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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.

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

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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
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46 also clearly biased towards forests <250 years of age. Our analysis suggests that there
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52 being generated by long-term monitoring networks and satellite based observations.

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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

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

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

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

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

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

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

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

Methods

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

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

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

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

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

Results

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

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

Discussion

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

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

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

The need for better data

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

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

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

Problems with defining mature forests

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

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

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

The future of forest biomass assessment

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

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

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Tables

Table 1 - Characteristics of studies used in this paper

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

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288 **Table 2 - Candidate mixed effect models for explaining global forest carbon**

289 **density. A=Age, T=Temperature, P=Precipitation**

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Formula	Model rank	df	log likelihood	AICc	$\Delta AICc$	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

Link to R-scripts used for analysis:

https://github.com/PhilAMartin/Liu_reanalysis

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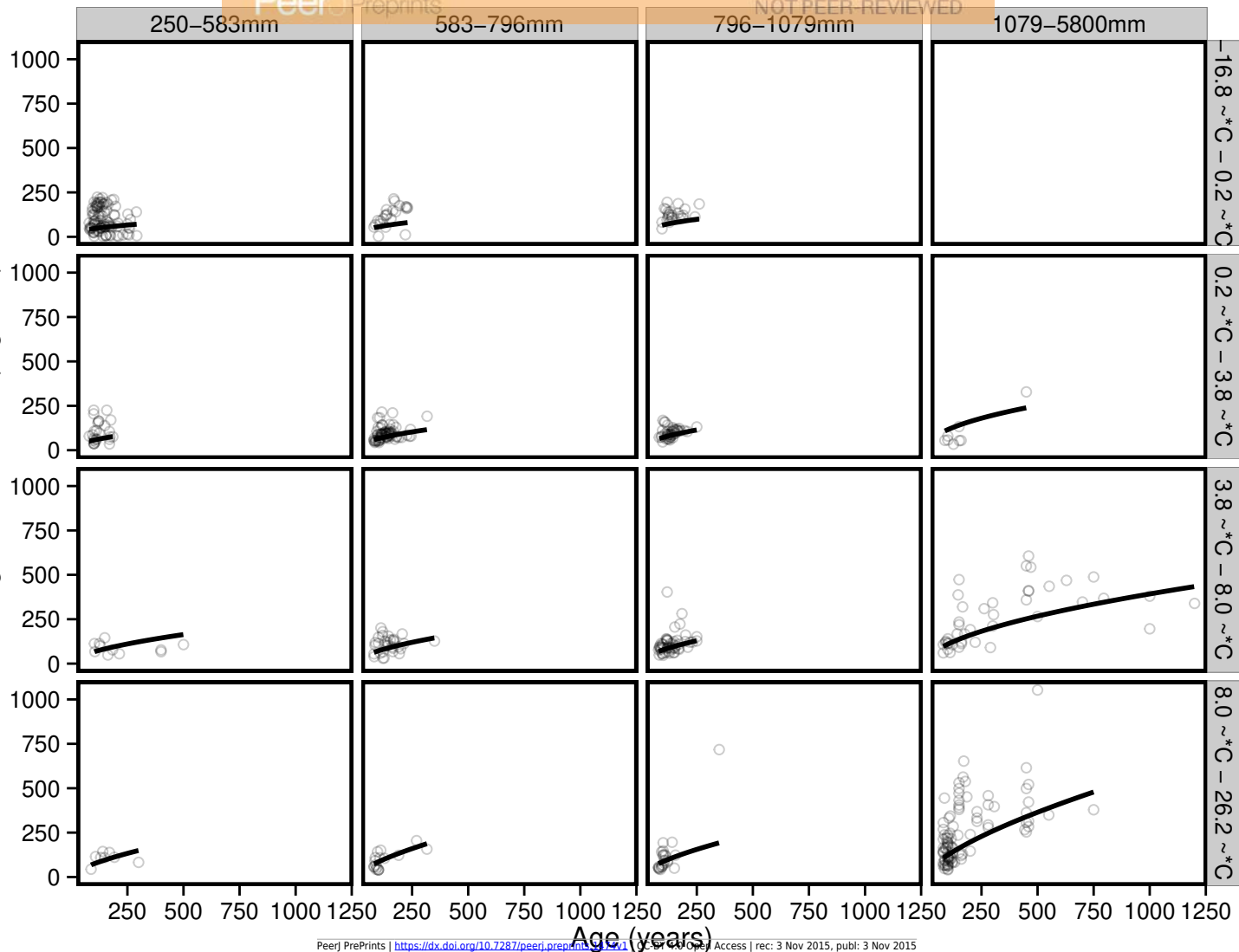
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Figure 1(on next page)

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)



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.

