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Can we set a global threshold age to define mature forests

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Globally mature forests appear to be increasing in biomass density. There is disagreement whether these increases are the result of increases in CO₂ concentrations or a legacy effect of previous land-use. Recently, it was suggested that a threshold of 450 years should be used to define mature forests and that many forests increasing in biomass may be younger than this. However, the study making these suggestions failed to account for interactions between forest age and climate. Here we revisit the issue to identify: (1) how climate and forest age control global forest biomass density and (2) whether we can set a threshold age for mature forests. Using data from previously published studies we modelled the impacts of forest age and climate on biomass density using linear mixed effects models. We examined the potential biases in the dataset by comparing how representative it was of global mature forests in terms of its distribution, the climate space it occupied and the ages of the forests used. Biomass density increased with forest age, mean annual temperature and annual precipitation. Importantly the effect of forest age increased with increasing temperature, but the effect of precipitation decreased with increasing temperatures. The dataset was biased towards Northern hemisphere forests in relatively dry, cold climates. The dataset was also clearly biased towards forests <250 years of age. Our analysis suggests that there is not a single threshold age for forest maturity. Since climate interacts with forest age to determine biomass density a threshold age at which they reach equilibrium can only be determined locally. We caution against using biomass as the only determinant of forest maturity since this ignores forest biodiversity which often takes longer to recover. Future study of the influence of climate on forest biomass should aim to use the data currently being generated by long-term monitoring networks and satellite based observations.

1 **Can we set a global threshold age to define mature forests?**

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28

29 Abstract

30 Globally, mature forests appear to be increasing in biomass density. There is
31 disagreement whether these increases are the result of increases in CO₂ concentrations
32 or a legacy effect of previous land-use. Recently, it was suggested that a threshold of
33 450 years should be used to define mature forests and that many forests increasing in
34 biomass may be younger than this. However, the study making these suggestions failed
35 to account for the interactions between forest age and climate. Here we revisit the issue
36 to identify: (1) how climate and forest age control global forest biomass density and (2)
37 whether we can set a threshold age for mature forests. Using data from previously
38 published studies we modelled the impacts of forest age and climate on biomass
39 density using linear mixed effects models. We examined the potential biases in the
40 dataset by comparing how representative it was of global mature forests in terms of its
41 distribution, the climate space it occupied, and the ages of the forests used. Biomass
42 density increased with forest age, mean annual temperature and annual precipitation.
43 Importantly, the effect of forest age increased with increasing temperature, but the effect
44 of precipitation decreased with increasing temperatures. The dataset was biased
45 towards Northern hemisphere forests in relatively dry, cold climates. The dataset was
46 also clearly biased towards forests <250 years of age. Our analysis suggests that there
47 is not a single threshold age for forest maturity. Since climate interacts with forest age to
48 determine biomass density, a threshold age at which they reach equilibrium can only be
49 determined locally. We caution against using biomass as the only determinant of forest
50 maturity since this ignores forest biodiversity which often takes longer to recover. Future
51 study of the influence of climate on forest biomass should aim to use the data currently
52 being generated by long-term monitoring networks and satellite based observations.

53

54

55 Introduction

56 Forests play an important role in the global climate system, covering nearly one-
57 third of the earth's terrestrial surface and accounting for over three-quarters of terrestrial
58 gross primary production (Pan et al., 2013). Forests also provide vital habitats for

59 biodiversity and supply a wide-range of ecosystem services upon which humans
60 depend, such as climate regulation via carbon storage in tree biomass (Foley et al.,
61 2007). Globally, mature forests appear to be increasing in biomass density, and are
62 responsible for approximately 29% of all carbon sequestration in forests (Pan et al.,
63 2011). Mature tropical forests, in particular, have increased in biomass by around 0.5
64 Mg C ha⁻¹ year⁻¹ (Baker et al., 2004; Lewis et al., 2009), though the rate of increase now
65 appears to be slowing (Brienen et al., 2015).

