_{Indiv} given

331   population level variability, Roxburgh *et al*., 2015) were used to examine improvement in

332   accuracy with decreasing level of generalisation in allometric models. We calculated for each

333   species dataset, the change in fit statistics (*RSME*, R^2 and *AIC*) between the $All_{universal}$ model and

334   each of the two levels of generalisations, i.e.: functional types model, and species-specific

335   model. For example, for a species of eucalypt such as *E. wandoo*, changes in fit statistics were

336   assessed for $(F_{Euc}) - (All_{universal})$, and for (Species-specific model for *E. wandoo*) $- (All_{universal})$.

337

338   ***Model performance***

339   One concern with the application of generalised (multi-species) allometric models, such

340   as those based on plant functional type, is that not all species are well represented by the model.

341   In some cases, this may lead to significant bias. To test bias frequency, predicted AGB_{Indiv} (and

342   its associated 95% confidence interval) was attained at D_{10} values of 10, 50 and 100 cm using

343   both species-specific models and the more generalised plant functional type or universal models.

344   If the 95% confidence interval of prediction using a generalised model largely overlapped with

345   that from the most accurate model (species-specific) for that species, then it was assumed that

346   significant bias had not been introduced.

347   As a final test of accuracy of allometric models, results were collated from 17 stands of

348 contrasting structure and environment where whole plots of vegetation were harvested to obtain

349 'true' and direct measurements of stand-based AGB_{Stand} (Table 2). Inventories of species and D

350 from each of these 17 stands were used to apply the models of best fit identified in this study,

351 and to sum the predicted AGB_{Indiv} to facilitate a comparison of observed and predicted AGB_{Stand}.

352 The relationship between observed and predicted AGB_{Stand} was used to determine the overall

353 accuracy and bias of generalised predictions at the stand-scale. These predictions were made

354 using three scenarios where the level of generalisation of the applied models differed. In the first

355 scenario, we used species identity of each individual to apply the relevant species-specific model

356 and then sum individual tree biomass to estimate AGB_{Stand}. For species where no species-specific

357 model was available, the appropriate plant functional type model was applied. Second, species

358 identification and/or species-specific models were assumed to be unavailable, and so only plant

359 functional type models were applied. Third, species identification, and models based on species

360 or plant functional type models were assumed to be unavailable, and so the universal model

361 ($All_{universal}$) was applied. Using plots of observed versus predicted AGB_{Stand}, the 1:1 line was used

362 to indicate the distribution of residuals, and display any bias. Model efficiencies (*EF*, Soares *et*

363 *al*. 1995, expressed as a percentage) were used to assess whether the prediction performance

364 differed among the three scenarios. In addition, we calculated slope and intercept of the line of

365 best fit between observed and predicted AGB_{Stand}, and the resulting prediction quality statistics

366 *RMSE* and *MAPE*, for each of the three scenarios.

367

368 **Results**

369 *Allometric models*

370   Even when based on D-alone, the model (Eq. 2) precisely predicted AGB_{Indiv} across the

371 entire database using either $All_{Universal}$, or any of the five categories of plant functional types:

372 F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ (Fig. 3). The amount of variation in $\ln(AGB_{Indiv})$ explained

373   by these simple generalised models was 94-98%, with errors (*RMSE*) of 0.19-0.49 (Table 3).

374   Back-transformation of ln(AGB$_{Indiv}$) predictions (using the MM correction factor) indicated

375   relatively high uncertainty in the prediction of AGB$_{Indiv}$ for any given tree or shrub of a given D

376   (see 95% confidence intervals of prediction, Fig. 4). However, these individual errors largely

377   cancel out when predictions are made across a wide range of data. Thus, these generalised

378   models provided reasonable accuracy across the datasets, explaining 84-96% of variation in

379   AGB$_{Indiv}$ (Fig. 4), with a *MAPE* range of 15-41% (Table 3).

380   There was some evidence that the simple power-law allometric model was not

381   appropriate for F$_{Other-L}$ plant functional types, with under-prediction of AGB$_{Indiv}$ in larger trees

382   and over-prediction of AGB$_{Indiv}$ in smaller trees. However, if small saplings (D_{130}<10 cm) were

383   excluded, the performance of the power-law model was satisfactory, with the RMSE of

384   ln(AGB$_{Indiv}$) prediction decreasing from 0.273 (data not shown) to 0.189 (Fig. 3).

385

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

387   Addition of H and/or ρ in a compound predictor variable in Eq. 2 did not markedly

388   influence model performance compared with the D-based model in predicting ln(AGB$_{Indiv}$), with

389   changes in *RMSE* and R^2 less than ±0.06 and ±0.02, respectively (Table 4). Similar results were

390   obtained for a sub-set of the data for which H or ρ were measured rather than estimated (see

391   values in parentheses, Table 4), noting that tests of ρ inclusion were based on limited data

392   because only 12% of the dataset had measured or estimated ρ values.

393

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

395   Since the addition of H and/or ρ in a compound predictor did not markedly influence

396   performance of the D-based model in predicting ln(AGB$_{Indiv}$), only models based on D were used

397   to test the benefits of including site-factor predictor variables. When compared to using D-alone,

398   accounting for site-factors resulted in negligible model improvements, with the increase in

399   explained variation of $\ln(AGB_{Indiv})$ being consistently $< 0.4\%$ (Table 5). For example,

400   accounting for whether or not the individual was from a young (< 20 years old) stand, or whether

401   or not the individual was from a stand that was managed, resulted in *RMSE* and *AIC* decreases of

402   < 0.03 and $< 5\%$, respectively. Furthermore, these site factors had negligible influence across all

403   models based on plant functional types where a majority of the individuals were from young

404   planted stands (e.g. F_{Multi}, $F_{Other-H}$, $F_{Other-L}$). Accounting for ecoregion reduced *RMSE* by $< 0.03\%$

405   and *AIC* by $< 8\%$. If ecoregion was added as supplementary variable, *Cp* was sometimes greater

406   than the number of explanatory variables used, suggesting a poor model fit. Inclusion of

407   numerical variables of MAT or MAP led to even less improvement in predictions, with *RMSE*

408   reduced by $< 0.01\%$, *AIC* reduced by $< 3\%$.

409

410   ***Levels of generalisation***

411   Addition of plant functional type as a categorical explanatory variable improved

412   performance of the $All_{Universal}$ model (*RMSE* reduced by 0.04, R^2 increased by 0.01%, and

413   negative changes in *AIC*, Table 6). As further evidence of improvements in prediction accuracy

414   by reducing level of generalisation, there was a consistent increase in fit statistics when, for each

415   plant functional type, the relevant plant functional type model was applied in place of the

416    $All_{Universal}$ model. When generalising at the level of plant functional type there was a decrease in

417   the *RMSE* of 0.01-0.25, with R^2 increasing by 0.00-0.05% (Table 6). Gains in accuracy when

418   generalising at the plant functional type level were particularly pronounced for $F_{Other-L}$ (or F_{Multi})

419   where increases in *RMSE* were 0.25 (or 0.05), compared to < 0.02 for the other categories of

420   plant functional type. When considering the reduced dataset for $F_{Other-L}$ (i.e. excluding saplings

421   with $D_{130} < 10$ cm, N=455), gains in accuracy were similarly larger when using a model specific

422   for that dataset than when applying the $All_{Universal}$ model (i.e. $\Delta RMSE$ of -0.162, ΔR^2 of 0.150,

423   data not shown).

Generic allometrics 16

424   Although results are not shown here, generalising at the level of sub-categories of plant

425   functional type (Fig. S1) showed little or no improvement in accuracy of $\ln(AGB_{Indiv})$ predictions

426   when compared to those obtained when using models generalised at the level of plant functional

427   type.

428   As expected, when applied to datasets restricted to focal species, the greatest accuracy of

429   prediction in $\ln(AGB_{Indiv})$ was attained using the least generalised model – i.e. models specific to

430   a given species. Compared to the $All_{Universal}$ model, plant functional type models yielded some

431   modest improvements, but were still not as good as species-specific models (Table 7). Gains in

432   accuracy of $\ln(AGB_{Indiv})$ predictions could be made by reducing the level of generalisation from

433   functional type to species, especially for F_{Shrub} and F_{Euc}.

434

435   *Model performance*

436   Fig. 5 illustrates the overlap of the 95% confidence interval of generalised model

437   prediction with that attained using the species-specific model for predicting $\ln(AGB_{Indiv})$ under

438   the scenarios of assuming an observed D_{10} of 10, 50 and 100 cm. On average, 74% (SD 14%) of

439   the confidence interval of prediction obtained using the models generalised at the level of plant

440   functional type overlapped with that attained using the species-specific model. Tested against the

441    $All_{Universal}$ model, this figure decreased to 67% (SD 13%), largely because two key species of

442    $F_{Other-L}$ were relatively poorly represented by the $All_{Universal}$ model. However for most tested

443   species, results were similar (with mean ±8%, SD 5%) when comparisons were made between

444   the confidence intervals of species-specific models and two alternative, more generalised

445   models.

446   Of the 53 species tested, only four (or 8%) had < 55% overlap in confidence intervals of

447   prediction obtained using generalised and species-specific models. These four species were

448   *Eucalyptus vegrandis*, *Acacia calamifolia*, *E. pilularis* and *E. muelleriana*. For *Acacia*

449   *calamifolia*, this was partly attributable to the relatively low *RMSE* of prediction of the species-

450   specific model resulting in relatively small confidence intervals of prediction relative to the more

451   generalised models. However, generalised multi-species models poorly represented the allometry

452   of all four of these species, indicating potential for significant bias in up to 8% of the tested

453   species generalised models were applied.

454   When allometry-predicted AGB_{Stand} was compared to that observed by direct whole-plot

455   harvesting across 17 contrasting stands (Table 2), prediction quality was not affected by

456   increasing the level of generalisation of models. Differences in efficiency of prediction of

457   AGB_{Stand} were < 1% between scenarios, while differences in *MAPE* were < 5.61% between

458   scenarios (Fig. 6).

459   Despite good overall prediction quality, allometry-predicted AGB_{Stand} introduced

460   significant bias, even when applying species-specific models. However, this bias was largely

461   independent of the level of generalisation of allometry applied. For example, for the Leos site,

462   where measured AGB_{Stand} was 113.6 Mg ha^{-1} (Table 2), the absolute prediction error (or bias)

463   was 24-36% regardless of the model applied.

464

465   **Discussion**

466   *Allometric models*

467   Results obtained here confirmed that a simple power-law model largely encapsulated

468   scaling laws common to most woody plants (e.g. Niklas, 2004). There may be bias in AGB_{Indiv}

469   prediction for any given individual tree or shrub. But across a wide range of individuals,

470   AGB_{Indiv} may be predicted using generalised allometric models with reasonable accuracy (i.e.

471   *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

472   explanatory variable. Despite these models being based on AGB_{Indiv} datasets that were larger,

473   and from a broader range of vegetation types than previously collated for Australia, the fit

474   statistics obtained were comparable to generalised allometric models for AGB_{Indiv} previously

475   developed for much smaller datasets (e.g. Williams *et al.*, 2005; Montagu *et al.*, 2005; Jonson &

476   Freudenberger 2011; Paul *et al*., 2013a,b).

477   Our results suggest that increasing the domain of application of generalised allometric

478   models for AGB_{Indiv} (i.e. being based on datasets from a wider range of ecoregions and from a

479   range of plant types etc.) does not substantially jeopardise their accuracy of prediction. Our

480   results provide further evidence of the effectiveness of generic AGB_{Indiv} allometric models

481   developed from large, compiled datasets, consistent with comparable studies in tropical forests

482   (Chave *et al*., 2005, 2014, Vieilledent *et al*., 2012); for different forest types in the U.S.A

483   (Chojnacky *et al*., 2014); and for different forest types in China (Ali *et al*., 2015). Development

484   of such generalised models is an appropriate approach to extending the geographical application

485   range of otherwise limited, and often localised, species-specific models. Collation of datasets to

486   develop such generalised allometric models seems preferable to either: (i) making parameters of

487   existing localised species-specific models available in a database to facilitate the selection of the

488   most appropriate models for new specific areas of interest (e.g. Ter-Mikaelian & Korzukhin,

489   1997; Zianis *et al*., 2005; Henry *et al*., 2013), or (ii) applying existing localised species-specific

490   models to generate pseudo-observations to develop more generalised models (e.g. Pastor *et al*.,

491   1984; Zianis & Mencuccini, 2004; Muukkonen 2007; Chojnacky *et al*., 2014).

492   In the present study, allometry-predicted AGB_{Indiv} tended to be least accurate for the

493   multi-stemmed plant functional types of F_{Shrub} and F_{Multi} (Table 3). Many others (e.g. Buech &

494   Rugg, 1995; Chojnacky & Milton, 2008; Paul *et al*., 2013a,b; Berner *et al*., 2015) found D to be

495   the strongest predictor of AGB_{Indiv} in such multi-stemmed individuals. However in allometric

496   models of AGB_{Indiv} for multi-stemmed trees, some workers (e.g. Mosseler *et al*., 2014; Matula *et*

497   *al*., 2015) used D of only a given number (e.g. 3 or 5 stems) of the largest stems, yet did not test

498   whether it resulted in an increased accuracy of prediction above that obtained if an equivalent D

499   was calculated and applied. Hence further work is required to assess alternative methods for

500   calculating D in multi-stemmed individuals, and determining the method that provides the

501   highest accuracy of prediction of AGB_{Indiv}. There is also a need to have clear and consistent

502   protocols for measurement of D.

503   Another aspect of these results that requires further investigation is whether there may be

504   improvement on the simple power-law model for tree species of relatively low wood density. For

505   the $F_{Other-L}$ category of species, a single simple power-law model did not accurately predict

506   AGB_{Indiv} across the full range of tree sizes. For these species, options for weighted non-linear

507   modelling should be investigated as an alternative to the power-law model provided here (i.e. for

508    $F_{Other-L}$ trees of $D_{130} > 10$ cm).

509

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

511   We found including H and ρ in addition to D in a compound predictor variable did not

512   markedly improve $\ln(AGB_{Indiv})$ predictions, even when using only measured values (Table 4).

513   This finding supports the conclusions of others (e.g. Molto *et al*., 2013; Sileshi, 2014; Kuyah &

514   Rosenstock, 2015) that using D alone is an appropriate predictor of AGB_{Indiv} as it minimises

515   costs associated with these additional biometric measurements, and also the uncertainty resulting

516   from measurement and prediction errors of H and/or ρ.

517   The fact that H is often correlated with D (e.g. Pérez-Cruzado & Rodríguez-Soalleiro,

518   2011; Mugasha *et al*., 2013; Ishihara *et al*., 2015) may largely explain why inclusion of H as an

519   additional predictor did not markedly influence the performance of the D-based models. Indeed

520   scaling theory of larger woody plants predicts that H scales with diameter to the 2/3 power

521   (Niklas & Spatz, 2004). Nonetheless, although the inclusion of H may not be necessary to

522   accurately predict AGB_{Indiv}, there is evidence that it may be beneficial to include in allometric

523   models of foliage biomass, which tends to be influenced by plant architecture (e.g. Picard *et al*.,

524   2015).

