1   The importance of large-diameter trees in the wet tropical rainforests of Australia

2   Short title: Large-diameter trees in Australian rainforests

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8   # Abstract

9   Large trees are keystone structures in many terrestrial ecosystems. They contribute

10 disproportionately to reproduction, recruitment and succession, and influence the structure,

11 dynamics, and diversity of forests. Recently, researchers have become concerned about evidence

12 showing rapid declines in large, old trees in a range of ecosystems across the globe. We used ≥10cm

13 diameter at breast height (DBH) stem inventory data from 20, 0.5 ha forest plots spanning the wet

14 tropical rainforest of Queensland, Australia to examine the contribution of large-diameter trees to

15 above ground biomass (AGB), richness, dominance, mortality and recruitment. We show

16 consistencies with tropical rainforest globally in that large-diameter trees (≥70 cm DBH) contribute

17 much of the biomass (33%) from few trees (2.4% of stems ≥10cm DBH) with the density of the

18 largest trees explaining much of the variation (62%) in AGB across plots. Measurement of AGB in the

19 largest 5% of trees allows plot biomass to be predicted with ~85% precision. In contrast to rainforest

20 in Africa and America, we show that a high proportion of species are capable of reaching a large-

21 diameter in Australian wet tropical rainforest resulting in weak biomass hyperdominance (~10% of

22 species account for 50% of the biomass) and high potential resilience to regional disturbances and

23 global environmental change. We show that the high AGB in Australian tropical forests is driven

24 primarily by the relatively high density of large trees coupled with contributions from significantly

25 higher densities of medium size trees. Australian wet tropical rainforests are well positioned to

26 maintain the current densities of large-diameter trees and high AGB into the future due to the

27 species richness of large trees and a high density of replacement smaller trees.

2

Introduction

28

29 Large trees are keystone structures in many terrestrial ecosystems including urban areas and

30 agricultural systems [1]. They play a critical ecological role, storing large quantities of carbon,

31 dominating canopies, providing food, shelter, habitat, and nesting cavities, and modulating

32 microclimates and hydrological processes [2-5]. In forest ecosystems, large trees also contribute

33 disproportionately to reproduction, recruitment and succession, and influence the structure,

34 dynamics, and diversity of forests [6, 7]. Recently, researchers have become concerned about

35 evidence showing rapid declines in large, old trees in a range of ecosystems across the globe [8].

36 Several reasons for this decline have been suggested including higher mortality rates in response to

37 drought [9, 10] and cyclones [11], and the effects of fragmentation [12], logging, land clearing and

38 agricultural intensification [2, 13].

39 Tropical forests make an important contribution to the global carbon cycle and the aboveground

40 carbon balance of these forests is largely governed by the growth and mortality of individual trees

41 [14]. Large trees in tropical forests have been shown to be particularly vulnerable to effects of

42 fragmentation and lagged-mortality arising from damage sustained during logging activities [12, 15].

43 However, in tropical forests not subject to significant human-disturbance, evidence for decline in

44 large trees is limited and long-term datasets are rare. Several authors have noted overall increases in

45 mortality in trees across tropical forest plots in America and Asia though large trees have not been

46 reported to be disproportionately affected [16]. Over 8.5 years, the mortality rate of trees >40m in

47 height in lowland American rainforest was less than half the landscape-scale average for all canopy

48 trees [5]. These authors suggest low mortality rates may be attributed to species-specific traits such

49 as high wood density or delayed reproduction that increases survival through all life stages,

50 increasing the probability of attaining tall heights. Alternatively (or in concert), low mortality in tall

51 trees may be due to ecological advantages such as escape from physical damage from branch falls of

52 lower stature trees or greater light interception which increases carbon gain [5]. It has been

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53 suggested [8] that elevated plant-growth rates in tropical forests, possibly resulting from rising

54 atmospheric CO_2, might result in larger numbers of large trees, particularly where other human

55 disturbances are limited.

56 Large trees store large quantities of carbon and have been shown to drive variation in biomass in

57 tropical forests across both the Neo- and Paleotropics [4, 17, 18]. Large trees (≥70 cm diameter at

58 breast height (DBH) stored, on average, 25.1, 39.1 and 44.5% of above ground biomass (AGB) in

59 South America, Southeast Asia and Africa, respectively, but represented only 1.5, 2.4 and 3.8% of

60 trees >10 cm DBH (Table 1, [4]). Large trees also accumulate carbon much faster than smaller trees

61 [19]. Large trees have been recently described as being 'biomass hyperdominant', that is, the

62 functions of storing and producing carbon are concentrated in a small number of tree species [20].

63 For example, in tropical forest plot datasets from the Amazon and Africa, just ~1% [20] and 1.5% of

64 tree species [17] were responsible for 50% of carbon storage and productivity. Understanding the

65 dynamics of these large trees, and their response to changing environmental conditions, is clearly

66 important for predicting the long-term functioning of tropical ecosystems as well as carbon storage

67 and cycling.

68 **Table 1. Large-diameter tree (>70 cm DBH) and AGB characteristics of Australian, Asian, American**

69 **and African tropical rainforest.**

	Mean AGB (Mg/ha)	Number of large stems/ha	Contribution of large trees to AGB (%)	Percentage of large stems
Australia[#]	590.5±169.0	18.4±5.4	32.7	2.4
Asia*	393.3±109.3	13.4±6.7	39.1	2.4
Amazon*	287.8±105.0	7.5±5.3	25.1	1.5
Africa*	418.3±91.8	15.8±5.4	44.5	3.8

70 #This study

4

71   *[4]

72   Australian wet tropical forests have among the highest biomass of tropical forests globally. On

73   average, AGB in Australian lowland rainforest (<600 m) is 1.7 times higher than in lowland

74   Amazonian forest, and between 1.2 and 1.3 times higher than in African and Asian lowland forests

75   (Table 1, [4]). Interestingly, AGB values in Australian lowland forests are also considerably higher

76   than those in Papua New Guinea [21], our nearest neighbour and most phylogenetically similar

77   rainforest. Comparisons are similar or more pronounced in upland forests (600-1000 m) [22-24] and

78   highland forests (1000-1500 m) [23, 25, 26]. We have monitored growth, recruitment and mortality

79   of stems (≥10 cm DBH) in 20, 0.5 ha plots in the wet tropical rainforest of Australia for nearly 5

80   decades [27]. Here, we assess the contribution of large trees to carbon storage on our plots and

81   examine changes in mortality and recruitment. We also discuss the role of large trees in the high

82   biomass estimates seen in Australian wet tropical rainforest. We compare our results with those for

83   tropical forests globally, highlighting convergent and divergent patterns. We demonstrate, 1) broad

84   consistencies with other tropical rainforest globally confirming the importance of large-diameter

85   trees to the carbon cycle, and 2) some divergence from other tropical rainforest globally, notably

86   high species richness of large-diameter trees resulting in low biomass hyperdominance by species

87   and some uncertainty in estimating AGB from the largest trees.

