Topographic and biotic factors determine forest biomass spatial distribution in a subtropical mountain moist forest

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ABSTRACT

A mechanistic understanding of factors driving forest biomass will help stewards manage carbon storage in forests. We examined the potential biotic and topographic factors in regulating subtropical forest carbon storage. We utilized data from the Badagongshan 25 ha (500 × 500 m) forest dynamics plot to examine the factors regulating the spatial variation of large trees and forest biomass. We mapped forest biomass and large tree biomass distributions and applied variation partitioning analysis to examine a suite of topographic and biotic factors related to the distributions. The average biomass of the 25 ha plot is 252.7 Mg/ha but varied substantially from 39.16 to 1024.53 Mg/ha in the 20 × 20 m quadrats. Overall, large tree (diameter at breast height ⩾25 cm) density accounted for 71% of variation in forest biomass distribution. Variance partitioning showed that biotic, topographic and spatial factors altogether explained 64.8% and 57.5% of the variation in the distribution of forest biomass and large tree density, respectively. Fractions of variance explained by the convexity and topographic wetness index (TWI) were much larger than other topographic variables in both distributions. For biotic variables, stem density and wood specific gravity were important in predicting forest biomass and large tree density distributions. Both biomass and large tree density showed an increasing trend with increasing convexity, stem density and wood specific gravity, but decreased as TWI increased. Convexity and TWI explained more variation among topographic variables, indicating that water deficiency may play an important role in shaping the distribution of forest biomass and large tree density. In conclusion, the crucial relationship between forest biomass and large tree density distribution should attract more attention, and suggests a mechanistic control of forest carbon storage that may help provide options in forest carbon management.

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1. Introduction

A clear understanding of forest carbon balance and its driving forces at multi-scales is an essential step toward predicting effects of climate change and formulating policy on forest carbon management (Pan et al., 2011; Yu et al., 2014), but also is fundamental for benchmarking global land models (Luo et al., 2012). Forests have been shown to be carbon sinks in the Northern Hemisphere, but their status as sinks remains uncertain (Ciais et al., 1995; Lewis et al., 2009). Subtropical forests comprise a vast area in China

and have been recognized as important carbon pools and sinks (Fang et al., 2001; Yu et al., 2014). Overall forest cover is increasing rapidly due to natural regeneration and reforestation in China's subtropical forests in recent years. However, old-growth forests in this area, which always have high species diversity, are in an accelerated loss (Brandt et al., 2012). Therefore, there is a pressing need to quantify and monitor the magnitude of carbon storage or release during forest recovery (Holl and Zahawi, 2014), both for natural forests and plantations (Ruiz-Jaen and Potvin, 2011).

Mapping forest biomass spatial distribution is essential for reducing uncertainties in forest ecosystem carbon cycle models; it has been studied extensively on continental (Barredo et al., 2012) and global levels (Kindermann et al., 2008), but seldom been conducted at the local scale (McEwan et al., 2011; Meyer et al.,

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2013), especially in subtropical forest. Mapping forest biomass distribution with spatially-explicit information for each recorded individual can specifically describe biomass variance along a topographic gradient and detect fine scale relationships of potential factors influencing the distribution. In recent decades, a large number of forest dynamic plots have been established with standard sampling protocols in boreal, temperate, and tropical forest (Barredo et al., 2012). These plots range from 2 ha to 120 ha (mean size: 25 ha) in size and are appropriate to characterize the spatial distribution of forest biomass and examine the factors regulating forest carbon storage, and provide a platform for monitoring temporal change in biomass pools at larger scale (Anderson-Teixeira et al., 2015). Despite numerous studies linking environmental factors to above-ground biomass (AGB) (Laurance et al., 1999; Holl and Zahawi, 2014), there remains little information on belowground biomass and forest biomass spatial distribution.

Large trees have attracted considerable attention from ecologists in tropical and temperate forests, given their disproportionate importance to structure, function and dynamics in forest ecosystems (Lutz et al., 2012; McIntyre et al., 2015). Although only a small proportion of total abundance in a forest, large trees disproportionately possess much of the forest wood volume and biomass (Slik et al., 2013). Therefore, density of large trees may be a potential predictor in explaining the observed local to regional-scale differences of forest biomass (Paoli et al., 2008; Slik et al., 2010) and annual net change of AGB (Sist et al., 2014). Further, the proportion of biomass stored in large trees in mature forest can be tested as a criterion to assess potential carbon storage for forests in recovery stages (Brown et al., 1997). Additionally, some studies have found that large trees were vulnerable to climate change (e.g. drought stress (Slik et al., 2010)) and thus will potentially lead to loss of forest carbon as climate changes. Therefore, describing the distributions of large trees and seeking potential regulating factors is important to understand forest carbon storage.