66 Some researchers have hypothesised that increased CO₂ concentrations in the
67 atmosphere as a result of human activities have stimulated the growth of trees in
68 mature forests, resulting in increased biomass (Lewis et al., 2009). However, other
69 researchers reject these claims, hypothesising that that many mature forests are in fact
70 undergoing secondary succession following 'unseen' disturbances that occurred either
71 hundreds of years ago (Brncic et al., 2007; Muller-Landau, 2009) or as a result of
72 extreme weather such as El Niño events (Wright, 2005). If many supposedly mature
73 forests are recovering from previous human influence, then this may account for
74 observed increases in biomass density (Wright, 2005). It is thus unclear whether the
75 mature forests in studies that showed increases in biomass were actually old enough to
76 achieve a state of relative equilibrium, which can take decades to centuries. However,
77 until recently there has been no attempt to determine whether there are methods that
78 could be applied globally to enable forests recovering from disturbances to be
79 distinguished from relatively stable mature forests.

80 Recently Liu et al. (2014) attempted to address this issue by (i) assessing how
81 climate and forest age affect forest biomass density, and (ii) using this analysis to define
82 an age threshold for mature forests. The authors concluded that the biomass density of
83 mature forest stands was highest in areas with a mean annual temperature of c. 8-10°C
84 and mean annual precipitation between 1000 and 2500 mm (Liu et al., 2014). In
85 addition, the authors further suggested that forest biomass carbon density increased
86 with stand age, plateauing at approximately 450 years of age (Liu et al., 2014).
87 However, given that previous work has shown that climate strongly influences both
88 biomass accumulation (Johnson, Zarin & Johnson, 2000; Anderson et al., 2006;
89 Anderson-Teixeira et al., 2013) and the maximum biomass attainable by a forest

90 (Stegen et al., 2011) it seems unlikely that there is a single global age threshold that
91 can be used to define mature forests. Rather if such thresholds are used, they will need
92 to be defined in areas with relatively homogenous climates where accumulation rates
93 and maximum attainable biomass vary relatively little.

94 To address these issues we use the same data as Liu et al. (2014) to revisit the
95 questions:

- 96 1. How do climate and forest age control the biomass density of global forests?
- 97 2. Can we use this to set an age threshold for mature forests globally?

98 While the analyses we present here use the same data as Liu et al. (2014), we
99 improve on their analyses by considering interactions between precipitation,
100 temperature and estimated forest age. Our work shows that these interactions improve
101 model fit considerably, as well as indicating that establishment of a single age threshold
102 for mature forests is ecologically unrealistic.

103

104 **Methods**

105 The data we used for this study were taken from Liu et al. (2014) in which the
106 authors tested global-scale correlations between mature forest carbon stocks (biomass
107 density), stand age and climatic variables using data collected from previous studies.
108 Here we used this data on aboveground biomass (AGB, Mg ha⁻¹) along with estimated
109 forest age (years), mean annual precipitation (mm), mean annual temperature (°C) and
110 geographic location (Longitude and Latitude).

111 To examine our first question of how forest biomass is determined by climate and
112 forest age we used linear mixed effect models (LMMs). First, we tested whether
113 accounting for methodological differences between studies and spatial autocorrelation
114 improved model performance compared to null models. To do this we fitted a model
115 with a dummy random effect and compared the corrected Akaike Information Criteria
116 (AICc) value to our null models, which included study level random effects and a matrix
117 to account for spatial autocorrelation. Using the random effects structure deemed most
118 parsimonious we then tested the effects of temperature, precipitation and forest age on
119 AGB by running all possible LMMs that included two way interactions. Forest age was
120 log transformed as increases in AGB with age tend to be non-linear (Martin, Newton &

121 Bullock, 2013). All explanatory variables were standardised following Schielzeth (2010),
122 by subtracting the mean from each value and dividing by the standard deviation. This
123 method allows easier interpretation of coefficients and improves model convergence. To
124 reduce heteroscedasticity in model residuals we log transformed the response variable.

125 Models were ranked by AICc and model averaging performed using all models
126 with an $\Delta AICc \leq 7$ to produce coefficient estimates (Burnham & Anderson, 2002;
127 Burnham, Anderson & Huyvaert, 2010). These coefficient estimates were subsequently
128 used to predict AGB in relation to stand age, precipitation and temperature. Based on
129 our results we then inferred an answer to our second question, relating to thresholds in
130 forest maturity. If interactions between climate and forest age were considered
131 important we determined that it was not possible to set a global age threshold by which
132 to define mature forests without considering their local characteristics.