525   We make two suggestions as to why inclusion of ρ did not improve the predictive ability

526   of the D-based model. The first is possible measurement errors. For example, ρ varies with

527   height (e.g. Pérez-Cruzado & Rodríguez-Soalleiro, 2011; Wiemann & Williamson, 2014), and

528   with stand age or rates of growth (e.g. Ilic *et al*., 2000). Hence database-derived ρ values may

529   have been erroneous due to the height and/or age at which ρ was measured (e.g. Molto *et al*.,

530   2013). Second, most of our dataset was obtained from temperate regions, where ρ is typically

531   less variable than, for example, among tropical trees (Swenson & Enquist, 2007). This is

532   consistent with ρ having greater predictive potential in AGB_{Indiv} models for tropical trees (Chave

533   *et al*., 2014) than was found in this study.

534

535   *Inclusion of site-factor predictor variables*

536   Our study indicated that including site-related factors such as characteristics of the stand

537   (stand age and management), and climatic characteristics (e.g. MAP, MAT), did not markedly

538   improve the predictive ability of D-based models (increased R^2 of <1%, Table 5). These results

539   provided support to findings that while the allocation of AGB_{Indiv} and plant architecture (i.e. the

540   D-H relationship) may vary with site factors as individuals optimize their growth strategies, the

541   impact on total AGB_{Indiv} allometry appears to be negligible (e.g., António *et al*., 2007; Peichl &

542   Arain, 2007; Feldpausch *et al*., 2011, 2012; Banin *et al*., 2012; de Miguel *et al*., 2014; Gonzalez-

543   Benecke *et al*., 2014; Moncrieff *et al*., 2014; Hulshof *et al*., 2015). This may be due to the

544   compensatory relationship between stem and canopy mass resulting in similar AGB_{Indiv} for trees

545   of the same D, but different partitioning to leaves, branches and stems (e.g. Kuyah *et al*., 2013).

546   Hence, results obtained here support the claim that generalised models can be based on plant

547   functional types rather than site factors such as climatic zones (Ngomanda *et al*., 2014).

548   These findings contrast with previous research showing that the inclusion of additional

549   stand-related variables such as stand age, density and/or productivity in allometric models may

550   provide more accurate AGB_{Indiv} predictions (Callaway *et al*., 1994; De Lucia *et al*., 2000; Genet

551   *et al*., 2011; Alvarez *et al*., 2012; Lopez-Serrano *et al*., 2015). Such improvements are often

552   interpreted as climatic impacts influencing predicted AGB_{Indiv} via changes in the tree architecture

553   (H-D relationship, e.g. Chave *et al*., 2014), and have led to recent debates over potential trade-

554   offs between practical application and loss of accuracy when simple power-law models are used

555   in preference to more complex models of AGB_{Indiv} (e.g. Sileshi, 2014; Picard *et al.*, 2015).

556   Results obtained here indicate that this trade-off of loss of accuracy with the application of

557   simple power-law models was relatively minor.

558

559   *Levels of generalisation*

560   Compared to the most generalized model ($All_{Universal}$), the largest gains in predictive

561   ability were attained when categorising the dataset at the level of species, but with little loss of

562   accuracy when generalised to the level of plant functional type (Tables 6 & 7). These results

563   were therefore consistent with previous work showing that generic multi-species models perform

564   almost as well as the species-specific ones developed for that region (e.g. Feller 1992; Williams

565   *et al.*, 2005; Montagu *et al.*, 2005; Mugasha *et al.*, 2013; Paul *et al.*, 2013a,b; Mbow *et al.*, 2014;

566   Ali *et al.*, 2015).

567   It is often suggested that plant functional attributes (e.g. ρ, apical dominance, and canopy

568   architecture) may be genetically constrained as a result of adaption to environmental factors (e.g.

569   Onoda *et al.*, 2010; van Gelder *et al.*, 2006; Banin *et al.*, 2012). Such phylogenesis may account

570   for differences in the AGB_{Indiv} allometry between trees and shrubs found here, and by others (e.g.

571   Paul *et al.*, 2013a). Species of F_{Shrub} of relatively large size (e.g. D_{10} ca. 30-90 cm) had slightly

572   lesser AGB_{Indiv} than trees of the same D (Fig. 3). In contrast, multi-stemmed species (F_{Multi})

573   tended to have relatively high AGB_{Indiv} for a given D (Fig. 3). This may be attributable to their

574   typical architecture of a large proportion of relatively heavy branches/small stems (e.g. Paul *et*

575   *al.*, 2013b) of relatively high ρ (Table 1).

576   Although including ρ in compound predictor variables offered no measurable

577   improvement to D-based models (Table 4), phylogenesis resulting in divergent stem anatomy

578   and ρ may also largely account for the differences in AGB_{Indiv} allometry between angiosperms

579   and gymnosperms found here (i.e. $F_{Other-L}$ departing strongly from the $All_{Universal}$ model, Tables 6

580   & 7) and by others (e.g. Chojnacky *et al.*, 2014; Hulshof *et al.*, 2015). Lower average values of ρ

581   for species of $F_{Other-L}$ (Table 1) explain why, for a given D, the AGB_{Indiv} was relatively low when

582   compared to most other tree species, particularly F_{Euc} (Fig. 3). Although less evident from ρ

583   measurement and estimates collated due to the high uncertainties in these datasets, such

584   differences in stem anatomy may also be one of the reasons why species of F_{Euc} (average ρ 0.77

585   g cm^{-3}, Table 1) of large size (e.g. $D_{10} > 50$ cm) had relatively high AGB_{Indiv} for a given D when

586   compared to species of $F_{Other-H}$ (average ρ 0.67 g cm^{-3}, Table 1) (Fig. 3).

587   There is evidence that ρ varies greatly among species in Australia (e.g. Onoda *et al.*,

588   2010). Further refinement and consistency in protocols used to measure ρ is required to confirm

589   whether, as observed by others (e.g. van Breugel *et al.*, 2011; Fayolle *et al.*, 2013; Chojnacky *et*

590   *al.*, 2014), ρ may be more similar within than between different plant functional types, resulting

591   in each having a unique AGB_{Indiv} allometry. Hence, although ρ was found not to impact the

592   model directly via a compound predictor variable, it may nonetheless have an indirect impact via

593   influencing categories (i.e. groups of species, or plant functional types) upon which generalised

594   models are developed.

595

596   *Model performance*

597   Species datasets for which we had confidence in prediction of AGB_{Indiv} using species-

598   specific models (i.e. 53 species where $N > 50$) provided a test for bias in predictions with the

599   application of more generalised models. Most (92%) demonstrated no significant bias, with the

600   95% confidence interval of prediction obtained using generalised allometry overlapping with that

601   attained using the species-specific model in 55-85% of the cases (Fig. 5). In contrast, species-

602   specific models appeared to avoid risks of significant bias in AGB_{Indiv} in about 8% of the species

603   studied. Thus, to minimise the potential for significant bias when accurate predictions are

604   required at the *individual* level, representative species-specific models (i.e. $N > 50$, Roxburgh *et*

605   *al.*, 2015) should be used when these are available (e.g. Table S3). However because allometry-

606   predicted AGB_{Indiv} are generally used to derive AGB_{Stand}, user decision on whether the additional

607   costs associated with developing new species-specific models is justified should be based on the

608   extent to which these more specific models improve accuracy (and particularly, reduce bias) at

609   the *stand* level.

610   Stand-level validation of allometric models showed that there was relatively little added

611   benefit (*EF* of AGB_{Stand} prediction increasing by <1%, and *RMSE* and *MAPE* decreasing by <

612   3.2 Mg ha^{-1} and < 5.6%, respectively) of using species-specific models when compared to more

613   generalised models (Fig. 6). The stand of Leos (observed AGB_{Stand} of 113.6 Mg ha^{-1}) remained

614   an outlier regardless of which level of generalisation was used in the allometric models applied

615   to individuals in this stand. These results indicate that a good *individual*-level model does not

616   necessarily translate into much improved *stand*-level predictions. Hence, when allometry-

617   predicted AGB_{Stand} estimates are required for new stands, added field-measurement costs and

618   model uncertainty associated with obtaining species-specific data and calibrating model

619   coefficients for each new species-specific model are generally unwarranted. Costs and possible

620   uncertainties in stand-based estimates can be minimised through the application of more

621   generalised models that are based on a much smaller number of parameters (e.g. only two when

622   applying the most generalised model), irrespective of the number of species within the stand.

623   This study has advanced the development and testing of generalised allometric models

624   for prediction of total AGB_{Indiv} for a wide range of plant functional types found across a diversity

625   of ecoregions in Australia. Simple power-law generic models were precise, even when based on

626   trunk diameter as the sole predictive varaible. Given the insubstantial influence of site factors

627   (e.g. whether the stand was relatively young or managed, ecoregion, MAP and MAT) on

628   AGB_{Indiv} allometry, a next line of enquiry is to rigorously evaluate this finding by extending the

629   replication of individuals from some of the relatively under-sampled combinations of plant

630   functional type and ecoregion (e.g. individuals of $F_{Other-H}$ from tropical and subtropical regions,

631   Fig. 2) or stand-types (e.g. individuals of F_{Multi} from relatively mature and unmanaged stands).

632   Although species-specific models significantly reduced bias in AGB_{Indiv} in about 8% of

633   the species tested, results obtained from validation of allometric models against 17 stands that

634   had AGB_{Stand} directly measured showed that a good individual-level model does not necessarily

635   translate into much improved stand-level predictions. Across these contrasting sites where direct

636   measurement (destructive stand harvest), the application of more generalised allometric models

637   resulted in predictions of stand-level AGB that were almost as accurate as species-specific

638   models. Furthermore, it is possible that for stands of mixed species, due to the smaller sample

639   size and larger overall number of model coefficients to parameterise, uncertainties associated

640   with the propagation of errors (including measurement, model-fitting and prediction errors) may

641   be larger with the application of multiple species-specific models compared to a single

642   generalised multi-species model. This hypothesis is being tested in a forthcoming paper.

643   Additionally, sample sizes of > 50 are required for constructing each species-specific model

644   (Roxburgh *et al.*, 2015), resulting in significant costs associated with development of models for

645   each new species. For such mixed species stands, likely higher uncertainties and costs negate the

646   slight gain in average accuracy of AGB_{Stand} prediction when applying multiple species-specific

647   models when compared to a generalised multi-species model.

648   It is therefore recommended that generalised multi-species models be applied when cost-

649   effective predictions of AGB_{Stand} are required across multiple mixed species stands. The most

650   generalised model ($All_{Universal}$) tested here was based on D_{10} by necessity, and yet D

651   measurement at this height is known to be sub-optimal for many single-stemmed tree species.

652   Hence for practical reasons, models generalised at the level of plant functional groups (Eq. 4a-e,

653   reported here using the Baskerville *CF*) are recommended for application in both Australia, and

654   for validation in similar ecoregions in other continents.

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

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

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

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

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

660   There are two exceptions to the recommendation of application of Eq. 4. First, where the

661   trade-off between accuracy and cost effectiveness is relatively high, such as when estimating

662      $\text{AGB}_{\text{Stand}}$ for a given high carbon stand comprising only one or two dominant species. In such

663   circumstances, additional costs associated with obtaining species-specific models may warrant

664   the improved accuracy of $\text{AGB}_{\text{Stand}}$ prediction. Second, where $\text{AGB}_{\text{Stand}}$ is required for stands

665   dominated by species suspected of not conforming to the generalised plant functional groups

666   models. Another line of enquiry to pursue is to build improved species-specific models to expand

667   the testing done here that found 8% of species did not conform to generalised plant functional

668   type models.

669   As with all allometric models, to avoid bias in $\text{AGB}_{\text{Indiv}}$ predictions, recommended

670   models in this study should only be applied within their valid diameter range as indicated by the

671   maximum D sampled (e.g. Table 3, Table S3). Further sampling is required to extend the D

672   range of allometric models to both increase the replication (and confidence) of prediction of

673   larger sized trees (D_{130} >50 cm), and to account for some of the variation in $\text{AGB}_{\text{Indiv}}$ due to

674   hollows or piping of larger over-mature trees or trees affected by termites (e.g. Rayner *et al.*,

675   2014; Monda *et al.*, 2015).

676

677   **Acknowledgements**

687

688   **References**

689   Ali A, Xu MS, Zhao YT, Zhang QQ, Zhou LL, Yang XD, Yan ER (2015) Allometric biomass

690   equations for shrub and small tree species in subtropical China. *Silva Fennica,* **49**, 1-10.

691   Alvarez E, Duque A, Saldarriaga J *et al.* (2012) Tree above-ground biomass allometries for

692   carbon stocks estimation in the natural forests of Colombia. *Forest Ecology and Management*,

693   **267**, 297–308.

694   António N, Tomé M, Tomé J, Soares P, Fontes L (2007) Effect of tree, stand, and site variables

695   on the alllometry of *Eucalyptus globulus* tree biomass. *Canadian Journal of Forest Research*,

696   **37**, 895-906.

697   Arthur M, Hamburg SP, Siccama TG (2001) Validating allometric estimates of aboveground

698   living biomass and nutrient contents of a northern hardwood forest. *Canadian Journal of

699   Forest Research*, **31**, 11–17.

700   Attiwill P (1979) Nutrient Cycling in a *Eucalyptus obliqua* (L'hérit.) Forest. III. Growth,

701   Biomass, and Net Primary Production. *Botany*, **27**, 439-458.

702   Banin L, Feldpausch TR, Phillips O L *et al.* (2012) What controls tropical forest architecture?

703   Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, **21**,

704   1179–1190.

705   Ballantyne AP, Andres R, Houghton R *et al.* (2015) Audit of the global carbon budget: estimate

706   errors and their impact on uptake uncertainty. *Biogeosciences*, **12**, 2565–2584.

707   Baskerville GL (1972). Use of logarithmic regression in the estimation of plant biomass.

708   *Canadian Journal of Forest Research*, **2**, 49–53.

709   Basuki T, van Laake P, Skidmore A, Hussin Y (2009) Allometric equations for estimating the

710   above-ground biomass in tropical lowland Dipterocarp forests. *Forest Ecology and*

711   *Management*, **257**, 1684–1694.

712   Berner LT, Alexander HD, Loranty MM, Ganzlin P, Mack MC, Davydov SP, Goetz SJ (2015)

713   Biomass allometry for alder, dwarf birch, and willow in boreal forest and tundra ecosystems

714   of far northeastern Siberia and north-central Alaska. *Forest Ecology and Management*, **337**,

715   110–118.