Topography is a good predictor in forest ecosystems which usually relates to other variables that directly influence plant growth, such as soil type, soil water content, soil nutrients (Luizão et al., 2004), and light availability (Larsen and Speckman, 2004). Water tables in transition between slope and valley have been associated with topographic and soil factors (de Toledo et al., 2012), and more uprooted and snapped large trees were associated with valleys and steep slopes (Ferry et al., 2010); especially large trees were more prone to be uprooted on steep slopes. In this study, we introduced two topographic variables: topographic wetness index (TWI) and vertical distance from the channel network (VDCN) (Tarboton, 1997) that have not been previously used in forest biomass studies. These two variables are important in quantifying effects of topography on hydrological processes when hydrological data are lacking (Punchi-Manage et al., 2013). Rainfall is abundant in this area, so quadrats with better drainage may favor large tree survival (i.e. less likely to be uprooted). Therefore, we assume that these two variables could influence distributions of forest biomass and large trees.

Wood specific gravity is an important functional trait of tree species and can influences forest ecosystem carbon storage processes. Small shifts in average wood specific gravity could lead to large changes in forest carbon storage, which potentially contributes to climate change (Larjavaara and Muller-Landau, 2010). In an Amazonian forest, wood specific gravity accounted for a large part of the variance in above-ground biomass along an east–west gradient (Baker et al., 2004), but Stegen et al. (2009) found no consistent relationship between wood specific gravity and above-ground biomass across four Neotropical forests. Intuitively, species with different functional traits can coexist with each other and better partition resources, suggesting species-rich forests can increase the capacity of carbon storage in forest ecosystems (Kirby and

Potvin, 2007; McEwan et al., 2011). However, the influence of wood specific gravity and species diversity on subtropical forest carbon storage has seldom been examined.

The objectives of this study are to: (1) Estimate the forest biomass and map the spatial distribution of forest biomass in the Badagongshan (BDGS) 25 ha plot; (2) Evaluate how much spatial variation can be explained by the density of large trees; and (3) Identify topographic and biotic factors related to the spatial distribution of large trees and forest biomass in subtropical forests.

2. Materials and methods

2.1. Study sites description

Our study site is located in the Badagongshan National Nature Reserve (BNNR) in the North of Wuling Mountains, central China (29°46.041′ N, 110°5.248′ E). The forest in the BNNR is a typical old-growth subtropical evergreen broad-leaved forest that is well protected. Forest canopy height is about 15 m above the ground with little human disturbance in the core zone after the 1950s. This area is characterized as monsoonal humid subtropical climate; average annual precipitation is 2105 mm, mean annual temperature is 11.5 °C with a range from 0.1 in January to 22.8 in July, and average number of rain days is 176, comparable to tropical rainforest. These meteorological data were obtained at an elevation about 1300 m in the reserve. Terrain in this area is relatively complex and undulate characterized by steep slopes, deep valleys, and flat tops.

The BDGS forest dynamic plot (Fig. 1), a 25 ha (500 × 500 m) plot in the core zone of BNNR, was established in 2011 as a node of Chinese Forest Biodiversity Monitoring Network (http://www.cfbiodiv.org/). Elevation in BDGS plot ranges from 1369.6 m to 1470.9 m and slopes of the 20-m quadrats range from 3.5° to 68.5°. Within the plot, all standing woody stems with DBH ⩾ 1 cm were tagged, mapped, measured, identified to species and geographic coordinates documented following standard field procedures (Condit, 1998); liana and bamboo individuals were not included in this inventory. According to the census, there were 238 tree species belonging to 114 genera and 53 families. A total of 186,556 stems were counted, and the average DBH of BDGS plot trees was 5.41 cm, while DBH of the largest tree was 117 cm. Mean stem density was 7418 individuals per ha and mean basal area was 164.5 m^2 ha^{-1}. Dominance of major species in decreasing order of basal area were *Cyclobalanopsis multinervis*, *Rhododendron stamineum*, *Fagus lucida Rehder*, *Cyclobalanopsis gracilis*, *Sassafras tzumu*.