133 It is important in analyses that combine data from multiple sources to determine
134 whether the data being used show signs of bias that might influence a study's results.
135 One example of such a bias is if data is not representative of an overall population
136 which it seeks to represent (Tuck et al., 2014). In the case of our study such bias may
137 be caused by an over or underrepresentation of particular forest ages, certain climates
138 and particular geographic regions. To test for this we (i) examined the age distribution of
139 forests using histograms; (ii) determined the climate space encompassed by the sites
140 used in this study compared to that occupied by forests globally; (iii) and examined the
141 geographical distribution of study sites. For the comparison of the forest climate space
142 we binned the data on precipitation into bins of 200 mm and mean annual temperature
143 into bins of 1°C. We then used a global grid with a resolution of 0.5 decimal degrees to
144 identify where forest was present based on the globcover 2009 dataset (Bontemps et
145 al., 2011). We determined the mean total precipitation and mean annual temperature in
146 each grid cell where forest was present using WorldClim (Hijmans et al., 2005). We then
147 compared the percentage of our data contained within each temperature and
148 precipitation bin with the percentage area of global forests contained in each bin.
149 All analyses were conducted in R version 3.2.1 (R Development Core Team, 2008) and
150 with models producing using the nlme (Pinheiro et al., 2015) and MuMIn packages
151 (Barton, 2015).

152

153 Results

154 Our model averaged results indicated positive relationships between AGB and
155 the logarithm of forest age (slope=0.24, SE=0.02, $P<0.001$), mean annual temperature
156 (slope=0.18, SE=0.04, $P<0.001$) and total annual precipitation (slope=0.32, SE=0.04,
157 $P<0.001$). Importantly, the slope related to forest age increased with mean annual
158 temperature (interaction term=0.06, SE=0.02, $P=0.018$). In addition, the positive effect
159 of total annual precipitation on AGB was reversed at higher temperatures (interaction
160 term=-0.12, SE=0.02, $P<0.001$). The interaction term between total precipitation and
161 forest age was not significant (-0.02, SE=0.02, $P=0.439$). Models included in the model
162 averaging process had reasonable descriptive power with conditional R^2 values varying
163 from 0.18 to 0.24. Predictions using model averaged coefficients did not show a clear
164 plateauing of AGB at any age (Figure 1), contrary to the findings of Liu et al. (2014).
165 These models also showed much greater descriptive power than those of Liu et al.
166 (2014), as models containing only age, precipitation and temperature were poorly
167 supported ($\Delta AICc=112.41$, 114.17 and 139.99 respectively).

168 There are clear biases in the dataset we used for this analysis. Tropical and
169 Southern Hemisphere forests are under-represented, relative to the area which they
170 cover (Figure 2a). While the data we used also covered a wide range of climatic
171 conditions there was a bias towards forests found in relatively cold, dry climates and
172 away from warmer, wetter climates (Figure 2b). The dataset we used was also clearly
173 biased towards younger forests, containing relatively few stands > 250 years of age
174 (Figure 2c) (although we note that the ages of many tropical sites appear to be
175 uncritical reference to Luysaert et al. (2007) , where the ages of the trees in a range of
176 minimally disturbed tropical forests was reported as being between 100-165 years old).

177

178 Discussion

179 Our results indicates that climate and forest age interact to determine
180 aboveground biomass density in global mature forests. This study is, to our knowledge,
181 the first to quantitatively show this interaction. Previous studies have shown that
182 biomass accumulation rate of regrowing forests depend on precipitation and

183 temperature (Johnson, Zarin & Johnson, 2000; Anderson et al., 2006; Anderson-
184 Teixeira et al., 2013) and that climate is an important constraint of biomass in mature
185 forests (Stegen et al., 2011). Our work builds on these suggesting that biomass of
186 mature forests depends on their age, as well as the climate they experience. We show
187 that forests experiencing higher temperatures accumulated biomass more rapidly, in
188 agreement with previous studies (Anderson-Teixeira et al., 2013). However, our results
189 also suggested that there is little interaction between forest age and annual
190 precipitation. Taken together these results support the findings of Anderson et al. (2006)
191 that, on a global scale, temperature differences drive the majority of differences in rates
192 of biomass accumulation. However, reality is likely to be more complex than our results
193 suggest. For example, Stegen et al. (2011) suggested that water deficits resulting from
194 interactions between precipitation and temperature are a primary limiting factor of the
195 biomass that can be attained by mature forests.