716   BoM (2015). Bureau of Meteorology Gridded climatological data. Climate Data Services,

717   Melbourne 3001, Australia.

718   Buech RR., Rugg DJ (1995) Biomass relations for components of five Minnesota shrubs.

719   Research Paper NC-325. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North

720   Central Forest Experiment Station

721   Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in Model

722   Selection, *Sociological Methods & Research*, **33**, 261–304.

723   Búrquez A, Martínex-Yrízar A (2011). Accuracy and bias on the estimation of aboveground

724   biomass in the woody vegetation of the Sonoran Desert. *Botany*, **89**, 625–633

725   Brown S, Gillespie A, Lugo, A. (1989) Biomass estimation methods for tropical forests with

726   applications to forest inventory data. *Forest Science*, **35**, 881–902.

727   Callaway RM, Delucia EH, Schlesinger WH (1994) Biomass allocation of montane and desert

728   ponderosa pine: An analog for response to climate-change. *Ecology*, **75**, 1474–1481.

729   Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science*, **320**,

730   1456-1457.

731   Carter JL, White DA (2009) Plasticity in the Huber value contributes to homeostasis in leaf

732   water relations of mallee Eucalypt with variation to groundwater depth. *Tree Physiology*, **29**,

733   1407-1418.

734   Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and

735   scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society*

736   *B: Biological*, **359**, 409–420.

737   Chave J, Andalo C, Brown S *et al*. (2005) Tree allometry and improved estimation of carbon

738   stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.

739   Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide

740   wood economics spectrum. *Ecology Letters*, **12**, 351-366.

741   Chave J, Réjou-Méchain M, Búrquez A *et al*. (2014). Improved allometric models to estimate

742   the aboveground biomass of tropical trees. Global Change Biology, **20**, 3177–3190.

743   Chen Q, Laurin GV, Valentini R (2015) Uncertainty of remotely sensed aboveground biomass

744   over an African tropical forest: Propagating errors from trees to plots to pixels. *Remote

745   Sensing of Environment*, **160**, 134–143

746   Chojnacky, D.C., Milton, M. (2008) Measuring Carbon in Shrubs. *In*: Hoover CM (ed) Field

747   measurements for forest Carbon Monitoring: A Landscape-Scale Approach. Humana Press,

748   New York, pp 45-72.

749   Chojnacky, D.C., Heath, L.S., Jenkins, J.C (2014) Updated generalized biomass equations for

750   North American tree species. *Forestry*, **87**, 129–151.

751   Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot

752   data. *Ecological Applications*, **12**, 3-7.

753   Clifford D Cressie N, England JR, Roxburgh SH, Paul KI (2013) Correction factors for

754   unbiased, efficient estimation and prediction of biomass from log-log allometric models.

755   *Forest Ecology and Management*, **310**, 375–381.

756   Cook RD (1979) Influential Observations in Linear Regression. *Journal of the American

757   Statistical Association*, **74**, 169–174.

758   De Lucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation in

759   pines. *Global Change Biology*, **6**, 587–593.

760   De Miguel S, Pukkala T, Assaf N, Shater Z (2014) Intra-specific differences in allometric

761   equations for aboveground biomass of eastern Mediterranean *Pinus brutia*. *Annals of Forest*

762   *Science*, **71**,101–112.

763   DSWPC (2015) Australia's ecoregions map. Department of Sustainability, Environment, Water,

764   Populations and Communities (adapted from World Wildlife Fund, WWF). Last accessed

765   September   2015.   Commonwealth   of   Australia,   Canberra.

766   https://www.environment.gov.au/system/files/pages/1716eb1c-939c-49a0-9c0e-

767   8f412f04e410/files/ecoregions_1.pdf

768   Enquist BJ, Kerhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA (2007) A general

769   integrative model for scaling plant growth, carbon flux, and functional trial spectra. *Nature*

770   *Letters*, **449**, 218-222.

771   Fayolle A, Doucet JL, Gillet JF, Bourland N, Lejeune P (2013) Tree allometry in Central Africa:

772   testing the validity of pantropical multi-species allometric equations for estimating biomass

773   and carbon stocks. *Forest Ecology and Management*, **305**, 29–37.

774   Feldpausch TR, Banin L, Phillips OL *et al*. (2011) Height diameter allometry of tropical forest

775   trees. *Biogeosciences*, **8**,1081–1106.

776   Feldpausch TR, Lloyd J, Lewis SL *et al*. (2012) Tree height integrated into pantropical forest

777   biomass estimates. *Biogeosciences*, **9**, 3381–3403.

778   Feller M (1992) Generalized versus site-specific biomass regression equations for *Pseudotsuga*

779   *menziesii* var. *menziesii* and *Thuja plicata* in coastal British Columbia. *Bioresource*

780   *Technology*, **39**, 9-16.

781   Forrest W, Ovington J (1970) Organic Matter Changes in an Age Series of *Pinus radiata*

782   Plantations. *Journal of Applied Ecology*, **7**, 177-186.

783   Genet A, Wernsdörfer H, Jonard M *et al*. (2011) Ontogeny partly explains the apparent

784   heterogeneity of published biomass equations for *Fagus sylvatica* in central Europe. *Forest*

785   *Ecology and Management*, **261**, 1188–1202

786   George SJ, Harper RJ, Hobbs RJ, Tibbett M (2012) A sustainable agricultural landscape for

787   Australia: A review of interlacing carbon sequestration, biodiversity and salinity management

788   in agroforetry systems. *Agriculture, Ecosystems and Environment*, **163**, 28-36.

789   Gitay H, Noble IR (1997) What are functional types and how should we see them? In: Smith,

790   T.M., Shugart, H.H. & Woodward, F.I. (eds.) Plant functional types: their relevance to

791   ecosystem properties and global change, pp. 3-19. Cambridge University Press, Cambridge.

792   Gonzalez-Benecke CA, Gezan SA, Albaugh TJ *et al.* (2014) Local and general above-stump

793   biomass functions for loblolly pine and slash pine trees. *Forest Ecology and Management*,

794   **334**, 254-276.

795   Hatanaka N, Wright W, Loyn RH, Nally RM (2011) Ecologically complex carbon: Linking

796   biodiversity values, carbon storage and habitat structure in some austral temperate forests.

797   *Global Ecology and Biogeography*, **20**, 260-271.

798   Haverd V, Raupach MR, Briggs PR *et al.* (2013) The Australian terrestrial carbon budget.

799   *Biogeosciences*, **10**, 851-869.

800   Henry M, Picard N, Trotta C *et al.* (2011) Estimating tree biomass of sub-Saharan African

801   forests: a review of available allometric equations. *Silva Fennica*, **45**, 477–569.

802   Henry M, Bombelli A, Trotta C *et al.* (2013) GlobAllomeTree: international platform for tree

803   allometric equations to support volume, biomass and carbon assessment. *iForest—*

804   *Biogeosciences and Forestry*, **6**, 326–330.

805   Holland PG (1969) Weight Dynamics of Eucalyptus in the Mallee Vegetation of Southeast

806   Australia. *Ecology*, **50**, 212-219.

807   Houghton RA, House JI, Pongratz J *et al.* (2012) Carbon emissions from land use and land-cover

808   change. *Biogeosciences*, **9**, 5125–5142.

809   Hulshof CM, Swenson NG, Weiser MD (2015) Tree height–diameter allometry across the

810   United States. *Ecology and Evolution*, **5**, 1193-1204.

811   Husch B, Beers TW, Kershaw JA (2003) Forest Menstruation, 4th edition. John Wiley and Sons.

812   Ilic J, Boland D, McDonald M, Downes G, Blakemore P (2000) Wood Density Phase 1: State of

813   Knowledge. National Carbon Accounting System Technical Report No 18. Australian

814   Greenhouse Office, Canberra, Australia.

815   Ishihara MI, Utsugi H, Tanouchi H *et al.* (2015) Efficacy of generic allometric equations for

816   estimating biomass: a test in Japanese natural forests. *Ecological Applications*, **25**, 1433–

817   1446.

818   Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for

819   United States tree species. *Forest Science*, **49**, 12–35.

820   Jonson JH, Freudenberger D (2011) Restore and sequester: estimating biomass in native

821   Australian woodland ecosystems for their carbon-funded restoration. *Australian Journal of*

822   *Botany*, **59**, 639–652.

823   Ketterings, QM, Coe R, van Noordwijk M, Ambagau Y, Palm CA (2001) Reducing uncertainty

824   in the use of allometric biomass equations for predicting above-ground tree biomass in mixed

825   secondary forests. *Forest Ecology and Management*, **146**, 199–209.

826   Kuyah, S., Dietz, J., Muthuri, C., van Noordwijk, M., Neufeldt, H (2013) Allometry and

827   partitioning of above- and below-ground biomass in farmed eucalyptus species dominant in

828   Western Kenyan agricultural landscapes. *Biomass and Bioenergy*, **55**, 276-284.

829   Kuyah S, Rosenstock TS (2015) Optimal measurement strategies for aboveground tree biomass

830   in agricultural landscapes. *Agroforestry Systems*, **89**, 125-133.

831   Le Quéré C, Moriarty R, Andrew RM *et al.* (2015) Global carbon budget. *Earth System Science*

832   *Data*, **7**, 47–85.

833   Lopez-Serrano FR, Garcia-Morote A, Andres-Abellan M, Tendero A, del Cerro A (2005) Site

834   and weather effects in allometries: a simple approach to climate change effect on pines.

835   *Forest Ecology and Management*, **215**, 251–270.

836   Mallows CL (1973) Some Comments on CP. *Technometrics*, **15**, 661–675.

837   Matula, R., Damborska, L., Nečasova, M., Geršl, M., Šrámek, M. (2015) Measuring biomass and

838   carbon stock in resprouting woody plants. PLOS ONE, DOI:10.1371

839   Mbow C, Verstraete MM, Sambou B, Diaw AT Neufeldt H (2014) Allometric models for

840   aboveground biomass in dry savanna trees of the Sudan and Sudan–Guinean ecosystems of

841   Southern Senegal. *Journal of Forest Research*, **19**, 340–347.

842 Miranda de SC, Bustamante M, Palace M, Hagen S, Keller M, Ferreira LG (2014) Regional

843   Variations in Biomass Distribution in Brazilian Savanna Woodland. *Biotropica*, **46**, 125–138.

844 Molto Q, Rossi V, Blanc L (2013) Error propagation in biomass estimation in tropical forests.

845   *Methods in Ecology and Evolution*, **4**, 175–183.

846 Moncrieff GR, Lehmann CER, Schnitzler J *et al.* (2014) Contrasting architecture of key African

847   and Australian savanna tree taxa drives intercontinental structural divergence. *Global Ecology*

848   *and Biogeography*, **23**, 1235–1244.

849 Monda Y, Kiyono Y, Melling L, Damian C, Chaddy A (2015) Allometric equations considering

850   the influence of hollow trees: A case study for tropical peat swamp forest in Sarawak.

851   *Tropics*, **24**, 11-22.

852 Montagu K, Düttmer K, Barton C, Cowie A (2005) Developing general allometric relationships

853   for regional estimates of carbon sequestration—an example using *Eucalyptus pilularis* from

854   seven contrasting sites. *Forest Ecology and Management*, **204**, 115-129.

855 Moore JR (2010) Allometric equations to predict the total above-ground biomass of radiata pine

856   trees. *Annuals of Forest Science*, **67**, 806-817.

857 Mosseler A, Major J, Labrecque M, Larocque G (2014) Allometric relationships in coppice

858   biomass production for two North American willows (Salix spp.) across three different sites.

859   *Forest Ecology and Management*; **320**, 190–196.

860 Mugasha WA, Eid T, Bollandsås OM, Malimbwi RE, Chamshama SAO, Zahabu E, Katani JZ

861   (2013) Allometric models for prediction of above- and belowground biomass of trees in the

862   miombo woodlands of Tanzania. *Forest Ecology and Management*, **310**, 87-101.

863 Muukkonen P (2007) Generalized allometric volume and biomass equations for some tree

864   species in Europe. *European Journal of Forest Research*, **126**,157–166

865 Ngomanda A, Obiang NLE, Lebamba J *et al.* (2014) Site-specific versus pantropical allometric

866   equations: Which option to estimate the biomass of a moist central African forest? *Forest*

867   *Ecology and Management,* **312**, 1–9.

868   Niklas KJ (2004) Plant allometry: is there a grand unifying theory? *Biological Review*, **79**, 871-

869   889.

870   Niklas KJ, Spatz HC (2004) Growth and hydraulic (not mechanical) constraints govern the

871   scaling of tree height and mass. *Proceedings of the National Academy of Sciences of the*

872   *United States of America*, **101**, 15661–15663.

873   Onoda Y, Richards AE, Westoby M (2010) The relationship between stem biomechanics and

874   wood density is modified by rainfall in 32 Australian woody plant species. *New Phytologist*,

875   **185**, 493-501.

876   Paul KI, Roxburgh, SH, England JR *et al.* (2013a) Development and testing of allometric

877   equations for estimating above-ground biomass of mixed-species environmental plantings.

878   *Forest Ecology and Management*, **310**, 483-494.

879   Paul KI, Roxburgh, SH, Ritson P *et al.* (2013b) Testing allometric equations for prediction of

880   above-ground biomass of mallee eucalypts for southern Australia. *Forest Ecology and*

881   *Management*, **310**, 1005-1015.

882   Paul KI, Roxburgh SH, de Ligt R *et al.* (2015a). Estimating temporal changes in carbon

883   sequestration in plantings of mallee eucalypts: Modelling improvements. *Forest Ecology and*

884   *Management*. 335, 166–175.

885   Paul KI, Roxburgh SH, England JR *et al.* (2015b) Improved models for estimating temporal

886   changes in carbon sequestration in above-ground biomass of mixed-species environmental

887   plantings. *Forest Ecology and Management*, **338**, 208-218.

888   Paul, K.I., Peck, A., Spencer, B., *et al*. (2015c). Australian Individual Tree Biomass Library,

889   Version 1. 10.4227/05/566629ADA95DA. Obtained from Australian Ecological Knowledge

890   and Observation System Data Portal (ÆKOS, http://www.portal.aekos.org.au/), made

891   available by Commonwealth Scientific and Industrial Research Organisation, Australian

Generic allometrics 34

892   Government Department of Agriculture and Food, Westralian Department of Parks and

893   Wildlife, South Australian Department of Environment, Water and Natural Resources,

894   Victorian Department of Primary Industries, Queensland Department of Science, Information

895   Technology, Innovation and the Arts, Southern Cross University. Accessed 9th December

896   2015.

897 Pastor J, Aber JD, Melillo JM (1984) Biomass prediction using generalized allometric regression

898   for some northeast tree species. *Forest Ecology and Management*, **7**, 265-274.