2.2. Height–Diameter allometric relationships and wood specific gravity

AGB models used in this study require height data for each stem, but measuring individual heights was not practical. Instead, we measured a subset of individuals' heights and developed Height–Diameter allometric models for 25 dominant species and a community level mixed-species model to estimate height data for each stem in the plot. Choice of species for height measurement was based on importance values ((relative abundance + relative total area)/2) from inventory data. Height was measured using a measuring pole for trees below 15 m and a Vertex IV (http://www.haglofcg.com) for taller trees. The Vertex IV Hypsometer uses ultrasound to measure distances; heights are calculated trigonometrically using angle. In all, 1810 individual heights were collected for 60 dominant species: at least 20 individuals for each species. We developed Height–Diameter allometric models with nonlinear equations for 25 dominant species and a
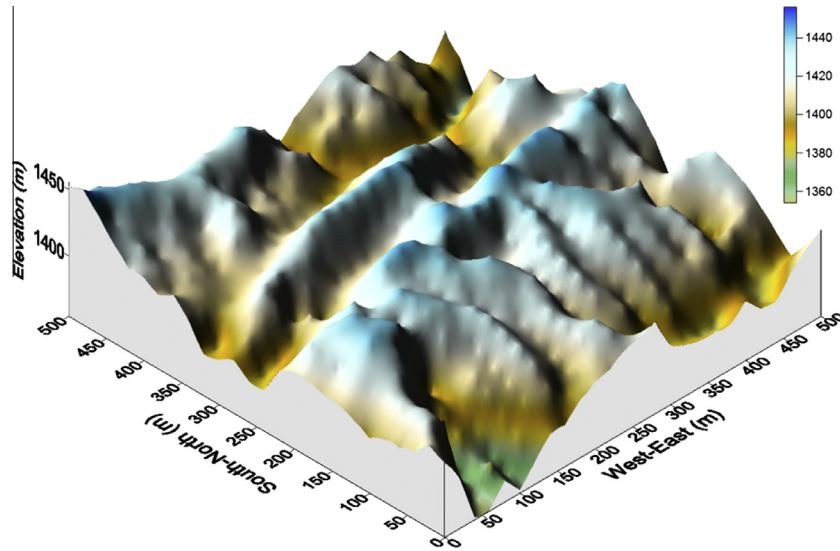
Fig. 1. Three-dimensional surface topographic map of 25-ha (500 × 500 m) Badagongshan forest dynamic plot (After Wang et al., 2014a.)

mixed-species model, then selected the best model shape for all candidate models. Because model shape between DBH and H was not consistent among species (Feldpausch et al., 2011), five types of non-linear candidate models were used to predict tree height: (1) log-linear; (2) log–log; (3) Michaelis–Menten function; (4) Weibull function; and (5) Gompertz function. Relative squared error (RSE) and the Akaike information criterion (AIC) were used to evaluate candidate models. Model comparison based on these statistics showed that log–log models performed better than the remaining four models in 15 of the 26 models, so we selected the log–log model shape as the best model to fit our data for all 25 species-specific models and the mixed-species models (Table A1).

For the wood specific gravity for each species, we collected 147 samples of 41 species, at least 5 samples each of the 25 dominant species, and calculated the mean wood specific gravity for these species. For remaining species, we calculated a mean value for all species together (Table B1). We used these data sets to estimate forest biomass for each stem in the plot.

2.3. Forest biomass estimate and mapping

For BDGS plot, we used measurements of diameter, total tree height and wood specific gravity to estimate forest biomass. A suite of models were developed to estimate forest above-ground and belowground biomass of the BDGS plot. Models developed were based on 147 sampling trees from 25 subtropical common species, and these sampling trees were selected from around the reserve. Results of model comparison between the models used in this study and other subtropical models showed that these models give a robust estimate for the BDGS plot (Xu et al., accepted for publication).

Models used in this study were as follows:

$$AGB = \exp(-2.334 + 2.118\ln(D) + 0.5436\ln(H)$$
$$+ 0.5953\ln(\rho)); \quad R^2 = 0.95. \tag{A.1}$$

$$BGB = \exp(-2.80346 + 2.0441\ln(D)); \quad R^2 = 0.924 \tag{A.2}$$

DBH is the tree diameter at breast height (cm), H is the total tree height (m), and ρ is wood specific gravity (g/cm^3).