196 In contrast to the recent study of Liu et al. (2014) we found that it is not possible
197 to set a threshold age at which forests can be considered mature. Since our results
198 indicated that aboveground biomass density was best determined by models that
199 included interactions between climate and stand age, any threshold age for mature
200 forests must be determined at a relatively local scale. Accumulation of biomass varies
201 locally with soil nutrient content and drainage, distance to other forest patches and
202 previous land-use (Norden et al., 2015). In addition, local effects such as priority effects,
203 herbivore density, invasive species, pathogen presence and edge effects can all result
204 in unpredictable successional pathways (Norden et al., 2015). As such, predicting the
205 age at which forests can be considered mature may be difficult, even at a local scale.

206

207 **The need for better data**

208 Though our analysis is an improvement on that performed by Liu et al. (2014) we
209 were limited by the representativeness of the data used. These data comprised few
210 tropical forest sites, were biased towards relatively cold, dry forests and very few forests
211 >250 years of age were included in the dataset. The lack of data from tropical forests
212 limits the generality of this analysis meaning that we have little confidence about
213 extrapolating our results to the tropics. This is particularly important as tropical forests

214 store approximately one third of global terrestrial carbon (Dixon et al., 1994) and appear
215 to be increasing in biomass (Baker et al., 2004; Lewis et al., 2009). As such, our
216 analysis and that of Liu et al. (2014) can say nothing about whether the recent
217 increases in biomass in apparently mature tropical forests may be a result of recovery
218 from past disturbances as Liu et al. suggested. The relative lack of data for forests >250
219 years of age in our study limits our conclusions, given that forests are often thought to
220 take 100-400 years to reach maturity (Guariguata and Ostertag 2001).

221 Critically, the setting of any threshold requires accurate aging of forests. This is
222 not a trivial task. In mature forests trees are recruited as other die, creating a complex
223 patchwork of differently aged trees (Chazdon, 2014). As such, defining the age of a
224 forest using the oldest tree (as studies that we used data from did) will likely only be
225 accurate in relatively young forests where tree ages do not differ greatly. However, in
226 mature forests where all pioneer individuals have been replaced, the age of the oldest
227 tree no longer provides a useful determinant of forest age. Thus, the precision of our
228 estimates for younger forest are undoubtedly greater, and more useful, than for older
229 forests. Furthermore, as most tropical trees lack annual growth rings, ¹⁴C dating is the
230 only feasible way to currently age most tropical trees and this is prohibitively expensive
231 in many cases.

232

233 **Problems with defining mature forests**

234 While in the future it may be possible to determine at what age forest biomass
235 becomes relatively stable, we advise against using this as a definition of forest maturity
236 for three reasons. Firstly, while carbon storage in the form of biomass is important from
237 the perspective of alleviating the impacts of climate change, it tends to recover relatively
238 quickly. In tropical secondary forests, community composition of tree species can take
239 >150 years to recover, with biomass recovering in approximately 100 years (Martin,
240 Newton & Bullock, 2013). Thus, while biomass accumulation is important, using it alone
241 to define forest successional stage may lead to forests being classified as mature, when
242 they are still undergoing the latter stages of succession.

243 Secondly, though mature forests can appear to be relatively stable when
244 observed at a single point in time, they never reach equilibrium. Over decadal time

245 scales even apparently mature forests rarely show stable biomass (Valencia et al.,
246 2009), and are influenced by changes in climate and changes in local land use. Thirdly,
247 old-growth forests are defined as forests which do not contain any individual trees that
248 colonised immediately following allogenic disturbances (Chazdon, 2014). As such
249 forests that contain remnant cohorts of long-lived pioneer species should be considered
250 as late successional rather than old-growth forests (Chazdon, 2014). Thus, examining
251 changes in biomass is likely to be of little use in separating late successional forests
252 such as these from true old-growth.

253

254 **The future of forest biomass assessment**

255 The results of this study and the work by Liu et al. (2014) highlight that better,
256 more spatially representative data is needed in order to understand the relationship
257 between forest biomass and climate at a global scale. To improve this knowledge
258 biomass data such as those used in this study, and from long term monitoring plots, are
259 being collected across the globe (Anderson-Teixeira et al., 2015; Brienen et al., 2015).
260 Although ease of data accessibility can vary, much is freely available (e.g.
261 <https://www.forestplots.net/>) and its use would substantially strengthen the conclusions
262 of studies such as ours.