899 Peichl M, Ar MA (2007) Allometry and partitioning of above- and belowground tree biomass in

900   an age-sequence of white pine forests. *Forest Ecology and Management*, **165**, 317–326.

901 Pérez-Cruzado C, Rodríguez-Soalleiro R (2011) Improvement in accuracy of aboveground

902   biomass estimation in *Eucalyptus nitens* plantations: Effect of bole sampling intensity and

903   explanatory variables. *Forest Ecology and Management*, **261**, 2016–2028.

904 Picard N, Saint-André L, Henry M (2012) Manual for building tree volume and biomass

905   allometric equations: from field measurement to prediction. Food and Agricultural

906   Organization of the United Nations, Rome, and Centre de Coopération Internationale en

907   Recherche Agronomique pour le Développement, Montpellier, 215 pp.

908 Picard N, Rutishauser E, Ploton P, Ngomanda A, Henry M (2015) Should tree biomass allometry

909   be restricted to power models? *Forest Ecology and Management*, **353**, 156-163.

910 Poulter B, Frank D, Ciais P *et al.* (2014) Contribution of semi-arid ecosystems to interannual

911   variability of the global carbon cycle. *Nature*, **509**, 600-603.

912 Rayner L, Ellis M, Taylor JE (2014) Hollow occurrence and abundance varies with tree

913   characteristics and among species in temperate woodland *Eucalyptus*. *Austral Ecology*, **39**,

914   145–157.

915 Resh S, Battaglia M, Worledge D, Ladiges S (2003) Coarse root biomass for eucalypt plantations

916   in Tasmania, Australia: sources of variation and methods for assessment. *Trees - Structure*

917   *and Function*, **17**, 389-399.

918 Richards GP, Evans DMW (2004) Development of a carbon accounting model (FullCAM Vers.

919   1.0) for the Australian continent. *Australian Forestry*, **67**, 277-283.

920 Roxburgh SH, Paul KI, Clifford D, England JR, Raison RJ (2015) Guidelines for constructing

921   allometric models for the prediction of woody biomass: how many individuals to harvest?

922   *Ecosphere*, **6**, 1-27.

923 Shen H, Zhu Z (2008). Efficient mean estimation in log-normal linear models. *Journal of*

924   *Statistical Planning and Inference*, 138, 552–567.

925 Sileshi GW (2014) A critical review of forest biomass estimation models, common mistakes and

926   corrective measures. *Forest Ecology and Management*, **329**, 237-264.

927 Sillett SC, van Pelt R, Kramer RD, Carroll AL, Koch GW (2015) Biomass and growth potential

928   of *Eucalyptus regnans* up to 100 m tall. *Forest Ecology and Management*, **348**, 78–91.

929 Snowdon, P., Eamus, D., Gibbons, P., Khanna, P., Keith, H., Raison, J. and Kirschbaum, M.

930   (2000): Synthesis of allometrics, review of root biomass and design of future woody biomass

931   sampling strategies. National Carbon Accounting System Technical Report No. 17, Australian

932   Greenhouse Office, 113 pp.

933 Soares P, Tome M, Skovsgaard JP, Vanclay JK (1995) Evaluating a growth model for forest

934   management using continuous forest inventory data. *Forest Ecology and Management*, **71**,

935   251-265.

936 Specht RL, Specht A (2002) Structure, Growth and Biodiversity of Australian Plant

937   Communities. 2nd edition. Oxford University Press. 500pp.

938 Specht A, Specht RL (2013) Australia: Biodiversity of Ecosystems. *In*, The Encyclopedia of

939   Biodiversity Vol. 1 (ed. B. Levin, et al.) pp 291-306. Waltham, MA: Academic Press.

940 Swenson NG, Enquist BJ (2007) Ecological and evolutional determinates of a key plant

941   functional trait: wood density and its community-wide variation across latitude and elevation.

942   *American Journal of Botany*, **94**, 451-459.

943 Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree

944   species. *Forest Ecology and Management*, **97**, 1–24.

945   Vieilledent G, Vaudry R, Andriamanohisoa SF *et al*. (2012) A universal approach to estimate

946   biomass and carbon stock in tropical forests using generic allometric models. *Ecological*

947   *Applications*, **22**, 572–583.

948   Van Breugel M, Ransijn J, Craven D, Bongers F, Hall JS (2011). Estimating carbon stock in

949   secondary forests: Decisions and uncertainties associated with allometric biomass models.

950   *Forest Ecology and Management*, **262**, 1648-1657.

951   Van der Werf GR., Randerson JT, Giglio L *et al*. (2010) Global fire emissions and the

952   contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009).

953   *Atmospheric Chemistry and Physics*, **10**, 11707-11735.

954   Van Gelder HA, Poorter L, Sterck FJ (2006) Wood mechanics, allometry, and life-history

955   variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367-78.

956   Waterworth R, (2016) Testing allometrics from the southcoast of NSW, Australia. In prep.

957   Wiemann MC, Williamson GB (2014) Wood specific gravid variation with height and its

958   implications for biomass estimation. Research Paper FPL-RP-677. Madison, WI: U.S.

959   Department of Agriculture, Forest Service, Forest Products Laboratory. 9 p.

960   Wirth C, Schumacher J, Schulze E D (2004) Generic biomass functions for Norway spruce in

961   Central Europe- a meta-analysis approach toward prediction and uncertainty estimation. *Tree*

962   *Physiology*, **24**, 121-139.

963   Xiao X, White EP, Hooten MB, Durham SL (2011) On the use of log-transformation vs.

964   nonlinear regression for analyzing biological power laws. *Ecology*, **92**, 1887–1894.

965   Ximenes FA, Gardner WD, Richards GP (2006) Total above-ground biomass and biomass in

966   commercial logs following the harvest of spotted gum (*Corymbia maculata*) forests of SE

967   NSW. *Australian Forestry*, **69**, 213–222.

968   Zianis D, Mencuccini M (2004) On simplifying allometric analyses of forest biomass. *Forest*

969   *Ecology and Management*, **187**, 311–332.

970   Zianis D, Muukkonen P, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations

971   for tree species in Europe. *Silva Fennica Monographs*, **4,** 1-63.

972   Zanne AE, Lopez-Gonzalez G, Coomes DA et al. (2009) Global wood density database. Dryad.

973   Available at: http://hdl. handle. net/10255/dryad, 235 (accessed 1 November 2013)

974

1001   Different symbols for the scatter points represent the different categories of plant functional

1002   types (in (a)) or sub-categories of plant functional types (b-f) as defined in Fig. S1. Datasets with

1003 D_{130}<10 cm were not used in the $F_{Other-L}$ model. R^2 and RMSE refer to the linear regression of

1004   predicted *vs*. observed AGB.

1005

1006   **Fig 5** Box plots describing the Proportion of the 95% confidence interval (CI) of generalised

1007   allometry prediction overlapped by the 95% CI of species-specific allometry prediction when the

1008   level of generalisation was; (a) plant functional type, or (b) universal, $All_{Universal}$. These results

1009   are for prediction of $ln(AGB_{Indiv})$ using models (Eq. 2) across 53 species and a total of 92

1010   scenarios where D_{10} was assumed to be 10 cm ($N = 53$), 50 cm ($N = 28$), or 100 cm ($N = 11$).

1011   Note, species presented here are those reported in Table S3, each of which had an N > 50. Only

1012   species sampled to these larger sizes were represented in scenario of D_{10} of 50 and 100 cm.

1013

1014   **Fig 6** Relationship between total above-ground biomass (AGB_{Stand}) from whole-plot harvesting

1015   at 17 contrasting stands (Table 2) and that predicted for those stands through the application of

1016   three scenarios of increasing generalisation of allometric models applied: (a) information on

1017   species identity of each individual at each of the test sites was utilised, and for species that were

1018   represented by the 53 available species-specific models, these were applied (Eq. 2 using

1019   parameters given in Table S3), while for all other species, the appropriate plant functional type

1020   model was applied (Eq. 2 using parameters given for F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ in

1021   Table 3), (b) species identification and/or species-specific models were assumed to be

1022   unavailable, and so plant functional type models were applied (Eq. 2 using parameters given for

1023 F_{Shrub}, F_{Multi}, F_{Euc}, $F_{Other-H}$ and $F_{Other-L}$ in Table 3), and (c) species identification, species-specific

1024   models and plant functional type models were assumed to be unavailable, and so the universal

1025   model ($All_{Universal}$) was applied (Eq. 2 using parameters given for $All_{Universal}$ in Table 3). In all

1026   scenarios, the MM correction factor was applied when back-transforming predictions. Grey

1027   dashed line represents the 1:1 line. *EF* indicates model efficiency. Black solid line represents the

1028   line of best fit, with slope, intercept and fit statistics as shown. Values in parentheses are the 95%

1029   prediction interval of the slope and intercept.

1030 **Supplementary material**

1031 **Table S1** Number of individuals obtained for each plant functional type from various sources.

1032 *Indicates sources where data were sourced directly from the publication. References for

1033 published data sources are listed below.

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

Generic allometrics 42

Ximenes (2014)	~	~	44	~	~	44
Sudmeyer et al., (2008)	~	20	20	~	~	40
Turner & Lambert, (1983, 2008); Turner, (1986)	~	~	39	~	~	39
O'Grady et al., (2000)	~	~	31	6	~	37
Forrest & Ovington (1970)	~	~	~	~	36	36
Theiveyanathan S, pers. com.	~	~	36	~	~	36
O'Grady et al., (2006)	~	~	33	~	~	33
Jonson, (2010)	~	10	22	~	~	32
Stewart et al., (1979)	~	~	31	~	~	31
Zerihun, et al., (2006)	~	~	31	~	~	31
Groves, (1987)*	15	~	17	~	~	32
Snowdon et al., (2000)	~	~	29	~	~	29
Birk & Turner, (1992)	~	4	24	~	~	28
Hingston & Galbraith, (1998)	~	~	26	~	~	26
Bennett et al., (2014)	~	25	~	~	~	25
Bi et al., (2001) *	~	11	14	~	~	25
Dargavel, (1970)	~	~	~	~	25	25
Feller, (1980)	~	3	22	~	~	25
Bennett et al., (1997)*	~	~	24	~	~	24
Paul et al., (2008)	~	~	24	~	~	24
Specht & West, (2003)	~	~	12	6	6	24
Hingston et al. (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 et al., (1993)	~	~	20	~	~	20
Turner et al., (1989)	~	~	~	19	~	19
Holland, (1969)*	~	19	~	~	~	19
Zerihun & Montagu, (2004)	~	~	~	~	19	19
Carter & White, (2009)	~	18	~	~	~	18
Hamilton et al., (2005)	~	~	18	~	~	18
Barton & Montagu, (2006)	~	~	16	~	~	16
Resh et al., (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 et al., (1984)	~	~	~	~	11	11
Specht, (2000)	~	~	11	~	~	11
Guo et al., (2008)	~	~	~	~	10	10
Stewart et al., (1981)	~	~	~	~	10	10
Forrester et al., (2004)	~	8	~	~	~	8
Turner et al., (1986); Turner & Lambert, (2014)	~	~	6	~	~	6
Grove, (1988)	~	~	6	~	~	6
Rose B, pers. com.	3	1	2	~	~	6

Generic allometrics 43

Lewis, (1978)	~	~	5	~	~	5
Keith *et al.*, (2003)*	~	~	5	~	~	5
Westman & Rogers, (1977)	~	~	2	1	~	3
Baldwin & Stewart, (1987)	~	~	1	~	~	1
Total	*2,383*	*5,397*	*6,004*	*503*	*767*	*15,054*

1034   **Literature used to compile the database**

1035

1036   Adams MA, Attiwill PM (1988) Nutrient cycling in forests of north-east Tasmania. Research

1037   Report No. 1. Tasmanian Forest Research Council, Hobart, Australia.

1038   Applegate GB (1982) Biomass of Blackbutt (*Euclayptus pilularis* Sm.) forests on Fraser Island.

1039   Master of Natural Resources. University of New England.

1040   Ashton D (1976) Phosphorus in Forest Ecosystems at Beenak, Victoria. *Journal of Ecology*, **64**,

1041   171-186.

1042   Baldwin PJ, Stewart HTL (1987) Distribution, length and weight of roots in young plantations of

1043   *Eucalyptus grandis* W. Hill ex. Maiden irrigated with recycled water. *Plant Soil*, **97**, 243–252.

1044   Baker TG (1982) Studies on the Distribution and Cycling of Nitrogen in Forests. PhD thesis, The

1045   University of Melbourne.

1046   Baker TG, Attiwill PM, Stewart HTL (1984) Biomass equations for *Pinus radiata* in Gippsland,

1047   Victoria. *New Zealand Journal of Forestry Science*, **14**, 89–96.

1048   Barton C, Montague K (2006) Effect of spacing and water availability on root:shoot ratio in

1049   *Eucalyptus camaldulensis*. *Forest Ecology and Management*, **221**, 52-62.

1050   Barton C, Parekh J (2006) Biomass partitioning and basic density for selected species and sites.

1051   Report to Australian Greenhouse Office. Forest Resources, Science and Research, NSW

1052   Department of Primary Industries, Beecroft, NSW.

1053   Bartle J, Huxtable D, Peck A (2012) Productivity interactions of integrated oil mallee farming

1054   systems. Ed. K. Brooksbank. *In*: Hydrological impacts and productivity interactions of

1055   integrated oil mallee farming systems: Landscape scale effects of dispersed mallee plantings.

1056   RIRDC Publication No. 11/161. RIRDC Project No. PRJ-000477.

1057   Bastin G (2014) Arid zone allometry and spatial extrapolation with remote sensing. *Range*

1058   *Management Newsletter*, **14**, 8-16.

1059   Bennett LT, Weston CJ, Attiwill PM (1997) Biomass, nutrient content and growth response to

1060   fertilisers of six-year-old *Eucalyptus globulus* plantations at three contrasting sites in

1061   Gippsland, Victoria. *Australian Journal of Botany*, **45**, 103-121.

1062   Bennett R, Mendham D, Ogden G, Bartle J (2014). Enhancing tree belt productivity through

1063   capture of short-slope runoff water. *Global Change Biology Bioenergy*, **7**, 1107-1117.

1064   Bi H, Birk E, Turner J, Lambert M, Jurskis V (2001) Converting stem volume to biomass with

1065   additivity, bias correction, and confidence bands for two Australian tree species. *New Zealand*

1066   *Journal of Forestry Science*, **31**, 298-319.

1067   Bi H, Murphy S, Volkova L *et al.* (2015) Additive biomass equations based on complete

1068   weighing of sample trees for open eucalypt forest species in south-eastern Australia. *Forest*

1069   *Ecology and Management*, **349,** 106-121.

1070   Birk EM, Turner J (1992) Response of flooded gum (*E. grandis*) to intensive treatments:

1071   biomass and nutrient content of eucalyptus plantations and native forests. *Forest Ecology and*

1072   *Management*, **47**, 1-28.