A correction factor (CF) was used to unbias underestimates when models were back log-transformed; we calculated the CF using RSE values from each model based on the Eq. (A.3). The CF

for the AGB model (with height data), AGB model (without height data) and the BGB model was 1.015, 1.022 and 1.061, respectively.

$$CF = \exp\left(\frac{RSE^2}{2}\right) \tag{A.3}$$

2.4. Topographic and biotic factors

The BDGS plot was systematically divided into 625 quadrats (20 × 20 m). For each quadrat, we estimated six topographic factors: terrain convexity, slope, aspect, elevation, TWI and VDCN. The first four topographic factors were computed following the method in Wang et al. (2014b); another two topographic variables (TWI and VDCN) were derived using the SAGA GIS software (http://www.saga-gis.org). TWI is the ratio of upslope area for each quadrat to the local slope of that quadrat following Tarboton's Deterministic Infinity Method (Tarboton, 1997). The VDCN is the vertical distance above the channel network in the plot (Tarboton, 1997; Wang et al., 2014b). Lacking direct hydrological data, we used these two indexes (TWI and VDCN) to represent hydrologic processes and as a proxy for plant-available soil moisture (Punchi-Manage et al., 2013).

For each quadrat, we calculated the basal area weighted mean value of wood specific gravity (WSG). We used basal area, instead of biomass, to weight wood specific gravity because wood specific gravity was an input variable in the AGB model (Slik et al., 2013). Then we calculated species richness and density of stems for all 625 quadrats. We selected wood specific gravity, species richness, and stem density as biotic factors to examine the relationships to density of large trees and forest biomass.

2.5. Statistical analyses

Simple definitions of large trees in the literature varied, studies chose arbitrary thresholds such as DBH ⩾ 60 cm (Sist et al., 2014), 70 cm (Slik et al., 2013) or 30 cm (DeWalt and Chave, 2004), thresholds not favorable for this study. In the BDGS plot, only 31 individuals had DBH ⩾ 70 cm and only 105 individuals had DBH ⩾ 60 cm. In this study, the appropriate boundary for distinguishing between large and small trees was detected using total biomass with different sampling scales (0.5%, 1%, 2.5% and 5% of stems with maximum DBH). The analysis showed that coefficient

Table 1
Mean forest biomass (Mg/ha^{-1}) (±SD) values (smaller trees and big trees) of the BDGS plot at different sampling scales.

Percentage (%)	DBH (cm)	Forest biomass smaller trees	CV	Forest biomass large trees	Sample size
0.5	39.61	190.35 ± 80.83	0.4246	62.32 ± 71.76	625
1	33.1	162.04 ± 68.53	0.4229	90.64 ± 79.47	625
2.5	24.3	115.132 ± 46.71	0.4057	137.54 ± 90.45	625
5	17.95	85.24 ± 37.74	0.4427	167.74 ± 99.78	625

of variation (CV) for 2.5% of stems was lowest among all four scales (Table 1). The DBH for 2.5% of stems was 24.3 cm, so we selected 25 cm as a logical DBH threshold to distinguish large and small trees (Table C1). A simple linear regression was conducted to test the strength of the relationship between forest biomass and the density of large trees (DBH ⩾ 25 cm).

In order to quantify the relative contribution of topographic and biotic factors to the spatial distribution of large trees, a variance partitioning method with multiple regressions was used to separate the pure and shared fractions for each group of factors (Borcard et al., 1992). Specifically, we estimated the fraction of spatial variance in large tree density explained by six topographic variables (convexity, slope, aspect, elevation, TWI and VDCN), three biotic variables (WSG, richness and density) and two spatial variables (x and y coordinates). Due to the spatial autocorrelation of large tree density and the inherent interrelation among biotic factors and topographic factors, variation partitioning is the prevailing method to separate the pure and shared proportions explained by each set of factors.

To account for spatial autocorrelation, a principal coordinate neighbor matrix (PCNM) was applied to assess the spatial variation on a 20 m × 20 m scale. Eigenfunctions were computed using a principal coordinate analysis (PCoA) from a truncated Euclidean distance matrix, and then filtering negative values because only positive values can be used as predictors in regression and canonical analyses. Forward selection was used to select the significant ($P < 0.05$ after 999 simulations) biotic, topographic and PCNMs, and adjusted R^2 was computed to explain pure effects and joint effects for each group of factors.

All statistical analyses were conducted in R software (R Development Core Team, 2012). Community wood specific gravity was calculated by using the FD package (Laliberté et al., 2010). The 'pcnm' function in the vegan package (Oksanen et al., 2007) was used to create the PCNM variables and the 'forward. sel' function in the 'packfor' package (Dray et al., 2009) was used to perform the forward selection. Variation partitioning analyses were computed using the 'varpart' function in the vegan package (Oksanen et al., 2007).