263 Comprehensive global monitoring of spatial variation in biomass is only possible
264 through the use of remote sensing techniques. Vegetation indices such as the
265 normalized difference vegetation index (NDVI) are now available for over multiple
266 decades and have frequently been used as proxies to calculate biomass (e.g. Dong et
267 al., 2003). Models of aboveground biomass using lidar estimates of forest height and
268 structure are even more accurate than those using optical and spaceborne lidar data.
269 These improved models have recently allowed the production of pan-tropical maps of
270 forest carbon stocks (Saatchi et al., 2011; Baccini et al., 2012), although uncertainty
271 remains in these maps, particularly in areas with little field data (Mitchard et al., 2013).
272 To resolve many of these issues, the European Space Agency will, in around 2020,
273 launch the BIOMASS mission, which is specifically designed to measure aboveground
274 forest biomass and height at a spatial resolution of 200 m (Le Toan et al., 2011). This
275 instrument will provide unprecedented data on the spatial variability of forest biomass

276 on a global scale, and combined with ground-based measurements will allow for a much
277 more precise understanding of the relationship between forest biomass and climate.

278

279

280 **Tables**

281

282 **Table 1 - Characteristics of studies used in this paper**

283

Reference	Mean annual temperature (°C)	Mean annual precipitation (mm)	mean forest age (years)
(Bondarev, 1997)	-13.3	290	190
(Liu et al., 2011)	13.6	1235	87
(Chang et al., 1997)	-3.7	347	204
(China's Forest Editorial Committee, 1999)	-1.0	470	216
(Feng, Wang & Wu, 1999)	9.0	850	350
(Hudiburg et al., 2009)	7.8	2276	423
(Kajimoto et al., 2006)	-9.8	610	158
(Keeton et al., 2010)	7.0	800	217
(Keith, Mackey & Lindenmayer, 2009)	10.7	1593	500
(Liu et al., 2014)	-3.2	596	163
(Luo, 1996)	5.2	889	130
(Luyssaert et al., 2007)	7.3	1204	162
(Ma et al., 2012)	-0.1	618	137

(Tan et al., 2011)	11.3	1840	300
(Zhou et al., 2002)	-4.7	446	149
(Zhu et al., 2005)	-2.0	459	84

284

285

286

287

288 **Table 2 - Candidate mixed effect models for explaining global forest carbon**289 **density. A=Age, T=Temperature, P=Precipitation**

290

Formula	Model rank	df	log likelihood	AICc	Δ AICc	weight
A+T+P+A*T+T*P	1	10	-305.02	630.44	0	0.56
A+T+P+A*T+T*P+A*P	2	11	-304.61	631.7	1.26	0.3
A+T+P+T*P	3	9	-307.74	633.81	3.37	0.1
A+T+P+T*P	4	10	-307.74	635.88	5.44	0.04
A+T+P+A*T	5	9	-318.73	655.79	25.35	<0.01
A+T+P+A*T+A*P	6	10	-318.43	657.25	26.82	<0.01
A+T+P+A*P	7	9	-319.98	658.28	27.85	<0.01
A+T+P+A	8	8	-321.03	658.32	27.88	<0.01
A+P	9	7	-329.94	674.08	43.64	<0.01
A+P+A*P	10	8	-329.74	675.73	45.3	<0.01
A+T+A*T	11	8	-333.58	683.42	52.98	<0.01
A+T	12	7	-335.71	685.63	55.19	<0.01
T+P+T*P	13	8	-350.23	716.72	86.28	<0.01
T+P	14	7	-363.42	741.04	110.6	<0.01
A	15	6	-365.35	742.84	112.41	<0.01

P	16	6	-366.23	744.61	114.17	<0.01
T	17	6	-379.14	770.43	139.99	<0.01
Null model	18	5	-395.95	802.01	171.57	<0.01

291

292 **Link to R-scripts used for analysis:**293 https://github.com/PhilAMartin/Liu_reanalysis