1073   Brand BM (1999) Quantifying biomass and carbon sequestration of plantation blue gums in

1074   south western Australia. Dissertation for Bachelor of Science (Biology) at Curtain University

1075   of Technology.

1076   Brooksbank K, Goodwin A (2012) Assessment of below ground biomass accumulation in oil

1077   mallees. Chapter 3. *In*: Hydrological impacts and productivity interactions of integrated oil

1078   mallee farming systems: Landscape scale effects of dispersed mallee plantings. RIRDC

1079   Project No PRJ000477. Rural Industries Research and Development Corporation, Canberra.

1080   Cromer R, Williams E (1982) Biomass and Nutrient Accumulation in a Planted *E. globulus*

1081   (Labill.) Fertilizer Trial. *Australian Journal of Botany*, **30**, 265-278.

1082   Cromer RN, Cameron DM, Rance SJ, Ryan PA, Brown M (1993). Response to nutrients in

1083   *Eucalyptus grandis*. 1. Biomass accumulation. *Forest Ecology and Management*, **62**, 211-230.

1084   Dargavel JB (1970) Provisional tree weight tables for radiata pine. *Australian Forestry*, **34**: 131–

1085   140.

1086   England, JR, Theiveyanathan S, Falkiner RA, Paul KI, Polglase PJ, Koul VK, Larmour JS,

1087   Smith J, Stewart LG (2007) Water use, growth and carbon sequestration of environmental

1088   plantings. Final Report. Commercial Environmental Forestry Project. CSIRO, Canberra,

1089   Australia.

1090   Falster DS, Duursma RA, Ishihara MI *et al.* (2015) BAAD: a Biomass And Allometry Database

1091   for woody plants. *Ecology*, **96,** 1445–1445.

1092   Feller M (1980) Biomass and nutrient distribution in two eucalypt forest ecosystems. *Australian*

1093   *Journal of Ecology*, **5**, 309-333.

1094   Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of

1095   *Eucalyptus globulus* and *Acacia mearnsii. Forest Ecology and Management*, **193**, 81-95.

1096   Forrester DI, Collopy JJ, Beadle CL, Baker TG (2012) Interactive effects of simultaneously

1097   applied thinning, pruning and fertiliser application treatments on growth, biomass production

1098   and crown architecture in a young *Eucalyptus nitens* plantation. *Forest Ecology and*

1099   *Management*, **267**, 104-116

1100   Forrest WG (1969) Variations in the accumulation, distribution and movement of mineral

1101   nutrients in radiata pine plantations. Ph.D. Thesis. Australian National University, Canberra.

1102   Forrest W, Ovington J (1970) Organic Matter Changes in an Age Series of *Pinus radiata*

1103   Plantations. *Journal of Applied Ecology*, **7**, 177-186.

1104   Guo LB, Cowie AL, Montagu KD, Gifford RM (2008) Carbon and nitrogen in a native pasture

1105   and an adjacent 16-year-old *Pinus radiata* D. Don. Plantation in Australia. *Agriculture,*

1106   *Ecosystems and Environment*, **124**, 205-218.

1107   Green D (2013) Woody biomass levels within the Cobar Peneplain bioregion. A report prepared

1108   for Western Regeneration Pty Ltd. NSW Western Catchment Management Authority.

1109   Grove TS (1987) Nutrient uptake and growth of overstory trees and understory shrubs in

1110   developing stands of karri *Eucalyptus divericolor* F. muell. Forests. PhD Thesis. University of

1111   Western Australia, Perth, Australia.

1112   Grove TS (1988) Growth responses of trees and understorey to applied nitrogen and phosphorus

1113   in karri (*Eucalyptus diversicolor*) forest. *Forest Ecology and Management*, **23**, 87-103.

1114   Grove TS, Mendham DS, Rance SJ, Bartle J, Shea S (2007) Nutrient management of intensively

1115   harvested oil mallee tree crops. A report for the RIRDC/L&WA/FWPRDC Joint Venture

1116   Agroforestry Program. RIRDC Publication No. 07/084. Canberra, Australia.

1117   Hamilton SD, Brodie G, O'Dwyer C (2005) Allometric relationships for estimating biomass in

1118   grey box (*Eucalyptus microcarpa*). *Australian Forestry*, **68**, 267–273.

1119   Hawkins C, Carter J, Paul K *et al*. (2010) Farming Landscapes for the Future: Report to Avongro

1120   Wheatbelt Tree Cropping. Report to Department of Agriculture, Fisheries and Forestry. 106 p.

1121   Hingston F, Galbraith J (1998) Application of the process-based model BIOMASS to *Eucalyptus*

1122   *globulus* ssp. *globulus* plantations on ex-farmland in south western Australia. *Forest Ecology*

1123   *and Management*, **106**, 157-168.

1124   Hingston F, Galabraith J, Jones M (1990) Dimensional data for trees at several sites in northern

1125   Jarrah (*Eucalyptus marginata*) forest. DFFP Division of Forestry and Forestry Products User

1126   Series. No. 11.

1127   Hobbs TJ, Neumann CR, Tucker M, Ryan KT (2013) Carbon sequestration from revegetation:

1128   South Australian agricultural regions. DEWNR Technical Report 2013/14. Government of

1129   South Australia, through Department of Environment, Water and Natural Resources, Adelaide

1130   and Future Farm Industries Cooperative Research Centre.

1131   Jonson JH (2010) Carbon values of environmental tree plantings at the farm and catchment

1132   scales, and their economic implications to farming systems in the Central Wheatbelt of

1133   Western Australia. Thesis for Master of Science of Natural Resource Management, The

1134   University of Western Australia, Perth, Australia.

1135   Jonson JH, Freudenberger D (2011) Restore and sequester: estimating biomass in native

1136   Australian woodland ecosystems for their carbon-funded restoration. *Australian Journal of*

1137   *Botany*, **59**, 639–652.

1138　Keith H, Jacobsen K, Engalnd J, Smith J, Koul V (2003) Allocation of carbon belowground in

1139　　　native *Eucalyptus delegatensis* forest ecosystem carbon cycles. Third International

1140　　　Symposium on Dynamics of Physiological Processes in Woody Roots, Perth, September

1141　　　2003.

1142　Lambert MJ (1979) Sulphur relationships of native and exotic species. MSc(Hons) thesis,

1143　　　Macquarie Uni. 170pp.

1144　Lewis JW (1978) Ecological studies of coastal forests and its regeneration after mining. PhD

1145　　　Thesis, University of Queensland, Brisbane.

1146　O'Connell AM, Grove TS, Mendham S, Rance SJ (1999) Eucalypt plantations in south-western

1147　　　Australia. Site management and productivity in tropical plantation forests. *In*: Nambiar,

1148　　　E.K.S., Tiarks, A., Cossalter, C. and Ranger, J. (eds.). Site management and productivity in

1149　　　tropical plantation forests: a progress report. Centre for International Forestry Research,

1150　　　Bogor, Indonesia. 112 p.

1151　O'Grady A, Chen X, Eamus D, Hutley L (2000) Composition, leaf area index and standing

1152　　　biomass of eucalypt open forests near Darwin in the Northern Territory, Australia. *Australian*

1153　　　*Journal of Botany*, **48**, 629-638.

1154　O'Grady A, Worledge D, Battaglia M. (2006) Above- and below-ground relationships, with

1155　　　particular reference to fine roots, in a young *Eucalyptus globulus* (Labill.) stand in southern

1156　　　Tasmania. *Trees*, **20**, 531-538.

1157　Sochacki S, Harper R Smettem K (2007) Estimation of woody biomass production from a short-

1158　　　rotation bio-energy system in semi-arid Australia. *Biomass and Bioenergy*, **31**, 608-616.

1159　Paul KI, Jacobsen K, Koul V, Leppert P, Smith J (2008) Predicting growth and sequestration of

1160　　　carbon by plantations growing in regions of low-rainfall in southern Australia. *Forest Ecology*

1161　　　*and Management*, **254**, 205-216.

1162　Paul K, England J, Raison J *et al*. (2010) Improving Methods to Reliably Estimate C

1163　　　Sequestration by Environmental Plantings. Final report to NSW Department of Environment,

1164   Climate Change and Water.

1165   Paul KI, Roxburgh, SH, England JR *et al*. (2013a) Development and testing of allometric

1166   equations for estimating above-ground biomass of mixed-species environmental plantings.

1167   *Forest Ecology and Management*, **310**, 483-494.

1168   Paul KI, Roxburgh, SH, Ritson P *et al*. (2013b) Testing allometric equations for prediction of

1169   above-ground biomass of mallee eucalypts for southern Australia. *Forest Ecology and*

1170   *Management*, **310**, 1005-1015.

1171   Peck A, Sudmeyer R, Huxtable D, Bartle J, Mendham D (2012). Productivity of mallee

1172   agroforestry systems under various harvest and competition management regimes. RIRDC

1173   Project No PRJ-000729. Rural Industries Research and Development Corporation, Canberra.

1174   Rance S, Mendham D, Cameron D, Grove T (2012) An evaluation of the conical approximation

1175   as a generic model for estimating stem volume, biomass and nutrient content in young

1176   Eucalyptus plantations. *New Forests*, **43**, 109-128.

1177   Ritson P, Sochacki S (2003) Measurement and prediction of biomass and carbon content of

1178   *Pinus pinaster* trees in farm forestry plantations, south-western Australia. *Forest Ecology and*

1179   *Management*, **175**, 103-117.

1180   Ritson P, Clarke M, Killen A, Jeffery S (2015) Testing carbon farming opportunities for salinity

1181   management: A scientific report on the 'Pilot to test carbon driven solutions to salinity

1182   project'. Northern Agricultural Catchments Council (NACC), Western Australia.

1183   Sudmeyer RA, Abbott L, Jones H (2008) Phase Farming with Trees. Field validation of the

1184   cropping phase. RIRDC Publication No 08/122. RIRDC Project No DAW-104A. Rural

1185   Industries Research and Development Corporation, Canberra.

1186   Sudmeyer R, Daniels T (2010) The golden wreath wattle as an alternative to mallee eucalypt for

1187   alley systems. RIRDC Publication No. 10/071. Canberra, Australia.

1188   Specht A (2000) Technical Report Greenhouse Allies Project. Measurement of carbon

1189   sequestration in small non-industrial forest plantations. Report to the Australian Greenhouse

1190   Office, Canberra.

1191   Specht A, West PW (2003) Estimation of Biomass and Sequestered Carbon on Farm Forest

1192   Plantation in Northern New South Wales, Australia. *Biomass and Bioenergy*, **25**, 363-379.

1193   Stewart H, Flinn D, Aeberli B (1979) Above-ground biomass of a mixed eucalypt forest in

1194   eastern Victoria. *Australian Journal of Botany*, **27**, 725-740.

1195   Stewart HTL, Flinn DW, James JM (1981) Biomass and nutrient distribution in radiata pine. *In*:

1196   Proceeding of Australian Forest Nutrition Workshop "Productivity in Perpetuity". CSIRO,

1197   Melbourne.

1198   Turner J, Lambert MJ (1983) Nutrient cycling within a 27-year-old *Eucalyptus grandis*

1199   plantation in New South Wales. *Forest Ecology and Management*, **6**, 156-168

1200   Turner J, Lamber MJ (1986) Effects of forest harvesting removals on soil nutrient reserves in the

1201   Eden area, New South Wales. *Oecologia* (Berlin), **70**, 140-148.

1202   Turner J (1986) Organic matter accumulation in a series of *Eucalyptus grandis* stands. *Forest*

1203   *Ecology and Management*, **17**, 231-242.

1204   Turner J, Lambert MJ, Ryan PJ (1986) Nutrient cycling in a 42-year-old *Eucalyptus pilularis*

1205   forest and implications for management, State Forests of New South Wales Research Paper,

1206   Sydney, 13pp.

1207   Turner J, Lambert MJ, Kelly J (1989) Nutrient cycling in a New South Wales subtropical

1208   rainforest. *Annals of Botany*, **63**, 635-642.

1209   Turner J, Lambert MJ, Holmes GI (1992) Nutrient cycling in forested catchments in south-

1210   eastern New South Wales. I. Biomass accumulation. *Forest Ecology and Management*, **55**,

1211   135-148.

1212   Turner J, Lambert MJ (2008) Nutrient cycling in age sequences of two Eucalyptus plantation

1213   species. *Forest Ecology and Management*, **255**, 1701-1712.

1214   Turner J, Lambert MJ (2014) Analysis of nutrient use efficiency (NUE) in *Eucalyptus pilularis*

1215   forests. *Australian Journal of Botany*, **62**, 558-569.

1216   Waterworth R, (2016) Testing allometrics from the southcoast of NSW, Australia. In prep.

1217   Westman, WE, Rogers RW (1977) Biomass and structure of a subtropical eucalypt forest, north

1218   Stradbroke Island. *Australian Journal of Botany*, **25**, 171-191.

1219   Williams R, Zerihun A, Montagu K, Hoffman M, Hutley L, Chen X (2005) Allometry for

1220   estimating aboveground tree biomass in tropical and subtropical eucalypt woodlands: towards

1221   general predictive equations. *Australian Journal of Botany*, **53**, 607-619.

1222   Ximenes FA, Gardner WD, Richards GP (2006) Total above-ground biomass and biomass in

1223   commercial logs following the harvest of spotted gum (*Corymbia maculata*) forests of SE

1224   NSW. *Australian Forestry*, **69**, 213–222.

1225   Ximenes FA (2014) *Eucalyptus obliqua* biomass determination, Warra Tall Eucalypt SuperSite,

1226   200302. Australian SuperSite Network. http://www.tern-

1227   supersites.net.au/knb/metacat/lloyd.628.6/html

1228   Zerihun A, Montagu KD (2004) Belowground to aboveground biomass ratio and vertical root

1229   distribution responses of mature *Pinus radiata* stands to phosphorus fertilization at planting.

1230   *Canadian Journal of Forest Research*, **34**, 1883-1894.

1231   Zerihun A, Montagu K, Hoffmann M, Bray S (2006) Patterns of below- and aboveground

1232   biomass in *Eucalyptus populnea* woodland communities of northeast Australia along a

1233   rainfall gradient. *Ecosystems*, **9**, 501-515.