Materials and Methods

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Study sites

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90   The 20 CSIRO permanent study plots are situated in north-east Queensland, Australia, between

91   21.5°S, 149°E and 12.5°S, 143°E. The region is topographically diverse, and our dataset spans much

92   of the geographical and environmental variation. The climate is tropical with mean annual rainfall

93   ranging from 1200 mm to over 8000 mm on the higher coastal ranges. Seventeen of the plots are

5

94   located within the Wet Tropics bioregion which consists of narrow coastal plains flanked by rugged

95   mountains (to 1622 m) with extensive upland areas gradually sloping to the west. While covering

96   only 0.24% of the Australian continent, the Wet Tropics region contains high levels of diversity and

97   endemism of flora and fauna [28]. The plots were established between 1971 and 1980 in largely

98   undisturbed forest and have been resurveyed every 2-15 years through to 2016. For a full

99   description of the methodology and access to the data see [27]. At each census all stems ≥10 cm

100   diameter are measured at DBH and mortality of stems ≥10 cm is recorded. Each individual is

101   identified to species.

102

Defining large-diameter trees

104   For moist forests in the Amazon with AGB of 85 - 400 Mg/ha, trees ≥70 cm diameter were identified

105   as being important components of AGB [29]. Studies since have also defined large trees as ≥70 cm

106   DBH [4, 18, 30], however others have used a definition that is specific to the particular study or

107   forest type (e.g. >100 [31], >80 cm [32], 60-90 or >90 cm [15], and >60 cm [3]). In this study we

108   define a large tree as being ≥70 cm DBH to allow for relevant pan-tropical comparisons.

Above ground biomass estimates

110   Above ground biomass estimations are most accurate when they incorporate DBH, wood density

111   and tree height [33] and we consider equation 2 described by Chave et al. [34] to be the most

112   appropriate for AGB estimations in our forests. Unfortunately, height estimates for our plots were

113   only collected at establishment and in 1998. Therefore, we assessed two methods of deriving height

114   from DBH; 1) a pantropical equation that assumes a relationship between environmental stress and

115   tree height [34], and 2) an Australian moist forest equation developed from height diameter

116   relationships [31]. We compared these derived heights with our 1998 height data and heights

117   collected from 22,694 trees at the Robson Creek 25 ha rainforest plot [35] also located within the

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118   Wet Tropics Bioregion. The first equation considerably underestimated measured height, and the

119   second equation overestimated but approximated measured height (S1 and S2 Figs). We used the

120   derived heights from both sources in equation 2 in [34] and compared the resulting AGB estimations

121   to those using the actual measured heights from the 1998 and Robson Creek 25 ha data (S3 Fig).

122   Estimations from both sources were less accurate than simply using an equation for tropical moist

123   forests without height [33]. The latter is therefore used in this study:

124    $$(AGB)est = p \times \exp(-1.499 + 2.148\ln(D) + 0.207\,(\ln(D))2 - 0.0281(\ln(D))3)$$

125   Where p = wood density (g/cm³) and D = DBH (cm). Wood density values were taken from a

126   database compiled from the Australian literature and field collections. Values from the literature

127   were used if sourced from northern Australia. Where more than one measurement was available,

128   mean values were taken for a species. Where a species value was not available (n=19), the genus

129   mean was used (n=14). Where a genus mean was not available, the family mean was used (n=4).

130   Where a family mean was not available, the plot mean was used (n=1).

131   Data analysis

132   Trees in each plot were ranked by decreasing size according to their AGB and their contribution to

133   total AGB calculated. We calculated the number of species that collectively account for 50% of the

134   total biomass both at the plot and regional scale at the most recent survey.   The contribution of the

135   largest trees to total species richness for each plot was calculated.

136   We used linear regression to assess the variation in total AGB explained by the single largest tree in

137   each plot, and by the top 5, 10, 15 and 20% of largest trees in each plot.   Relative root mean square

138   errors were calculated to assess precision of the regression model.

139   Mortality and recruitment rates were calculated as per Condit, Ashton (36). Thus, for mortality:

140    $$m = \frac{\ln n_0 - \ln S_t}{t}$$

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141   For recruitment:

142     $$r = \frac{\ln n_t - \ln S_t}{t}$$

143   Where the census interval is t, n_o is the population size at time 0 and n_t is the population size at time

144   t. The number of survivors at time t is S_t. Mortality and recruitment rates were calculated for each

145   size class (large trees ≥70 cm DBH, medium trees 30-70 cm, and small trees <30 cm DBH) at each

146   census interval for each plot and then averaged by decade across all plots.

Results

148   Over all census periods, 81 species were recorded as large trees (≥70 cm), which is 16.6% of all

149   species in the dataset. Three species were strangler figs (*Ficus* sp.: Moraceae). The family Myrtaceae

150   had the highest number of large tree species (n=11), while the Sterculiaceae had the highest

151   proportion of species reaching large diameter status (42%, n=5). Species that grew into large trees

152   had a significantly lower wood density (mean = 0.59 g/cm^3) than species that did not (mean = 0.64

153   g/cm^3) (ANOVA $F_{(1, 488)}$ = 6.51, P = 0.011).