3. Results

Total forest biomass ranged widely from 39.16 to 1024.53 Mg/ha with a mean of 252.7 ± 108.7 Mg/ha in the 20 × 20 m quadrats of the BDGS plot; the maximum value of biomass was 26 times of that the minimum. In order to facilitate comparison with other studies, we estimated AGB of the BDGS plot at 214.3 ± 94.3 Mg/ha. Biomass among different diameter ranges followed a normal distribution (Shapiro–Wilk test; $p = 0.25$), and trees in the 20–25 cm DBH range accounted for more biomass than other diameter classes (Fig. 2). Although trees from 1 to 5 cm DBH accounted for 68.78% of stems, they accounted for only 3.35% of biomass.

Forest biomass and large tree biomass were highly variable in the BDGS plot (Fig. 3a and b). However, biomass changes were related to topography; the ridges always had higher biomass and the valleys lowest. Thus, topography, especially convexity may
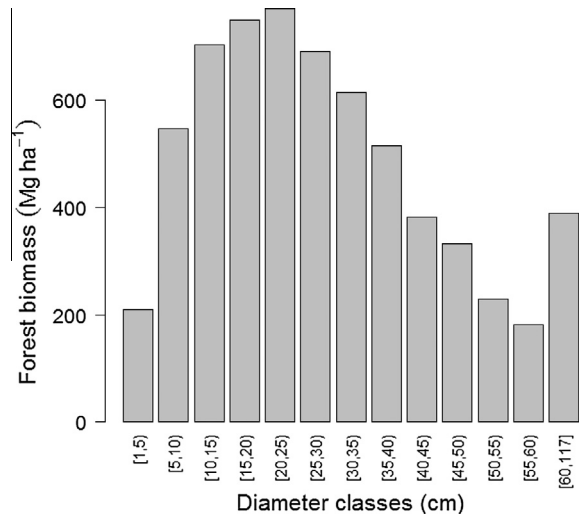

Fig. 2. Distribution of forest biomass among diameter classes in the Badagongshan plot.

play an important role in regulating the spatial distribution of forest biomass (Fig. 3a). Further, the spatial pattern of forest biomass and large tree biomass were highly overlapping. Patches with larger biomass always had higher densities of large trees (Fig. 3b).

Overall, large tree (DBH ⩾ 25 cm) density accounted for 71% of variation in forest biomass (Fig. 4; liner regression results: $y = 0.03x − 0.6785$; $R^2 = 0.7102$, $p < 0.001$).

Variance partitioning of forest biomass showed that 64.8% of the variation was explained by biotic, topographic and spatial factors together. Specifically, 43.3% of the variation was explained by biotic variables, 41.9% by topographic variables and 52% by spatial variables (76 PCNMs) (Fig. 5a). Among seven topographic variables, convexity and TWI were significant ($p < 0.01$) and explained 38.1% and 4% of biomass spatial variance, respectively. Stem density and WSG were significant ($p < 0.01$) biotic variables that explained 39.6% and 3.8% of biomass spatial variance, respectively (Table 2). Scatter plots of four significant predictors of biomass showed an increasing trend with increasing convexity, stem density and wood specific gravity, but decreasing trend as TWI increased (Fig. 6a–d).

Variance partitioning of the density of large trees showed that 57.5% of variance was explained by biotic, topographic and spatial factors together; 27.4% of variance was explained by biotic variables, and 32.3% and 47.3% of variance was explained by topographic and spatial variables (59 PCNMs), respectively (Fig. 5b). Factors related to large tree biomass distribution matched those of forest biomass. Convexity and TWI were significant ($p < 0.01$) and explained 30.7% and 1.8% of large trees distribution variance, respectively. Stem density and WSG were significant ($p < 0.01$) for biotic variables and explained 22.1% and 5.5% of large tree distribution variance, respectively (Table 2). Scatter plots showed that the same trends as between positive environment variables and large tree biomass, but the trends were not so obvious (Fig. 6e–h).