294

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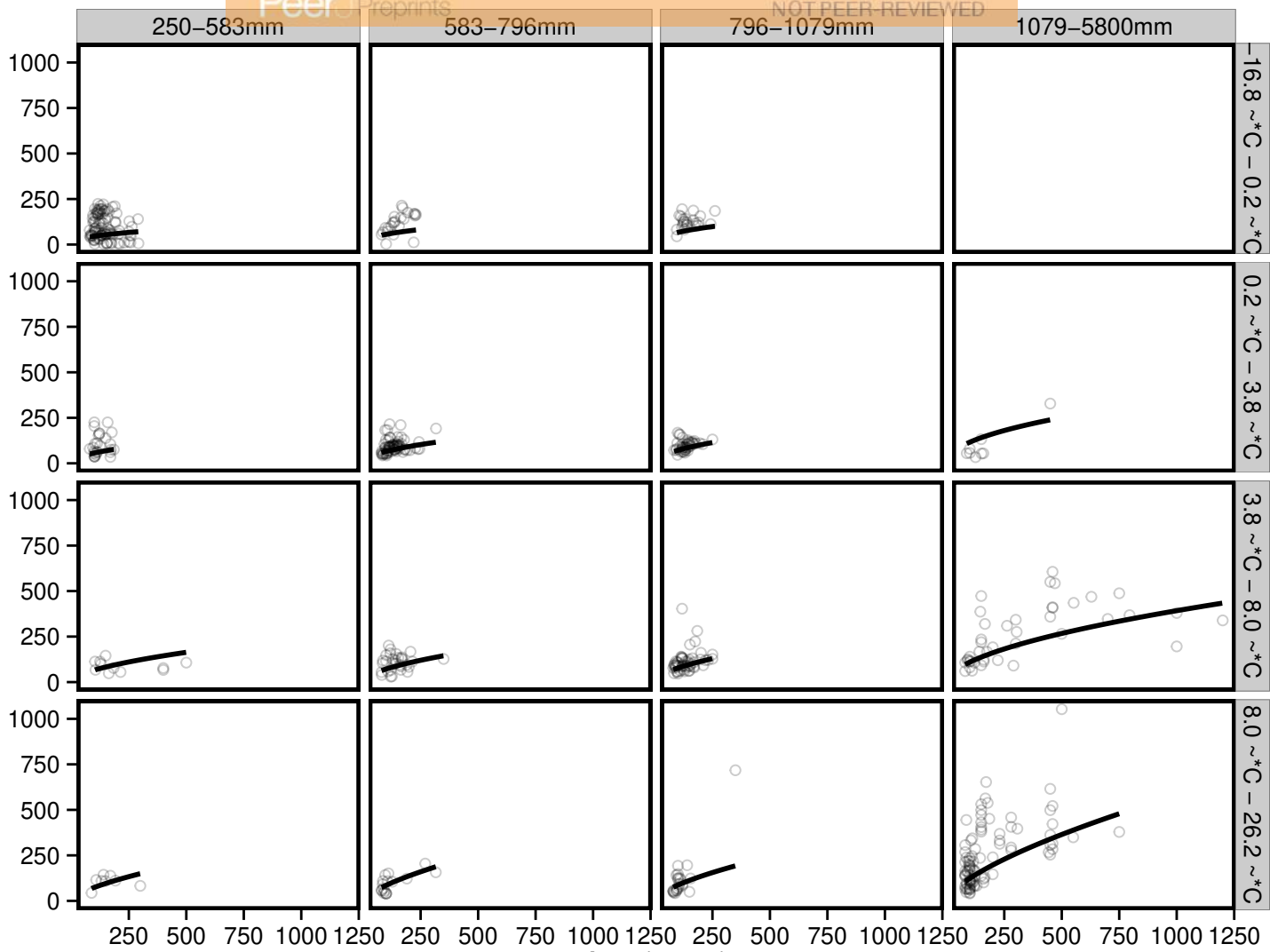
Figure 1(on next page)

Image of influence of age and climate on forest aboveground biomass

Relationship between forest age and aboveground biomass for differing climate spaces.

Panels represent binned mean annual temperature (rows) and total annual precipitation (columns). Bins represent quartiles so that each bin contains a similar number of data points. Points represent individual sites and solid lines predictions from model-averaged coefficients of models with a $\Delta AICc \leq 7$.

Aboveground biomass (Mg ha⁻¹)



Age (years)

2

Image showing potential biases in the dataset we used

Potential biases associated with the dataset we used for this study (a) - Spatial distribution of sites used in this study, showing lack of tropical sites. Green areas represent forest, dots sites used in this study. Dots are partially transparent to give an impression of site density. (b) - Climate space represented by data used in this study and forests globally (climate data from (Hijmans et al., 2005), forest cover data from (Bontemps et al., 2011) . Darker pixel colour indicates greater density of data, indicating a bias towards forests with low precipitation and low mean annual temperature. (c) - Distribution of sites used in this study by site age, showing a bias towards forests <250 years old.