154   Across the 20 plots the mean AGB at the last census was 590 ± 169 SD Mg/ha (range 307 – 909)

155   (Table 2). The size class 10 -20 cm DBH contributed 60.5% of the trees (Fig 1). At the last census the

156   size class 30 - 40 cm DBH contributed the most AGB of any 10 cm size class bracket (13.7%), a shift

157   from the first census where the 40 – 50 cm DBH size class contributed the most (15.0%) (Fig 2). The

158   total number of large trees was 169 at the first survey and 182 at the last survey. At the last census

159   the average number of large trees per hectare was 18.4 ±5.4 SD, comprising 2.4% of total trees, and

160   large trees accounted for 32.7% of AGB across all plots (range 0 – 52.3%). The mean proportion of

161   the total AGB accounted for by the cumulative number of largest trees increased rapidly reaching an

162   average of 49% for the 20 largest trees (5% of the trees) and 84% for the largest 100 trees (27% of

163   the trees) (Figs 3a and 3b).

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164 **Fig 1. Contribution to total trees number by size class across the 20 CSIRO permanent plots**. Note

165 the broken Y-axis.

166 **Fig 2. Contribution to total AGB by size class across the 20 CSIRO permanent plots.**

167 **Fig 3**. **Proportion of AGB accounted for by the largest trees.** (a) percent of largest trees and (b)

168 cumulative number of largest trees. Vertical lines indicate the (a) percent of largest trees accounting

169 for 50% and 80% of total AGB and (b) the proportion of AGB accounted for by the 20 and 100 largest

170 trees. The dashed lines represent ± 1 SD of the mean.

171 **Table 2**. **Above ground biomass and stem demographics of the 20 CSIRO permanent plots.**

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	First census					Last census			
Plot	Date	AGB (Mg/ha)	Number of stems	Number of stems ≥70 cm DBH	Largest stem (cm DBH)	Date	AGB (Mg/ha)	Number of stems	Number of stems ≥70 cm DBH	Largest stem (cm DBH)
ep18	1973	825	454	11	125.7	2016	838	427	13	120.5
ep19	1975	480	400	7	90.9	2016	307	387	3	87.8
ep2	1971	296	462	0	54.8	2015	343	511	0	55.4
ep29	1975	429	494	1	83.7	2015	478	409	2	98.6
ep3	1971	782	502	12	113.1	2015	814	466	15	118.0
ep30	1976	680	552	8	94.9	2013	674	550	10	94.2
ep31	1976	667	238	13	108.9	2013	537	191	6	118.7
ep32	1975	394	447	4	106.6	2015	421	402	5	119.0
ep33	1976	743	315	13	196.5	2015	806	250	23	122.7
ep34	1976	584	302	10	118.1	2016	530	259	10	122.9
ep35	1977	445	501	2	84.5	2016	551	399	5	92.2
ep37	1977	978	386	14	147.7	2013	909	440	12	158.8
ep38	1977	513	382	6	131.2	2016	505	324	7	134.4
ep4	1972	369	486	1	70.4	2016	456	454	6	87.0
ep40	1978	697	496	9	106.6	2013	627	414	9	120.6
ep41	1977	519	395	3	88.4	2015	589	314	5	77.8

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ep42	1977	547	243	17	134.8	2013	403	234	8	126.5
ep43	1978	730	387	16	127.3	2016	635	349	15	116.0
ep44	1980	675	439	11	109.3	2013	708	399	12	111.5
ep9	1972	638	441	11	121.2	2015	679	411	16	108.1
Mean±SD		599±172	416±87	8.5±5.2			590±169	379±93	9.1±5.6	

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174   The number of trees ≥70 cm DBH explained 62% of the variation in AGB across plots. The AGB of the

175   single largest tree in each plot explained 25% of the variation in total AGB across all plots and the

176   AGB of the top 5% of largest trees explained approximately 70% (Table 3).

177   **Table 3**. **Linear regression of plot AGB against number of trees per plot, AGB of the largest tree**

178   **per plot, and the largest 5, 10, 15 and 20% of trees in each plot.**

	R^2	F	Sig	rRMSE
Total number of trees	0.016	0.302	P=0.590	0.271
Number of trees ≥70 cm	0.616	28.92	p<0.001	0.169
Number of trees ≥70	0.006	0.1184	p=0.737	0.272
Largest tree	0.252	6.068	p<0.05	0.230
top 5%	0.692	40.424	p<0.01	0.151
top 10%	0.849	100.942	p<0.01	0.106
top 15%	0.916	196.604	p<0.01	0.079
top 20%	0.952	359.677	p<0.01	0.059

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180   Species richness was relatively high among the largest trees with the top 25 largest trees in a plot on

181   average accounting for nearly 25% of total species richness in that plot; the 100 largest trees in a

182   plot accounted for 56% of total species richness (Fig 4). At the last census, 123 species out of 443

183   (27.8%) contributed to the top 50% of total AGB across all plots. At the plot level, an average of 20%

184   of species contributed to the top 50% of AGB in the last census (range 3% to 44%). The mean DBH

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185   for biomass hyperdominant species was 74.7 cm ± 25.5 SD compared with non-biomass

186   hyperdominant species at 39 cm ± 27 SD.

187   **Fig 4**. **The proportion of total species accounted for by the cumulated number of largest trees.**

188   Results are displayed for each individual plot (coloured lines) with the heavy black line showing the

189   mean. Vertical lines indicate the proportion of species accounted for by the top 25 and top 100

190   largest trees.

191   The mean annual rate of mortality for large trees was higher than for small and medium size trees in

192   the first and last decade (decades beginning 1970 and 2010) and lowest in the decade beginning

193   1990 (Fig 5). Recruitment of large trees was also lowest in the 1970s but was higher than that for

194   small and medium trees for the remainder of the monitoring period, though variation was high due

195   to smaller overall numbers.

196   **Fig 5**. **Mean annual rate of mortality and recruitment across all plots during each decade for large**

197   **($\geq$70 cm dbh), medium (30-70 cm dbh) and small (<30cm dbh) trees.**

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Discussion

The contribution of large trees to above ground biomass

201   The role of a small number of large trees in driving forest biomass is now well recognised [3, 4, 18]

202   and the concentration of AGB in a limited number of large trees has been quantified recently across

203   the tropics [4, 17, 18, 37]. Despite Australian wet tropical rainforest holding considerably more

204   biomass than rainforests elsewhere in Asia, Africa and America, there are consistencies in the

205   contribution of the largest trees to biomass. Large-diameter trees ($\geq$70 cm DBH) contribute

206   approximately 33% of biomass and comprise 2.4% of trees $\geq$10 cm DBH in Australian wet tropical

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207   rainforest; within the range of values reported for Asian and African forests but significantly greater

208   than reported for Amazonian forests (Table 1, [3]). The density of the largest trees explains much of

209   the variation (~62%) in AGB across the plots, slightly less than the average pantropical estimate of

210   ~70% (excluding Australia) [4].