4. Discussion

4.1. Forest biomass in subtropical forest of China

One goal of this study was to estimate biomass density for the BDGS 25 ha plot, an old-growth subtropical evergreen and deciduous broad-leaved forest and compare the estimate with existing studies for the same forest type. Our estimate assumes that all biomass of each stem is located at the base of the tree. Lin et al. (2013)
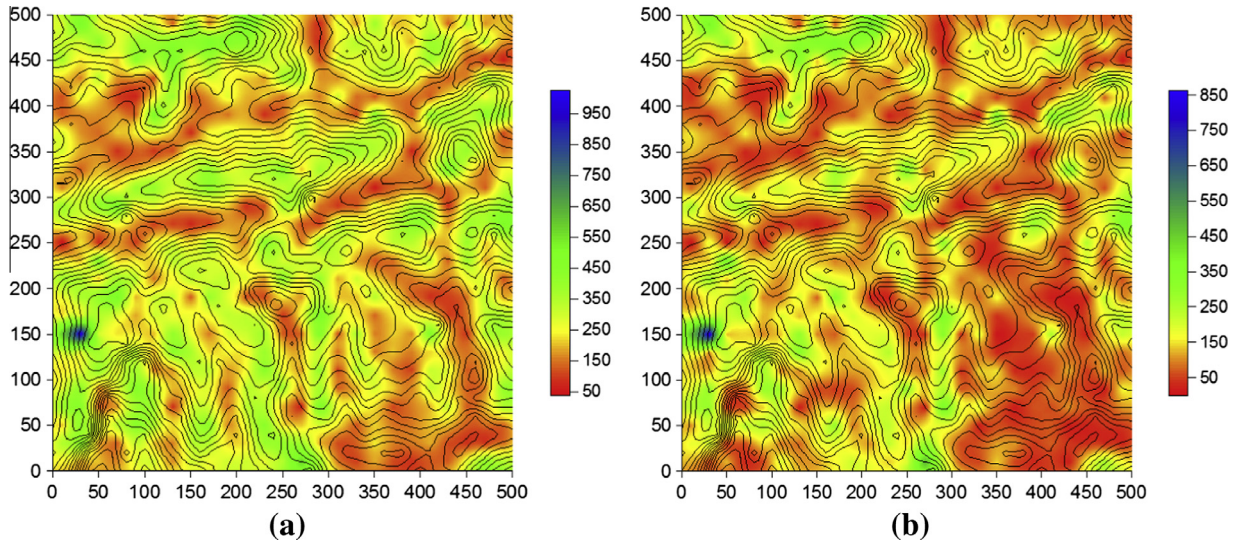
Fig. 3. Spatial distribution of forest biomass (Mg/ha) (a) and large trees biomass (DBH ⩾ 25 cm) (b) in the BDGS 25 ha plot. Contour lines in the map indicated elevation and the colors indicate biomass values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
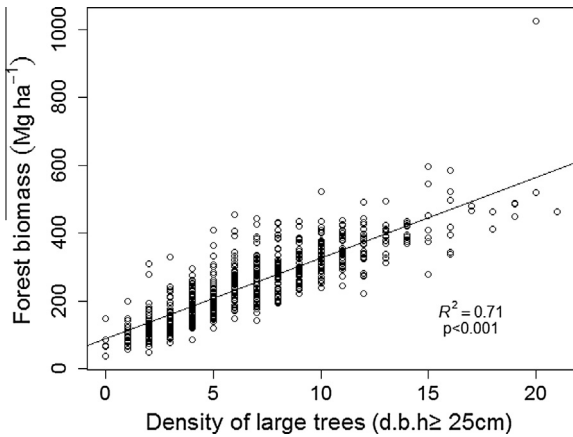

Fig. 4. Linear regression relationship between large tree density and forest biomass. The fitted line explained 71% of biomass spatial variance.

found a 4 ha sampling area effectively captured biomass spatial variances (error ±10%) in a 24 ha (400 m × 600 m) subtropical forest, so we believe our result from such a large sampling was a robust estimate for the same forest type in this area. A previous meta-analysis of subtropical forest biomass showed that AGB

ranged from 169 to 485 Mg/ha (Lin et al., 2012), but most of the estimates from these studies were based on only a few small and unrepresentative plots. According to the sampling method in Lin et al. (2013), only two of the 25 published studies met their criterion. To reduce sampling bias, combined with FDPs which have reported biomass in subtropical forest (McEwan et al., 2011; Lin et al., 2012), we suggest that the above-ground biomass value of subtropical old-growth evergreen broad-leaved forest in China is 210–230 Mg/ha.