1234

1235 Table S2 Empirical relationships used to 'gap fill' missing D and H measurements using the

1236 equation $Y = c + d\,X$, where X may be D (cm) or H (m). All relationships were highly

1237 significant ($P < 0.0001$), with no log-transformations required.

| Y	X	c	d	*RMSE*	R^2	N
D_{10}	D_0	0.445 (0.081)	0.879 (0.004)	2.584	0.973	1,540
	D_{30}	0.155 (0.047)	1.077 (0.003)	1.663	0.984	2,918
	D_{50}	0.395 (0.050)	1.122 (0.003)	2.007	0.972	4,353
	D_{130}	1.488 (0.074)	1.195 (0.004)	2.690	0.953	3,760
	H	1.201 (0.121)	2.099 (0.020)	6.671	0.574	8,283
D_{130}	D_0	0.414 (0.181)	0.683 (0.006)	3.577	0.930	991
	D_{10}	-0.577 (0.061)	0.798 (0.003)	2.198	0.953	3,760
	D_{30}	-0.397 (0.050)	0.854 (0.003)	1.849	0.970	3,366
	D_{50}	-0.494 (0.036)	0.912 (0.002)	1.516	0.976	4,686
	H	-2.834 (0.208)	1.924 (0.016)	11.297	0.683	7,003

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}	*Acacia calamifolia* (D_{10} < 16 cm)	-2.228 (0.094)	2.398 (0.055)	0.353	0.939	1.0520-1.0618	30.6	127
	Acacia hakeoides (D_{10} < 21 cm)	-2.255 (0.095)	2.181 (0.051)	0.341	0.944	1.0463-1.0572	28.4	111
	Acacia hemiteles (D_{10} < 9 cm)	-2.920 (0.107)	2.393 (0.077)	0.293	0.948	1.0273-1.0398	22.8	55
	Acacia kempeana (D_{10} < 26 cm)	-3.169 (0.042)	2.492 (0.025)	0.376	0.960	1.0689-1.0723	32.8	419
	Eremophila mitchellii (D_{10} < 37cm)	-2.716 (0.143)	2.261 (0.056)	0.370	0.933	1.0580-1.0679	32.6	119
	Eremophila sturtii (D_{10} < 35cm)	-2.848 (0.153)	2.194 (0.063)	0.482	0.926	1.0946-1.1165	46.0	98
	Geijera parviflora (D_{10} < 50 cm)	-2.515 (0.192)	2.312 (0.069)	0.452	0.917	1.0743-1.1028	43.4	105
	Senna artemisioides (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}	*Acacia acuminata* (D_{10} < 34 cm)	-3.003 (0.073)	2.516 (0.037)	0.373	0.960	1.0636-1.0701	33.8	193
	Acacia aneura (D_{10} < 49 cm)	-2.561 (0.126)	2.402 (0.045)	0.373	0.954	1.0577-1.0693	33.7	138
	Acacia harpophylla (D_{10} < 47 cm)	-2.789 (0.102)	2.570 (0.035)	0.262	0.982	1.0281-1.0332	21.3	102
	Acacia mearnsii (D_{10} <38 cm)	-2.381 (0.152)	2.348 (0.056)	0.296	0.964	1.0268-1.0416	25.0	67
	Acacia melanoxylon (D_{10} < 27 cm)	-2.928 (0.112)	2.478 (0.051)	0.245	0.979	1.0205-1.0277	21.2	53
	Acacia pycnantha (D_{10} < 26 cm)	-2.502 (0.118)	2.394 (0.063)	0.433	0.925	1.0781-1.0939	41.6	121
	Acacia saligna (D_{10} < 46 cm)	-3.075 (0.145)	2.424 (0.065)	0.420	0.899	1.0746-1.0891	41.0	159
	Eucalyptus incrassata (D_{10} < 27 cm)	-3.123 (0.203)	2.488 (0.088)	0.409	0.933	1.0686-1.0796	39.0	59
	Eucalyptus kochii (D_{10} < 28 cm)	-2.887 (0.049)	2.439 (0.021)	0.345	0.955	1.0553-1.0609	30.5	631

Generic allometrics 54

	Eucalyptus loxophleba (D_{10} < 37 cm)	-2.760 (0.037)	2.526 (0.017)	0.361	0.920	1.0651-1.0672	32.3	1,873
	Eucalyptus platypus (D_{10} < 31 cm)	-1.851 (0.193)	2.194 (0.079)	0.301	0.942	1.0327-1.0416	23.6	49*
	Eucalyptus polybractea (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$_{Euc}$	*Corymbia citriodora* (D_{130} < 34 cm)	-2.863 (0.053)	2.687 (0.053)	0.214	0.979	1.0169-1.0212	17.8	58
	Corymbia maculata (D_{130} < 140 cm)	-2.118 (0.033)	2.433 (0.020)	0.235	0.977	1.0255-1.0275	18.1	353
	Eucalyptus astringens (D_{130} < 29 cm)	-1.509 (0.251)	2.346 (0.094)	0.345	0.907	1.0429-1.0564	29.2	65
	Eucalyptus blakelyi (D_{130} < 71 cm)	-1.982 (0.091)	2.235 (0.046)	0.265	0.979	1.0210-1.0323	20.4	53
	Eucalyptus camaldulensis (D_{130} < 63 cm)	-2.147 (0.087)	2.371 (0.037)	0.332	0.966	1.0477-1.0545	28.7	144
	Eucalyptus cladocalyx (D_{130} < 52 cm)	-1.859 (0.144)	2.434 (0.065)	0.339	0.956	1.0405-1.0548	30.3	67
	Eucalyptus crebra (D_{130} < 50 cm)	-2.659 (0.090)	2.638 (0.033)	0.301	0.980	1.0376-1.0446	23.8	130
	Eucalyptus globulus (D_{130} < 64 cm)	-1.878 (0.024)	2.295 (0.013)	0.308	0.979	1.0466-1.0482	25.5	712
	Eucalyptus grandis (D_{130} <40 cm)	-1.576 (0.036)	2.181 (0.018)	0.318	0.969	1.0485-1.0512	26.4	477
	Eucalyptus largiflorens (D_{130} <54 cm)	-1.474 (0.123)	2.119 (0.052)	0.215	0.964	1.0142-1.0216	17.5	66
	Eucalyptus leucoxylon (D_{130} < 55 cm)	-2.394 (0.142)	2.526 (0.049)	0.276	0.981	1.0281-1.0353	23.4	55
	Eucalyptus melanophloia (D_{130} < 97 cm)	-3.004 (0.128)	2.699 (0.045)	0.276	0.982	1.0291-1.0362	23.3	71
	Eucalyptus melliodora (D_{130} < 92 cm)	-2.139 (0.051)	2.361 (0.020)	0.323	0.978	1.0490-1.0526	26.6	307
	Eucalyptus muelleriana (D_{130} < 100 cm)	-2.316 (0.121)	2.457 (0.036)	0.208	0.983	1.0177-1.0205	16.9	80
	Eucalyptus nitens (D_{130} < 30 cm)	-1.952 (0.157)	2.240 (0.056)	0.224	0.955	1.0130-1.0239	16.3	78
	Eucalyptus obliqua (D_{130} < 167 cm)	-2.866 (0.157)	2.609 (0.042)	0.325	0.968	1.0432-1.0520	28.9	131
	Eucalyptus occidentalis (D_{130} < 79 cm)	-2.203 (0.068)	2.517 (0.032)	0.385	0.951	1.0680-1.0757	34.5	329
	Eucalyptus pilularis (D_{130} < 129 cm)	-2.633 (0.071)	2.570 (0.023)	0.231	0.988	1.0237-1.0262	17.9	156
	Eucalyptus polyanthemos (D_{130} < 125 cm)	-1.907 (0.106)	2.298 (0.040)	0.365	0.980	1.0524-1.0637	32.0	69
	Eucalyptus populnea (D_{130} < 117 cm)	-1.799 (0.053)	2.304 (0.017)	0.262	0.986	1.0311-1.0342	22.4	242
	Eucalyptus regnans (D_{130} < 70 cm)	-2.576 (0.102)	2.559 (0.040)	0.259	0.987	1.0251-1.0310	22.0	55
	Eucalyptus saligna (D_{130} < 169 cm)	-2.131 (0.158)	2.425 (0.051)	0.255	0.975	1.0198-1.0302	21.9	60
	Eucalyptus sideroxylon (D_{130} < 72 cm)	-2.167 (0.183)	2.341 (0.064)	0.312	0.951	1.0362-1.0465	26.7	71
	Eucalyptus spathulata (D_{130} < 42 cm)	-1.347 (0.048)	2.231 (0.020)	0.209	0.979	1.0207-1.0217	16.7	279
	Eucalyptus tereticornis (D_{130} < 47 cm)	-2.368 (0.079)	2.428 (0.033)	0.237	0.975	1.0234-1.0274	18.6	145
	Eucalyptus vegrandis (D_{130} < 15 cm)	-1.179 (0.212)	2.189 (0.094)	0.216	0.908	1.0144-1.0216	18.0	57
	Eucalyptus viminalis (D_{130} < 30 cm)	-2.225 (0.053)	2.316 (0.024)	0.228	0.992	1.0240-1.0259	18.3	373
	Eucalyptus wandoo (D_{130} < 27 cm)	-1.807 (0.117)	2.202 (0.055)	0.365	0.957	1.0523-1.0640	29.8	73
F$_{Other-H}$	*Allocasuarina huegeliana* (D_{130} < 29 cm)	-1.545 (0.114)	2.193 (0.050)	0.256	0.974	1.0242-1.0303	20.5	55

Generic allometrics 55

	Callitris glaucophylla (D_{130} < 69 cm)	-1.638 (0.066)	2.176 (0.025)	0.276	0.983	1.0333-1.0374	21.4	131
	Casuarina obese (D_{130} < 13 cm)	-1.526 (0.135)	2.181 (0.057)	0.212	0.947	1.0096-1.0214	17.7	84
$F_{Other-L}$	*Pinus radiata* (10 < D_{130} < 49 cm)	-2.435 (0.087)	2.407 (0.031)	0.189	0.942	1.0162-1.0178	15.3	376
	Pinus pinaster (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.
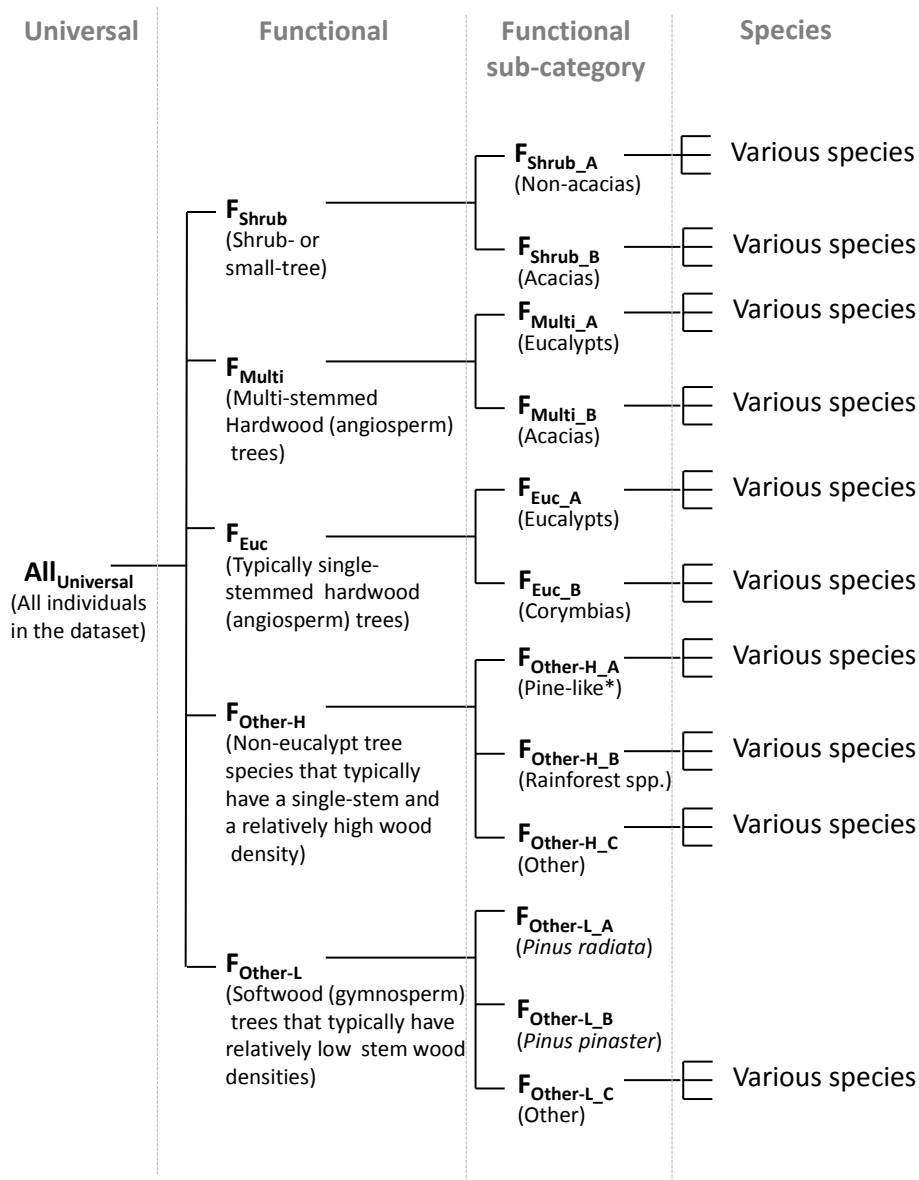
1

2   **Fig S1** Diagram depicting the categorisation of vegetation into five categories of functional type, and how these were further sub-

3   divided into sub-categories and species in order to assess four levels of generalisation of allometric models of AGB; (i) universal

4   (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$_{Shrub\_B}$,

5   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

6   53 species of the 274 studied were adequately sampled (i.e. *N* > 50). Definition of functional type sub-categories were as follows;

7   F$_{Shrub\_A}$ (61%): 40 different genera of shrubs or small trees, with the three most common genera of shrubs being *Eremophila*,

8   *Melaleuca* and *Senna*; F$_{Shrub\_B}$ (39%): Shrubs or small trees from the genus *Acacia;* F$_{Multi\_A}$ (76%): Mallee eucalypts. There were

9   32 species of mallee eucalypts, although the three most common species were *E. loxophleba*, *E. polybractea* and *E.kochii*; F$_{Multi\_B}$

10 (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

11 (in that they have foliage that resembles pine needles) genera of trees, including *Casuarina*, *Allocasuarina*, *Callitris* and

12 *Grevillea*. [Note: *Callitris* is a gymnosperm (softwood), but was included in this category given its very dense wood which is

1 similar to hardwood species]; $F_{Other-H\_B}$ (23%): 20 different rainforest tree genera of angiosperms; $F_{Other-H\_C}$ (9%): genera of

2 *Abrophyllum*, *Banksia*, *Erythrophleum*, *Lophostemon*, *Pittosporum* and *Terminalia;* $F_{Other-L\_A}$ (83%): *Pinus radiata* (the most

3 commonly established softwood plantation species in high rainfall regions of temperate Australia); $F_{Other-L\_B}$ (15%): *Pinus*

4 *pinaster* (the most commonly established softwood plantation species in low rainfall regions of Mediterranean Western

5 Australia); $F_{Other-L\_C}$ (2%): other species of softwood trees (e.g. species from the genera of either *Araucaria*, *Agathis* or *Pinus*).