211   However, the high biomass and stem density of Australian wet tropical rainforest results in some

212   inconsistencies with pan tropical rainforests in total AGB prediction from the largest trees. The AGB

213   of the single largest tree on each of our plots only explained 25% of the variation in AGB total across

214   all plots which is approximately half that in African forests [17] and in North and South American

215   forests [37]. The largest 5% of trees in a plot (ranging from 9 to 27 trees, average 18.5) explains 70%

216   of the variance across plots, lower than that for African forests where the largest 20 trees explain

217   87% of variance [17]. In our plots measurement of the top 10 to 15% of trees (average 38 to 58

218   trees) is needed to explain close to 90% of the variation in AGB across plots. Measurement of AGB

219   for the top 5% of trees allows an estimate of AGB total with approximately 85% precision (table 3),

220   similar to that reported for African forests [17] and slightly better than reported in a global tropical

221   forests analysis (excluding Australia) (~82% for the top 20 trees) [18].

222   We have shown [38] that the mean relative change in AGB in Australian wet tropical rainforest

223   shifted from predominantly positive to predominantly negative during the 40 year monitoring

224   period. Although the number of large trees across all plots in our current study increased by 8%

225   over the census period we saw a recent increased mortality and decreased recruitment of large

226   trees supporting a general trend of declining growth rates in Australian wet tropical rainforest.

227   However, this must be viewed with caution as small overall numbers of large trees in 0.5 hectare

228   plots (mean = 9.1± 5.6 SD) contribute considerable variation in rates of mortality and recruitment. In

229   addition, productivity in Australian wet tropical rainforest is primarily influenced by large scale

230   disturbance events [38]. Mortality and recruitment over the five decades of census was driven by

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231   three severe cyclones (1986, 2006 and 2010) and an extended dry period around 1986 that impacted

232   all but three plots and may not reflect trends over the longer term.

Biomass hyperdominance in large trees

234   Australian wet tropical rainforest does not appear to have strong biomass hyperdominance at the

235   species level. Nearly 28% of species accounted for the top 50% of biomass across our plots

236   compared with 1.5% for African forests plots [17] and 5.3% for Amazonian basin plots [20]. At the

237   plot level, biomass hyperdominance ranged from 3% to 44% (average 20%); again much higher than

238   the average 4.4% across African plots. A more realistic estimate for Amazonian-wide

239   hyperdominance was suggested as ~1% considering the estimated 16,000 tree species that occur

240   there [20]. We have far fewer plots in our dataset than those used in the Amazonian study, however

241   the wet tropical rainforest of Australia is far less extensive and our dataset spans much of the

242   geographical variation and environmental gradients across the region and includes ~31% of all

243   species ≥10 cm DBH in the region. Australian wet tropical rainforest covers 10 000 km^2 of the

244   Australian continent (compared with 5.3 million km^2 of Amazonian rainforest), and has an estimated

245   1450 tree species. If we consider our biomass hyperdominants are a reasonable representation of

246   the region as a whole, then ~10% of tree species contribute 50% of the carbon stock in Australian

247   wet tropical rainforest.

248   While examples of biomass hyperdominance are numerous in woodland communities in tropical

249   Australia, examples in wet tropical rainforest are harder to find. In our dataset, *Backhousia bancroftii*

250   accounts for the entirety of the top 50% of biomass in plot ep31, in part due to the species being less

251   susceptible to cyclone damage than other species in the community [39]. Other less extensive

252   examples of hyperdominance in the study area not represented in our plots are *Leptospermum*

253   *wooroonoorum* that is restricted to wet exposed mountain ridges, *Ceratopetalum virchowii* that

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254   dominates on a particular low nutrient soil, and *Alstonia scholaris* that resists frequent cyclone

255   disturbance allowing it to dominate on some exposed coastal slopes.

256   The relatively high diversity of species reaching a large size and contributing to biomass in Australian

257   wet tropical rainforest has significant implications for the ongoing resilience of these forests. The

258   loss of a single species or a group of closely related dominant species is unlikely to have the same

259   consequences for forest carbon storage and forest function as it would in African or Amazonian

260   forests. Due to the relatively small extent of our rainforest, a disturbance event such as a severe

261   cyclone or a regional drought has the potential to impact a large proportion of the area. Having a

262   high diversity of species in the largest size classes affords a greater level of resilience to such an

263   event as Australian wet tropical rainforest species display a range of responses to disturbance and

264   varied rates of recovery [39]. In addition, high taxonomic diversity safeguards against factors that

265   target particular taxa such as the introduced fungal pathogen Myrtle rust that only infects the family

266   Myrtaceae [40] and soil borne pathogens such as *Phytophthera* spp. that cause higher mortality in

267   large trees and species in the family Elaeocarpaceae [41].

268   ## Accounting for high AGB in Australian wet tropical rainforest

269   The high AGB in Australian wet tropical rainforest is largely a result of the high density of large-

270   diameter trees with the density of trees ≥70 cm DBH explaining ~62% of the variation in AGB across

271   plots. Australian wet tropical rainforest also have a significantly higher density of total (≥ 10 cm

272   DBH), small, and medium trees than forests in Africa, South-east Asia and America (Fig 6). Although

273   trees <70 cm DBH are not a good predictor of AGB in our plots (R^2 = 0.0065, Table 3), medium sized

274   trees (30-70 cm) contribute close to 50% of our total AGB and are seen as important contributors to

275   AGB in some forests across the tropics [18]. The high density of small and medium sized trees in

276   Australian wet tropical rainforest is likely due to the high frequency of large scale disturbance by

277   tropical cyclones [38] which initially result in increased mortality but subsequently allow recruitment

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278   and growth into small and medium size classes. This is also presumably why we rarely see emergent

279   trees in Australian wet tropical rainforests. There is also strong evidence that water use efficiency is

280   much higher in Australian wet tropical rainforest than in similar forests globally resulting in trees

281   rarely becoming water limited [42], most likely due to species evolving to survive in the generally dry

282   continent of Australia. This potentially allows greater production of AGB presuming variables such

283   as soil nutrients and solar radiation interception are not limiting.