4.2. Large trees as drivers of variation in forest biomass

In this study, the density of large trees accounted for more than 70% of spatial variation of forest biomass in subtropical forest, comparable to the results of Slik et al. (2013) which drew from three tropical forests. Thus, large trees capture most of the variance in biomass distribution in various geographic regions. Large trees stored 52.81% of forest biomass in the BDGS plot, but represented only 2.32% of stems larger than 1 cm DBH. Therefore, any factors that influence abundance and mortality of large trees likely plays an important role in carbon cycling in forest ecosystems. Forests with more large trees may have larger pools of stored carbon, and their preservation would protect most of the carbon pools in world forests (Lutz et al., 2012).
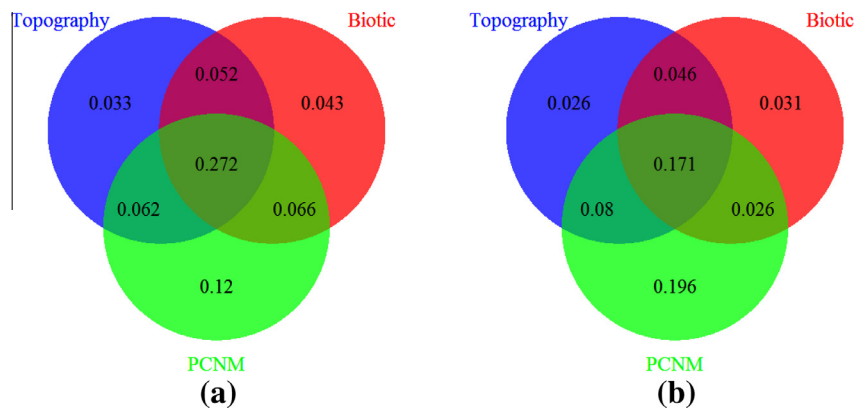

Fig. 5. Variance partition results of the forest biomass (a) and large tree density (b) against topographic, biotic and selected spatial variables.

Table 2
Topographic and biotic factors regulated the distribution of forest biomass and large tree density.

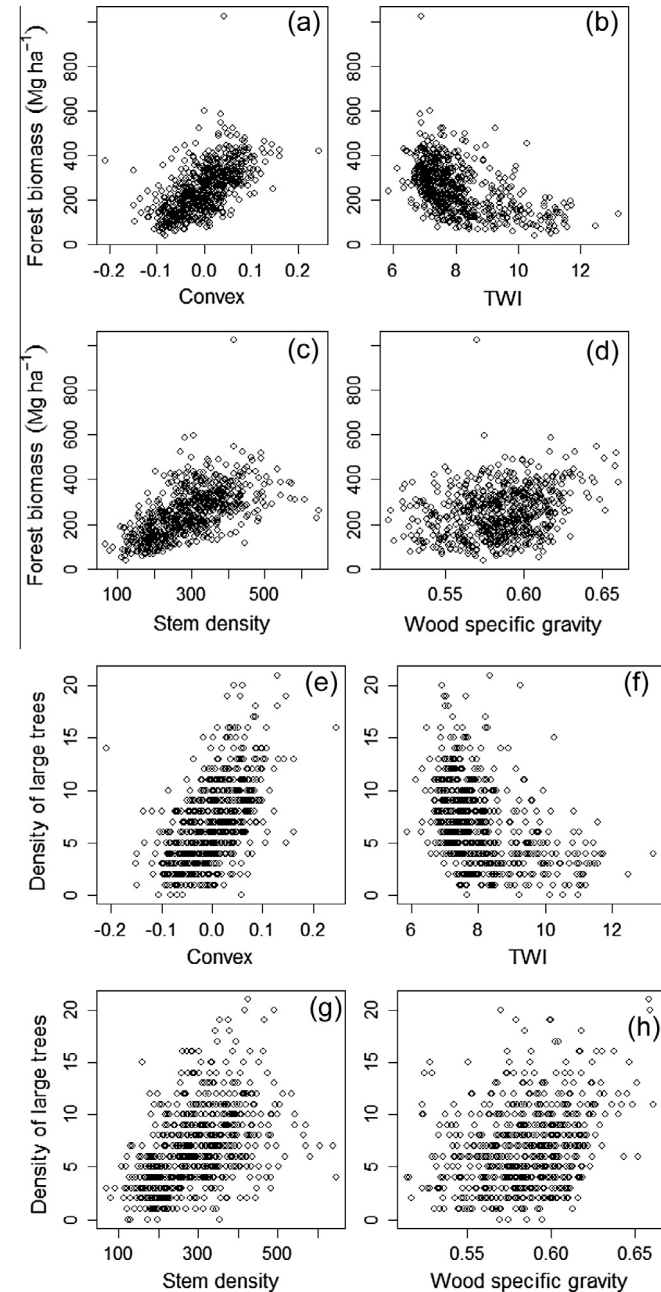| Factors	Forest biomass (Mg/ha^{-1})			Density of large tree		
	R^2	F	p value	R^2	F	p value
Topography						
Convex	0.381	382.7	<0001	0.307	276.3	<0001
TWI	0.04	42.99	<0001	0.018	16.64	<0001
Biotic factors						
Stem density	0.396	409	<0001	0.221	177	<0001
WSG	0.038	42.03	<0001	0.055	47.43	<0001

Fig. 6. Scatter plots demonstrating relationships of forest biomass (a–d) and density of large trees (e–h), and to four significant environmental predictors (convexity, TWI, stem density and wood specific gravity).