6

1 **Table 1** Characteristics of the entire dataset (All$_{Universal}$), or for each of the five plant functional types. Abbreviations as follows: '*N*', total number of individuals; '*D$_{10}$*' or '*D$_{130}$*', mean stem diameter

2 measured over bark at 10 cm or 130 cm height above the ground, respectively; 'H', mean height of the tallest part of a tree or shrub, irrespective of branch architecture; 'ρ', mean stem wood density

3 (based on limited direct measures with 88% derived from a global wood density database, see text); '*N* sites', number of field sites from which the trees or shrubs were harvested; '*N* spp.', number of

4 species that were harvested; '%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

5 managed rather than naturally regenerated without human intervention; 'MAT', long-term mean annual temperature, averaged across sites from which individuals were harvested; and 'MAP', long-

6 term mean annual precipitation, averaged across sites from which individuals were harvested. Where relevant, standard deviations (and for *D$_{10}$* and *D$_{130}$*, the range in values) are provided in

7 parentheses.

Type	N	D_{10} (cm)	D_{130} (cm)	H (m)	ρ (g cm^{-3})	N sites	N spp.	%Age < 20 yrs	%Managed	MAT (^{o}C)	MAP (mm yr^{-1})
All$_{Universal}$	15,054	15.2 (15.9; 0.3-203.4)	NA	7.0 (6.5)	0.77 (0.15)	826	274	64.4	71.6	16.8 (2.9)	619 (341)
F$_{Shrub}$	2,383	7.2 (6.7; 0.3-50.0)	NA	2.4 (1.7)	0.74 (0.10)	144	77	51.0	41.4	18.2 (2.6)	539 (343)
F$_{Multi}$	5,397	10.7 (6.8; 0.5-61.5)	NA	4.6 (2.5)	0.86 (0.11)	363	64	81.9	92.1	17.1 (1.9)	432 (158)
F$_{Euc}$	6,004	21.7 (21.0; 0.9-203.4)	16.9 (17.5; 0.5-169.0)	10.5 (8.0)	0.77 (0.11)	225	95	53.2	62.7	16.1 (3.3)	791 (344)
F$_{Other-H}$	503	20.2 (17.2; 1.6-123.4)	16.0 (14.0; 0.9-102.0)	8.8 (5.7)	0.67 (0.17)	59	33	39.6	57.6	19.0 (3.3)	779 (572)
F$_{Other-L}$	767	17.1 (10.4; 2.3-60.4)	13.0 (9.1; 0.7-49.3)	9.2 (6.2)	0.40 (0.02)	35	5	90.0	100.0	14.2 (2.3)	733 (281)

8

9

Generic allometrics 1

10 **Table 2** Summary of the main characteristics of 17 contrasting stands where whole plot AGB$_{Stand}$ harvesting was used to test the accuracy of generalised allometric models. Abbreviations included:

11 Location, latitude and longitude; AGB$_{Stand}$, measured stand-based above-ground biomass; MAP, mean annual precipitation; Plot N, plot area and number; Area, total area harvested across all plots

12 within the stand; Stand density, number of individuals per hectare of the stand, often based on measurements taken from a larger number of plots than those used for direct measurement of biomass;

13 BA, site average basal area; Tree N, number of live trees measured, often relatively small shrubs that were measured in bulk; Age, age of the stand, where 'MA' refers to mixed aged stands.

14 Regardless of whether stands were established in belts or block configuration, plot area calculations (ha) were based on the assumption that the outer edge of the plot was ½ the between-row distance

15 out from the outer row of trees.

Site	Location (decimal degrees)	AGB$_{Stand}$ (Mg ha^{-1})	MAP (mm)	Plot N	Area (ha)	Stand density (individuals ha^{-1})	BA (m^2 ha^{-1})	Tree N	Age (yr)	Type of stand
Pepal[1]	-33.4865 S, 117.7912 E	20.87	406	3	0.04	1,863	8.71	77	11	Belt monoculture planting of *E. loxophleba*
Bird[1]	-32.8515 S, 117.5892 E	37.68	376	3	0.03	1,356	11.92	38	11	Belt monoculture planting of *E. loxophleba*
Quicke[1]	-32.6736 S, 118.2361 E	77.63	339	3	0.02	1,894	25.55	29	14	Belt monoculture planting of *E. loxophleba*
Temby[1]	-33.1457 S, 117.7187 E	22.61	353	3	0.03	1,433	6.92	44	16	Block monoculture planting of *E. loxophleba*
Angel[1]	-30.1970 S, 117.1160 E	9.93	297	3	0.03	1,100	3.45	34	16	Block monoculture planting of *E. loxophleba*
Brotherony[1]	-33.1368 S, 146.6380 E	20.60	378	6	0.09	1,233	4.92	107	7	Block monoculture planting of *E. polybractea*
Gumbinnen[2]	-36.2447 S, 141.8148 E	19.13	347	6	0.22	2,282	4.38	523	10	Block planting of mixed species
Moorland B[2]	-35.3377 S, 139.6317 E	18.63	370	4	0.25	244	2.88	88	15	Block planting of mixed species
Moorland A[2]	-35.3377 S, 139.6317 E	19.95	370	4	0.25	139	2.52	50	20	Block planting of mixed species
Strathearn[2]	-35.0485 S, 149.2325 E	38.88	637	12	0.48	2,827	11.37	1,499	15	Block planting of mixed species
Moir[2]	-34.2809 S, 118.1820 E	42.38	439	12	0.48	2,708	4.72	1,449	20	Block planting of mixed species
Jenharwill[2]	-36.3958 S, 144.4304 E	69.12	406	6	0.05	6,456	16.92	304	12	Belt planting of mixed species
Leos[2]	-37.8381 S, 147.7582 E	113.60	626	10	0.11	845	26.61	96	16	Belt planting of mixed species
McFall[2]	-33.7290 S, 117.3217 E	189.55	438	3	0.03	2,440	30.50	111	22	Belt planting of mixed species
Mogo[3]	-35.7333 S, 150.0667 E	212.87	1,090	1	0.51	410	29.70	209	MA	Block native forest of mixed species
Clyde[3]	-35.4500 S, 150.2000 E	270.48	1,173	1	0.63	248	32.10	156	MA	Block native forest of mixed species
Flat Rock[3]	-35.4167 S, 150.3000 E	355.53	1,226	1	0.45	360	42.91	162	MA	Block native forest of mixed species

16 [3]Paul et al., (2013b); [2]Paul et al., (2013a); [3]Ximene et al., (2006) and Waterworth et al., (2016)

17   **Table 3** Fitted coefficients (and standard errors) and fit statistics of three levels of generalised allometric models for AGB_{Indiv} of the form given in Eq. 2, and using a predictor of D measured at

18   either 10 or 130 cm height. Here *RMSE*, R^2, *CF*, *MAPE*, and *N* refer to the standard error of the linear regression, adjusted coefficient of determination, bias correction factor, mean absolute

19   percentage error (based on back-transformed AGB_{Indiv} predictions), and sample size, respectively. All equations fitted were highly significant (P<0.001). The diameter range relevant to each model

20   is indicated in brackets (assuming a D_{10} of 0.3 cm). Parameters and performance of the species-specific allometric models are provided in the Table S3.

Model	D	ln(a)	b	RMSE	R^2	CF^2	CF^1	MAPE	N
$All_{Universal}$ (D_{10} < 203 cm)	D_{10}	-3.024 (0.010)	2.503 (0.004)	0.446	0.964	1.1042-1.1046	1.1013	40.7	15,054
F_{Shrub} (D_{10} < 50 cm)	D_{10}	-3.007 (0.017)	2.428 (0.009)	0.491	0.968	1.1268-1.1279	1.1281	39.3	2,383
F_{Multi} (D_{10} < 62 cm)	D_{10}	-2.757 (0.020)	2.474 (0.009)	0.389	0.937	1.0775-1.0785	1.0787	33.5	5,397
F_{Euc} (D_{130} < 169 cm)	D_{130}	-2.016 (0.013)	2.375 (0.005)	0.360	0.974	1.0664-1.0668	1.0668	34.5	6,004
$F_{Other-H}$ (D_{130} < 102 cm)	D_{130}	-1.693 (0.043)	2.220 (0.016)	0.293	0.973	1.0407-1.0433	1.0436	25.3	503
$F_{Other-L}$ (D_{130} < 49 cm)	D_{130}	-2.573 (0.073)	2.460 (0.025)	0.189	0.954	1.0169-1.0179	1.0180	15.4	455[3]

21   [1] Recommended MM *CF*

22   [2] Simpler Baskerville *CF* for reference

23   [3] 312 datasets with D_{130}<10 cm excluded in this model

Generic allometrics 3

24 **Table 4** Difference in fit statistics (*RMSE*, R^2 and change in *AIC*) when models based on *D*-alone were compared with models that used compound predictor variables. Values in parentheses are

25 results obtained when only a sub-set of the data were used: those for which *H* was measured (for application in the models based on D^2H), or for which both *H* and ρ were measured (for application

26 in the models based on $D^2H\rho$); these comparisons were based on relatively low *N*, particularly in relation to ρ (12% of all data). A negative change in *AIC* (ΔAIC) indicates that the first model is

27 better than the second, and vice versa for positve ΔAIC values.

Model	Comparison of models made	$\Delta RMSE$	ΔR^2	ΔAIC	N
All_Universal	(All_Universal using D_{10}-alone) − (All_Universal using $D_{10}{}^2H$)	-0.056 (-0.053)	0.010 (0.008)	-3,539 (-2,831)	15,054
	(All_Universal using D_{10}-alone) − (All_Universal using $D_{10}{}^2H\rho$)	-0.027 (-0.062)	0.004 (0.003)	-1,753 (-519)	15,054
F_Shrub	(F_Shrub using D_{10}-alone) − (F_Shrub using $D_{10}{}^2H$)	-0.007 (0.003)	0.001 (0.000)	-72 (26)	2,383 (2,191)
	(F_Shrub using D_{10}-alone) − (F_Shrub using $D_{10}{}^2H\rho$)	-0.013 (-0.044)	0.002 (0.005)	-121 (-73)	2,383 (405)
F_Multi	(F_Multi using D_{10}-alone) − (F_Multi using $D_{10}{}^2H$)	0.013 (0.016)	-0.004 (-0.005)	370 (352)	5,397 (4,102)
	(F_Multi using D_{10}-alone) − (F_Multi using $D_{10}{}^2H\rho$)	0.013 (-0.062)	-0.004 (0.003)	364 (-519)	5,397 (1,723)
F_Euc	(F_Euc using D_{130}-alone) − (F_Euc using $D_{130}{}^2H$)	-0.048 (-0.048)	0.008 (0.007)	-1,518 (-1,306)	6,004 (5,326)
	(F_Euc using D_{130}-alone) − (F_Euc using $D_{130}{}^2H\rho$)	-0.042 (-0.004)	0.007 (0.001)	-1,327 (-26)	6,004 (947)
F_Other-H	(F_Other-H using D_{130}-alone) − (F_Other-H using $D_{130}{}^2H$)	-0.080 (-0.095)	0.017 (0.020)	-244 (-249)	503 (440)
	(F_Other-H using D_{130}-alone) − (F_Other-H using $D_{130}{}^2H\rho$)	-0.056 (-0.158)	0.011 (0.050)	-176 (-43)	503 (55)
F_Other-L	(F_Other_L using D_{130}-alone) − (F_Other-L using $D_{130}{}^2H$)	-0.022 (-0.014)	0.003 (0.002)	-117 (-68)	767 (687)
	(F_Other-L using D_{130}-alone) − (F_Other-L using $D_{130}{}^2H\rho$)	-0.013 (0.036)	0.002 (-0.012)	-71 (9)	767 (26)

28

29

Generic allometrics 4

30 **Table 5** Fit statistics from general linear model analysis for assessing whether the allometric model represented by Eq. 2 was

31 improved by the inclusion of individual site-factors (and their interactions with ln(D)) as supplementary predictor variables.

32 Factors tested included: (i) binary categorical variable {0,1} of stand age ($Age<20_{[1,0]}$: relatively young at <20 yrs, or older), (ii)

33 binary categorical variable {0,1} of stand management ($Managed_{[1,0]}$: managed or 'natural'), (iii) categorical variable ecoregion

34 (see Fig. 1), (iv) numerical variable of mean annual temperature (MAT), and (v) numerical variable of mean annual precipitation

35 (MAP). Interactions of these site-factors with ln(D) were included in the model only where they were significant. Numbers in

36 parentheses are the number of parameters in the model (*Cp* values greater than this number indicate models of poor fit). 'n.s'

37 indicates the variable effects were not statistically significant (*P*>0.05). Note; *AIC* can only be compared across categories where

38 *N* is the same.

Model	Variables	*RMSE*	*R²*	*Cp*	*AIC*	*N*
All$_{Universal}$	ln(D_{10}) alone	0.446	0.964	2.00 (2)	-24,334	15,054
	+ Age<20$_{[1,0]}$	0.444	0.965	4.00 (3)	-24,490	15,054
	+ Managed$_{[1,0]}$	0.444	0.965	4.00 (3)	-24,492	15,054
	+ Ecoregion	0.421	0.968	6.93 (9)	-26,097	15,054
	+ MAT	0.446	0.964	4.00 (3)	-24,385	15,054
	+ MAP	0.443	0.965	4.00 (3)	-24,573	15,054
F$_{Shrub}$	ln(D_{10}) alone	0.492	0.968	2.00 (2)	-3,383	2,383
	+ Age<20$_{[1,0]}$	0.480	0.970	2.05 (3)	-3,495	2,383
	+ Managed$_{[1,0]}$	0.473	0.971	4.00 (4)	-3,564	2,383
	+ Ecoregion	0.465	0.972	6.77 (7)	-3,644	2,383
	+ MAT	0.483	0.969	4.00 (4)	-3,470	2,383
	+ MAP	0.486	0.969	4.00 (4)	-3,441	2,383
F$_{Multi}$	ln(D_{10}) alone	0.389	0.937	2.00 (2)	-10,177	5,397
	+ Age<20$_{[1,0]}$	n.s				
	+ Managed$_{[1,0]}$	n.s				
	+ Ecoregion	0.386	0.938	3.49 (6)	-10,263	5,397
	+ MAT	0.384	0.939	4.00 (4)	-10,317	5,397
	+ MAP	0.388	0.938	4.00 (4)	-10,211	5,397
F$_{Euc}$	ln(D_{130}) alone	0.360	0.974	2.00 (2)	-12,275	6,004
	+ Age<20$_{[1,0]}$	0.331	0.978	2.61 (3)	-13,291	6,004
	+ Managed$_{[1,0]}$	0.352	0.975	4.00 (4)	-12,532	6,004
	+ Ecoregion	0.350	0.975	11.6 (7)	-12,591	6,004
	+ MAT	0.359	0.974	4.00 (4)	-12,291	6,004
	+ MAP	0.359	0.974	4.00 (4)	-12,312	6,004
F$_{Other-H}$	ln(D_{130}) alone	0.293	0.973	2.00 (2)	-1,234	503
	+ Age<20$_{[1,0]}$	n.s				
	+ Managed$_{[1,0]}$	n.s				
	+ Ecoregion	0.290	0.974	5.92 (3)	-1,244	503
	+ MAT	0.289	0.974	4.00 (4)	-1,244	503
	+ MAP	0.290	0.974	4.00 (4)	-1,241	503
F$_{Other-L}$	ln(D_{130}) alone	0.273	0.979	2.00 (2)	-1,987	767
	+ Age<20$_{[1,0]}$	0.257	0.982	4.00 (4)	-2,078	767
	+ Managed$_{[1,0]}$	n.s				
	+ Ecoregion	0.272	0.980	6.12 (3)	-1,996	767
	+ MAT	0.272	0.980	4.00 (4)	-1,992	767

Generic allometrics 5

| | + MAP | 0.264 | 0.981 | 4.00 (4) | -2,038 | 767 |

39

Generic allometrics 6

40 **Table 6** Change in fit statistics (*RMSE*, R^2 and *AIC*) when the All$_{Universal}$ model was compared with either: (i) All$_{Universal}$ model

41 with the inclusion of a categorical variables for the five categories of plant functional type, using the entire dataset (first row), or

42 (ii) less generalised models of plant functional type model (F$_{Shrub}$, F$_{Multi}$, F$_{Euc}$, F$_{Other-H}$ or F$_{Other-L}$) when applied against each of the

43 plant functional type datasets. By necessity, all models here were based on D_{10}. A negative change in *AIC* (*ΔAIC*) indicates that

44 the first model is better than the All$_{Universa}$ model.