284   **Fig 6**. **A cross continental comparison of the number of trees per hectare ≥10 cm DBH.** From top to

285   bottom; all stems ≥10 cm DBH, stems 10 – 30 cm, stems 30 – 60 cm, stems >60 cm. CSIRO Australia

286   plots have significantly more stems in each comparisons except >60 cm DBH. Data is taken from

287   rainforest plots >10 ha in size, <18.0^0 north and south of the equator, and within the elevational

288   range of the CSIRO plots. Africa; 6 plots; [24, 43, 44], south-east Asia; 7 plots; [45-50], America; 8

289   plots: [51-54]. Stems >60 cm DBH are considered large due to the availability of relevant

290   comparative data.

291   Neither tree height, wood density, nor soil fertility appear to play a significant role in contributing to

292   higher biomass in Australian tropical forests. Mean canopy heights in Australian wet tropical

293   rainforest are in the order of 20-35 m [27, 35], emergent trees are rare, and asymptotic maximum

294   tree heights are similar to America and significantly lower than those in Asia and Africa [55]. The

295   mean wood density for species in our study is 0.63 g/cm^3, (± 0.16 SD, n = 443) with the most

296   frequent density class being 0.6-0.7 g/cm^3. This places wood density of Australian species higher

297   than reported means for tropical Africa (0.50 g/cm^3), Asia (0.57 g/cm^3), and America (0.60 g/cm^3) all

298   having the most frequent density class of 0.5-0.6 g/cm^3 [56]. However, applying slightly higher wood

299   density values to AGB estimations is unlikely to account for the high AGB in Australian wet tropical

300   rainforest particularly as we show that larger species have significantly lower wood densities. There

301   is no relationship between soil fertility and high AGB across our plots. Only one plot is considered

302   eutrophic (measured using exchangeable Ca and Total P%); ep33 of recent volcanic origin with an

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303 AGB of 806 Mg/ha. Fifteen of the remaining plots are on highly weathered soils and are considered

304 oligotrophic. Of these, ep18 and ep3 are ranked the second and third highest AGB. This broadly

305 contradicts a global pattern of increasing AGB with increasing soil fertility identified by Slik et al. [4].

306 Conclusion

307 We demonstrate that the contribution to AGB by the largest trees in Australian wet tropical

308 rainforest is generally consistent with that shown for tropical rainforest globally although the high

309 AGB and high contribution from smaller stems introduces some uncertainty in predicting AGB from

310 these large trees. We show that in stark contrast to African and Amazonian forest, our forests have

311 low biomass hyperdominance of larger trees. This puts them in a favourable position to withstand

312 effects of environmental change or large scale disturbance events. Finally, the high average AGB in

313 Australian tropical forests is driven primarily by the relatively high density of large trees coupled with

314 contributions from the higher densities of medium size trees.

315 Acknowledgements

321 References

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Supporting Information

492

**S1 Fig The relationship between measured tree height from 1998 CSIRO plot data and derived tree
height.** a) height derived from [34] equation 6a (grey circles; y = 3.444 + 0.477*x; r^2 = 0.6285) and, b)
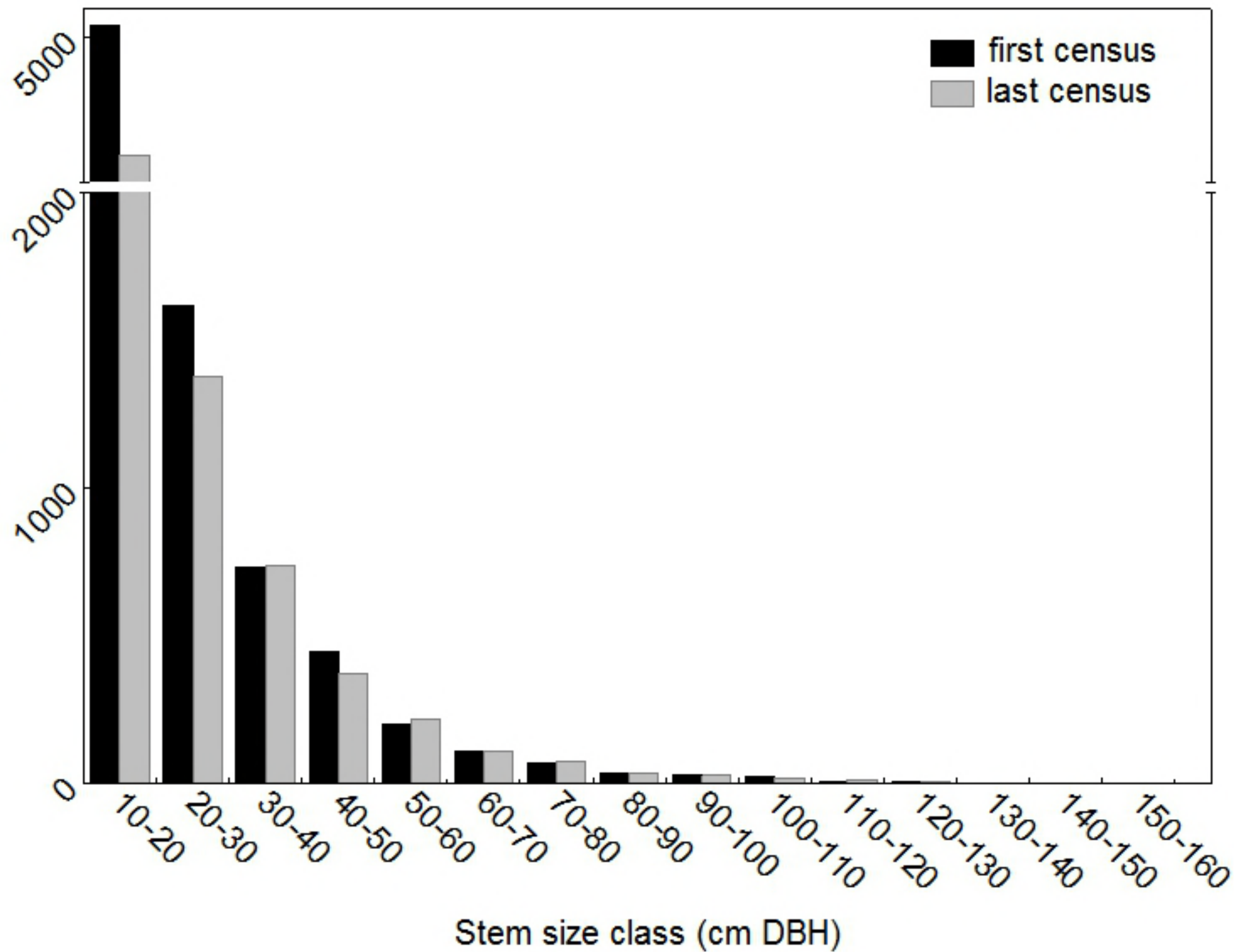height derived from [31] for Australian moist forest (back circles; y = 5.284 + 0.7766*x; r^2 = 0.6293).