Dataset	Model comparison	$\Delta RMSE$	ΔR^2	ΔAIC	N
All$_{Universal}$	(All$_{Universal}$ + Types) – (All$_{Universal}$)	-0.040	0.006	-2,836	15,054
F$_{Shrub}$	(F$_{Shrub}$) – (All$_{Universal}$)	-0.016	0.002	-155	2,383
F$_{Multi}$	(F$_{Multi}$) – (All$_{Universal}$)	-0.050	0.017	-1,311	5,397
F$_{Euc}$	(F$_{Euc}$) – (All$_{Universal}$)	-0.020	0.004	-602	6,004
F$_{Other-H}$	(F$_{Other-H}$) – (All$_{Universal}$)	-0.008	0.002	-25	503
F$_{Other-L}$	(F$_{Other-L}$) – (All$_{Universal}$)	-0.252	0.054	-1,019	767

45

46

Generic allometrics 7

47   **Table 7** Median changes in fit statistics (*RMSE*, R^2 and *AIC*) when the All_Universal model was compared with less generalised

48   models of either the relevant: (i) plant functional type model (F_Shrub, F_Multi, F_Euc, F_Other-H or F_Other-L), or (iii) model specific to the

49   species level. These models relate to data from 53 species having sufficient data for species-specific allometric models ('N

50   Species'), and by necessity, were based on D_{10}. Values in parentheses are standard deviations. *N* indicates the median number of

51   individuals represented by each species within each grouping of the dataset. A negative change in *AIC (ΔAIC)* indicates that the

52   first model is better than the All_Universal model, and vice versa for positve *ΔAIC* values.

| Dataset	Model comparison	N Species	Δ*RMSE*	ΔR^2	Δ*AIC*	*N*
All_Universal	(Types) – (All_Universal)	53	-0.026 (0.072)	0.006 (0.052)	-12 (146)	111
	(Species) – (All_Universal)	53	-0.080 (0.095)	0.027 (0.049)	-43 (184)	111
F_Shrub	(F_Shrub) – (All_Universal)	8	-0.015 (0.066)	0.004 (0.036)	-9 (30)	115
	(Species) – (All_Universal)	8	-0.088 (0.122)	0.039 (0.059)	-65 (52)	115
F_Multi	(F_Multi) – (All_Universal)	12	-0.062 (0.091)	0.019 (0.043)	-31 (277)	130
	(Species) – (All_Universal)	12	-0.068 (0.085)	0.028 (0.039)	-40 (294)	130
F_Euc	(F_Euc) – (All_Universal)	28	-0.025 (0.057)	0.006 (0.022)	-12 (74)	81
	(Species) – (All_Universal)	28	-0.101 (0.090)	0.019 (0.042)	-42 (144)	81
F_Other-H	(F_Other-H) – (All_Universal)	3	0.005 (0.016)	-0.003 (0.003)	4 (12)	84
	(Species) – (All_Universal)	3	-0.014 (0.013)	0.003 (0.002)	-5 (12)	84
F_Other-L	(F_Other-L) – (All_Universal)	2	-0.168 (0.018)	0.127 (0.044)	-49 (6)	219
	(Species) – (All_Universal)	2	-0.182 (0.008)	0.133 (0.040)	-55 (2)	219

53

Generic allometrics 8
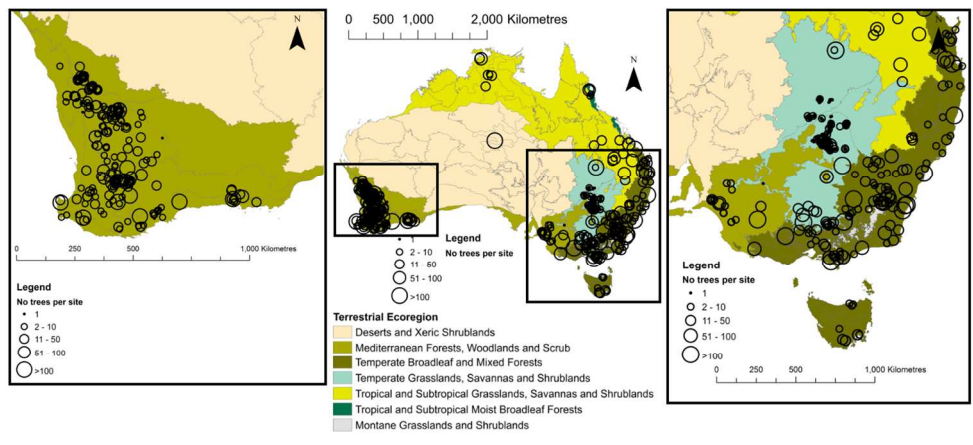
Figure 1
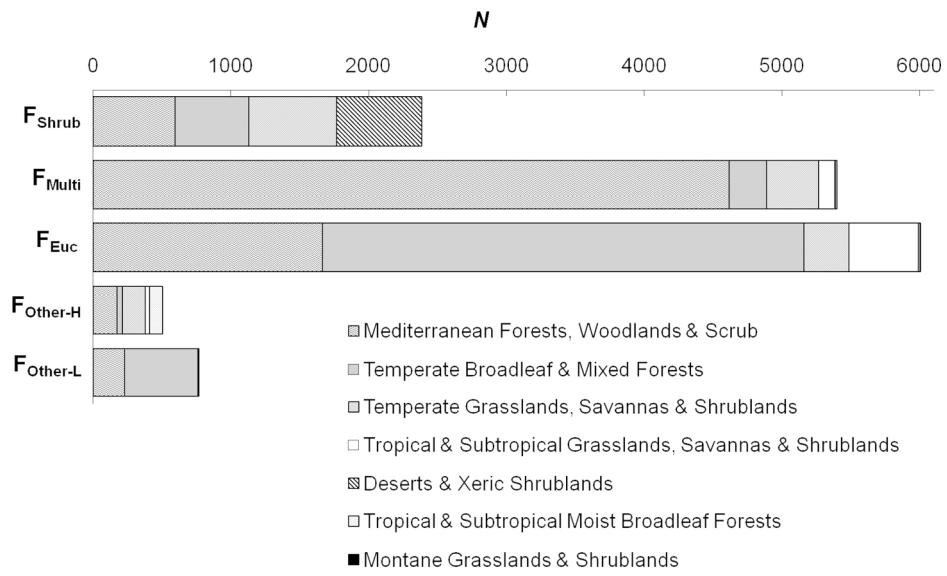168x75mm (300 x 300 DPI)

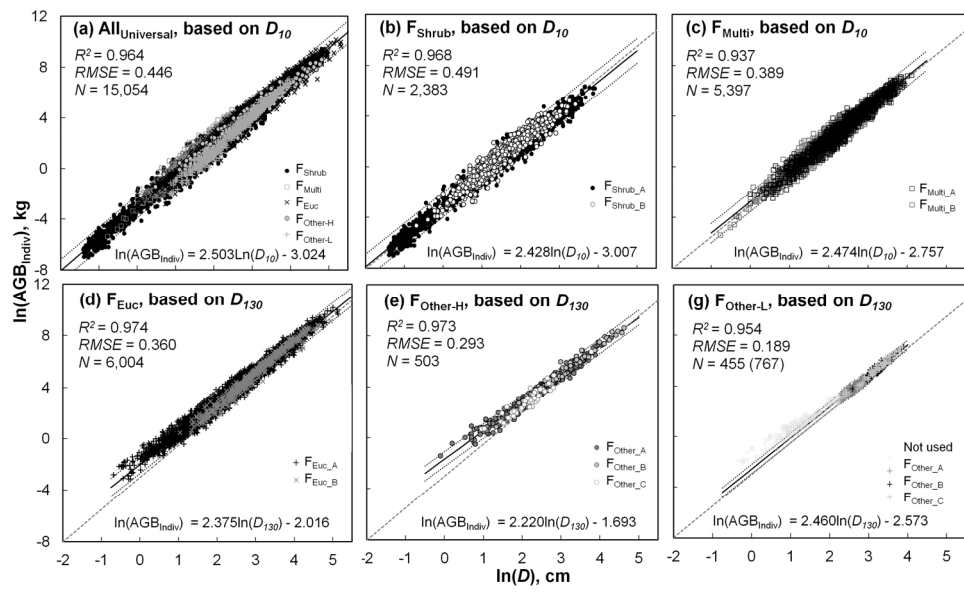Figure 2
168x100mm (300 x 300 DPI)
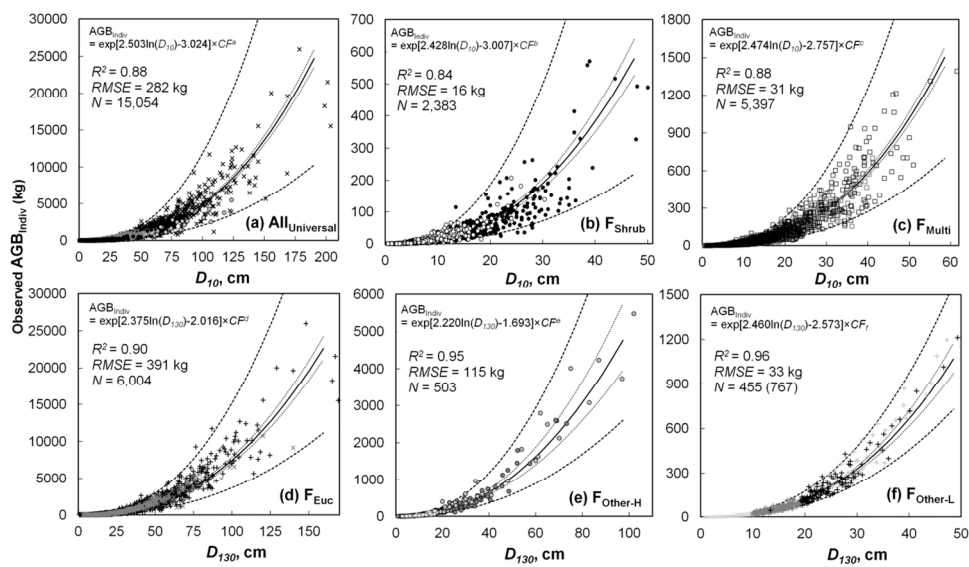
Figure 3
168x101mm (300 x 300 DPI)
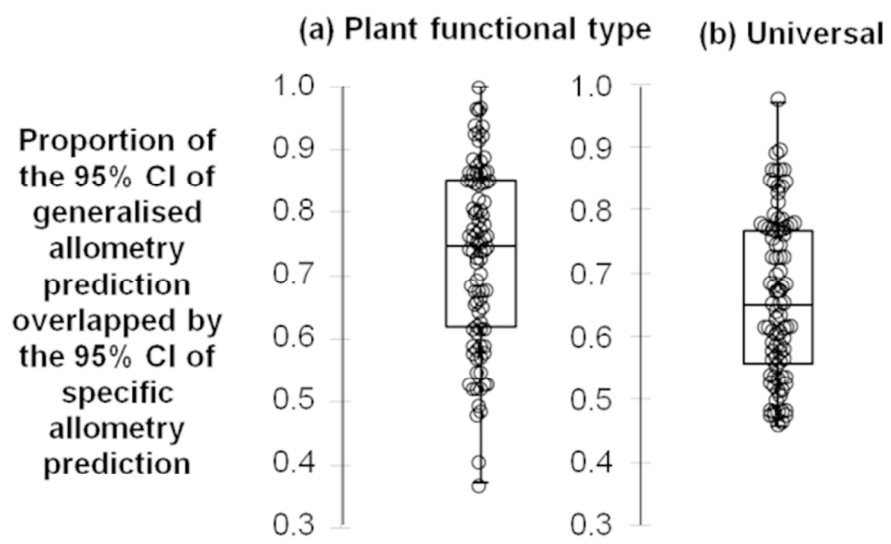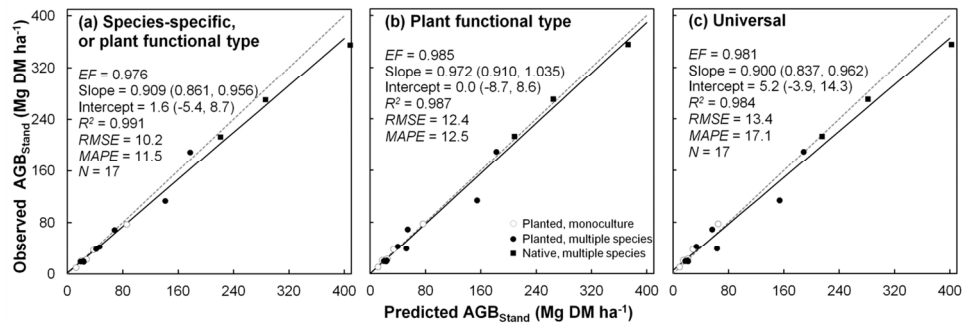
Figure 4
168x96mm (300 x 300 DPI)

Figure 5
80x46mm (300 x 300 DPI)

Figure 6
168x57mm (300 x 300 DPI)