**S2 Fig The relationship between measured tree height from Robson Creek 25 ha plot data [27] and
derived tree height.** a) height derived from [34] equation 6a (grey circles; y = 3.2759 + 0.478*x; p =
0.0000; r^2 = 0.6958 and, b) height derived from [31] for Australian moist forest (back circles; y =
5.4336 + 0.6638*x; p = 0.0000; r^2 = 0.6866).

**S3 Fig Relationship between estimated AGB using measured height, estimated AGB using derived
height and estimated AGB using [33] with no height.** a) estimated AGB using [34] equation 2 with
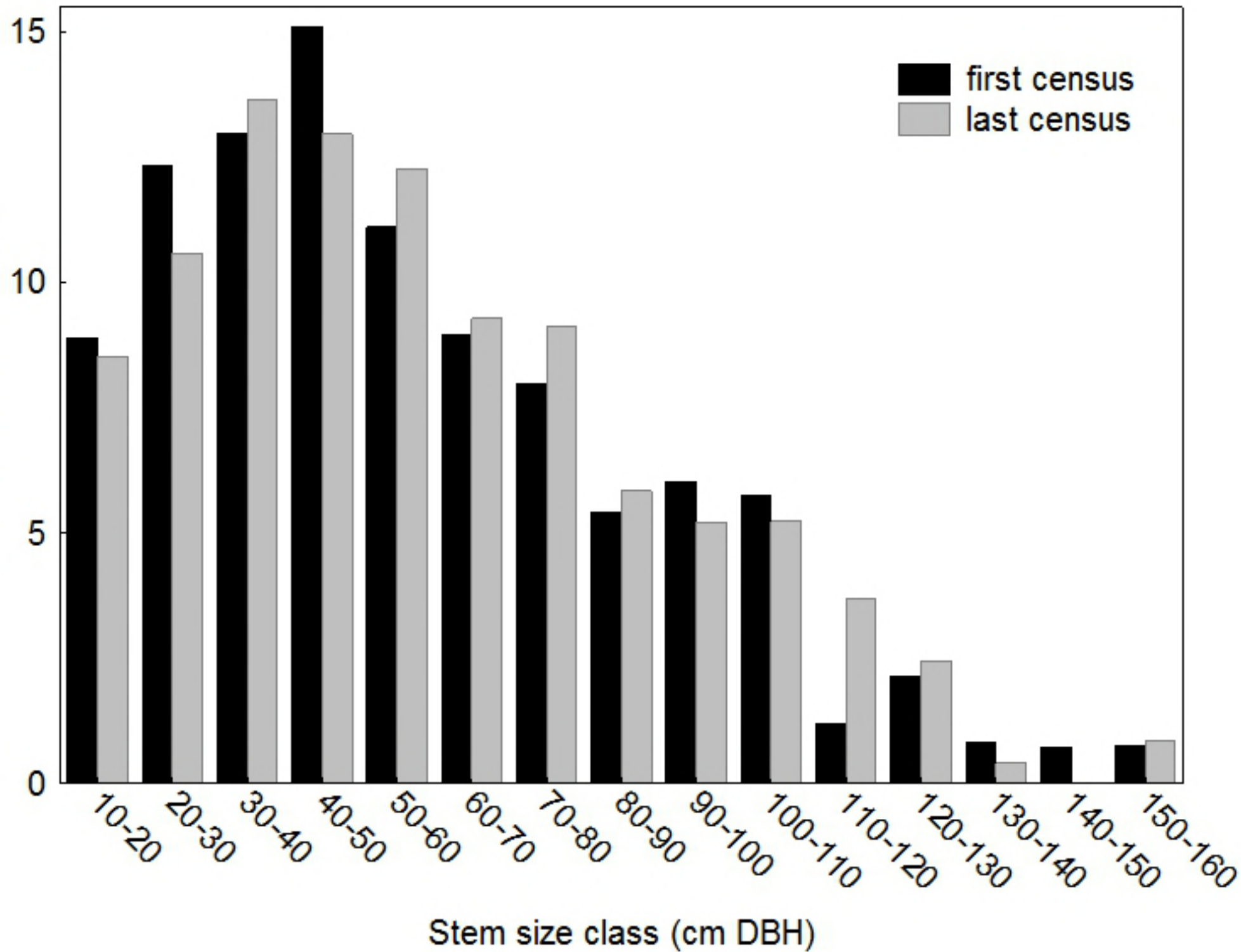
23

502   height derived from [34] equation 6a (triangles, dashed fit; y = 20.4771 + 0.6152*x; p = 0.0000; r^2 =

503   0.9462), b) estimated AGB using [34] equation 2 using height derived from [31] for Australian moist

504   forests (grey circles and fit; y = -59.9526 + 1.2396*x; r = 0.9793, p = 0.0000; r^2 = 0.9590). c) estimated

505   AGB using [33] for moist forests without height (black circles and fit; y = 1.2481 + 1.1607*x; r =

506   0.9852, p = 0.0000; r^2 = 0.9706).

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24
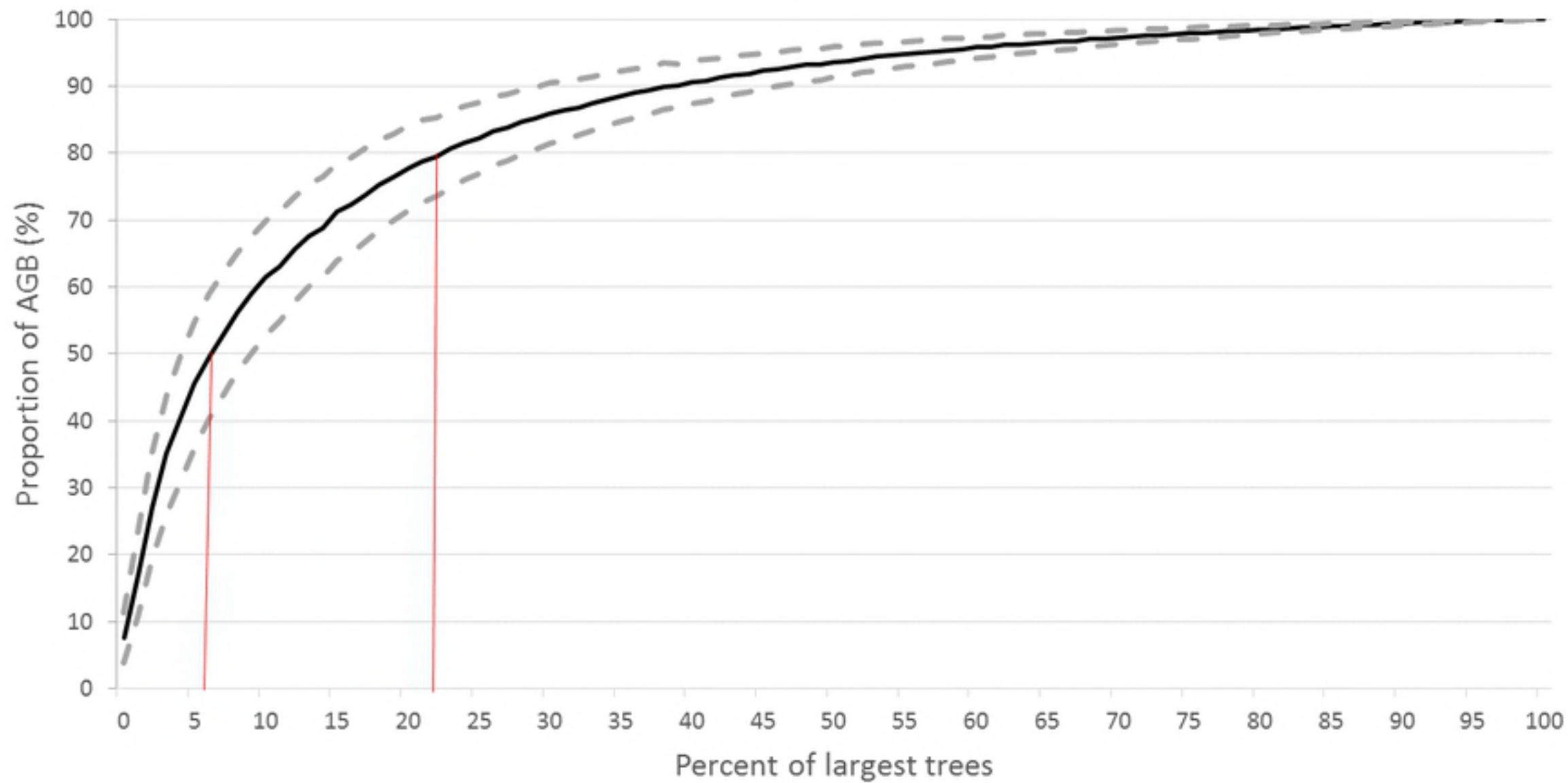
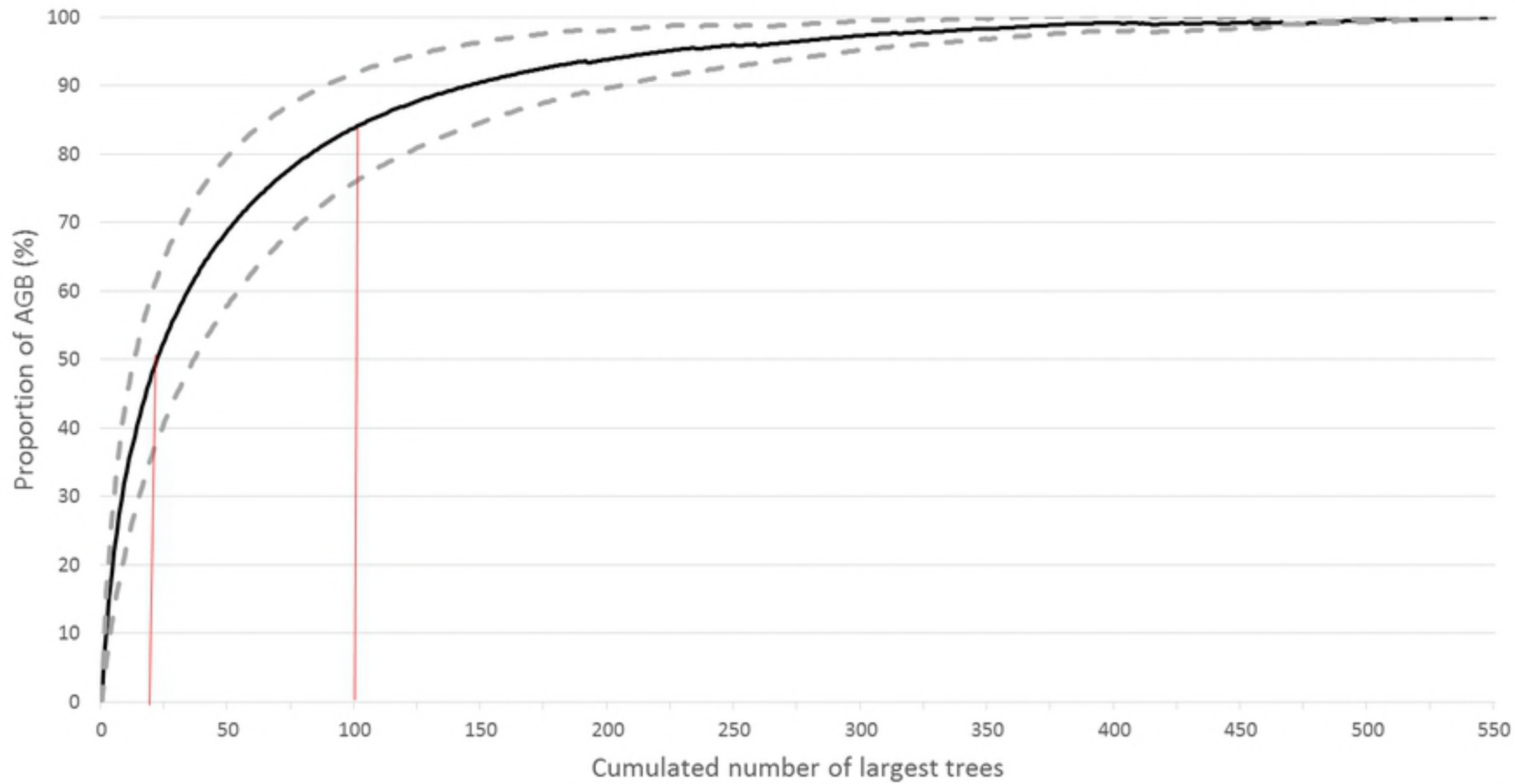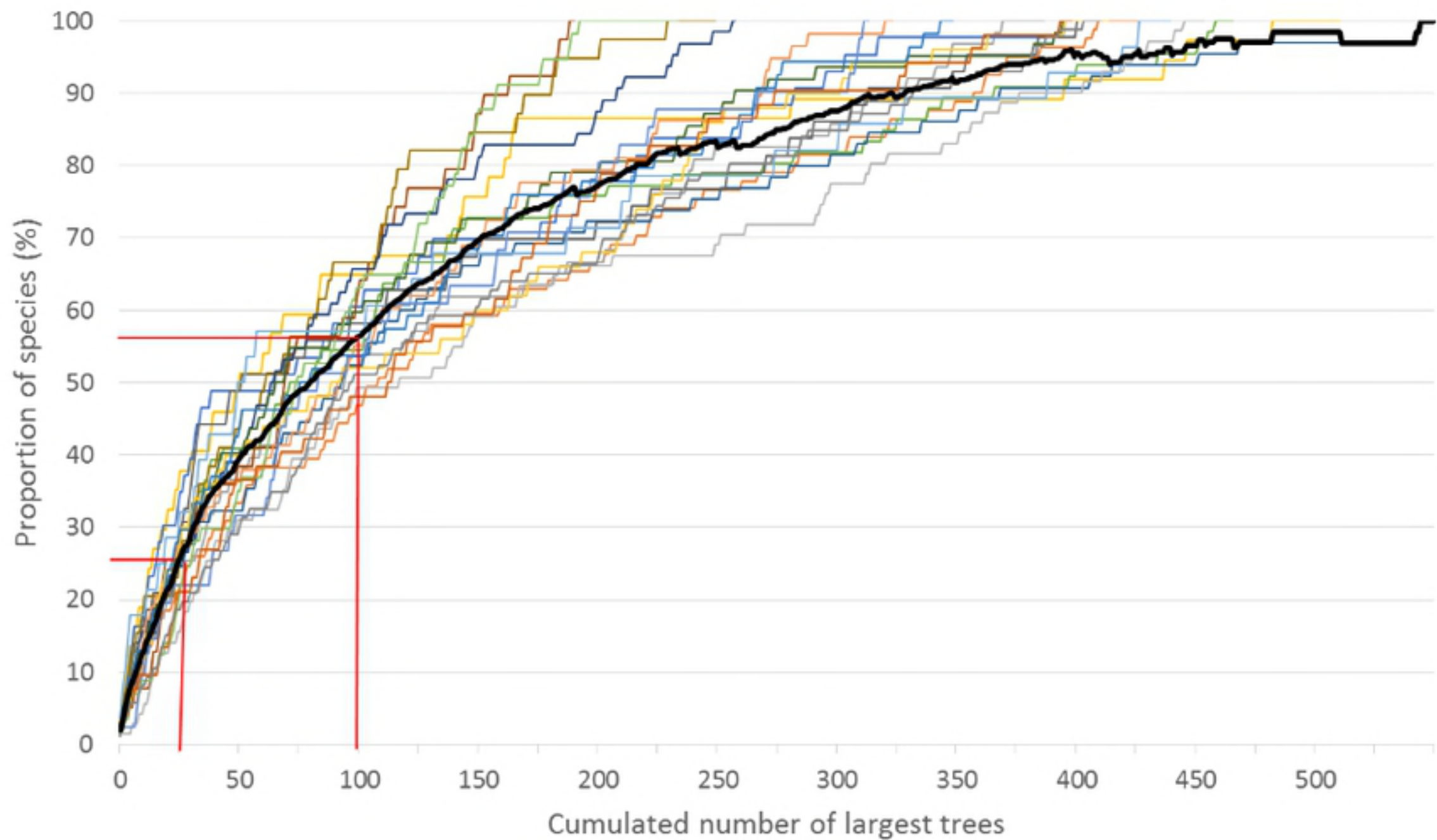Legend:
- first census (black)
- last census (gray)

Y-axis: Number of stems (5000, 2000, 1000, 0)

X-axis: Stem size class (cm DBH)
10-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, 90-100, 100-110, 110-120, 120-130, 130-140, 140-150, 150-160

Y-axis: Proportion of species (%)

X-axis: Cumulated number of largest trees

Legend: ep18, ep19, ep2, ep29, ep3, ep30, ep31, ep32, ep33, ep34, ep35, ep37, ep38, ep4, ep40, ep41, ep42, ep43, ep44, ep9, Mean