4.3. Topographic factors

Topography is a composite variable and can directly and indirectly affect the distribution of forest biomass, the density of large tree and stand dynamics due to plant physiological limitations (de Castilho et al., 2006; Baraloto et al., 2011). Species preference to a specified environmental variable would potentially affect forest biomass distributions. Therefore, the effects of topography on large trees and biomass distributions described here were not singly due to topography itself, but to several environmental factors related to topography (such as soil fertility and light condition). The BDGS plot provided explicit description of topographic conditions (six topographic variables) which we used as surrogates for environmental data (e.g. soil) lacking detail in this study. Partition variation results showed that topography explained 41.9% and 32.3% of variation in forest biomass and the density of large tree, respectively (Fig. 5a and b). Of the six topographic variables, convexity and TWI explained the majority of variation (Table 2).

In the BDGS plot, convexity indices varied from −0.21 to 0.245 with a mean of 0.00014, indicating an undulating topography in the plot. Forest biomass increased with convexity increasing; indicating that high biomass occurred in the quadrats with large convexity located the ridges, and ridges in the BDGS plot were relatively flat. McEwan et al. (2011) also found above-ground biomass was higher in quadrats with flat ridge terrain at a relatively low elevation in three FDPs. This result was further corroborated with above-ground biomass peaked on low ridges (Lin et al., 2012) and shallow slope in Marshall et al. (2012). Consistent results suggest that maximum biomass occurs on topographically flat ridges in subtropical forest.

Convexity is an important variable in regulating large tree density and indirectly affects biomass distributions. In the BDGS plot, large trees occurred more on the ridges than in the valleys (Fig. 6). Ferry et al. (2010) found more uprooted and snapped large trees along the steep slopes and in valleys perhaps due to shallow soil and steep slopes. Convexity also influenced dominant species' abundances and distribution in the BDGS plot (Wang et al., 2014a). For example, the ridge habitats were favorable for slower-growing species such as *Schima parviflora*, which can reach large sizes and thus large biomass in this area. However, heterogeneity of valley topography was greater (exposed large rocks and small streams are common), the shrub species *Hydrangea strigosa* and *Ficus heteromorpha* were common on down slopes and valley bottoms. Due to frequent disturbances, such as falling trees and streams flooding in the rainy seasons, these areas had a relatively high density of juvenile pioneer species and overall lower forest biomass (Ferry et al., 2010).

In this study, TWI also displayed a negative relationship with forest biomass and large tree density. Areas with a low potential for water accumulation had a high probability of maintaining high forest biomass and more large trees (Fig. 6). During rainy seasons, the rainfall in this area is heavy and soils are saturated. If the rainfall rate exceeds the limit of soil can infiltration, surface runoff occurs and loosened soil particles are transported down the valleys. The different waterlogged soil conditions may influence tree survival of the ridges, slopes and valleys differently (Marshall et al., 2012). In the plot inventory, we found more uprooted large trees in the slopes and valleys, but standing dead trees were more common on the ridge perhaps due to dry soil conditions, this also been found in Ferry et al. (2010). TWI also influenced tree species distributions in the BDGS plot, a previous study showed that seven of the ten dominant species were significantly associated with TWI and VDCN (Wang et al., 2014b). These common species typically accounted for a large fraction of biomass.

4.4. Biotic factors

In the BDG 25 ha plot, stem density varied markedly among quadrats from 68 to 647 stems and explained 39.6% of biomass variance. Within a certain range, forest biomass and large tree density increased with stem density increasing, and then decreased (Fig. 6). Therefore, maximum forest biomass can be predicted in the area based on certain stems and more large trees. Paoli et al. (2008) found that soil fertility had a significant effect on stem density and aboveground biomass, but the same soil variables may have opposite effects on different size classes. Therefore, we speculated that the large variation in stem density and forest biomass could be partly explained by soil fertility. On fertile soils, relaxed nutrient limitations could facilitate tree growth and increase tree size and/or stem density, and thus lead to higher biomass: e.g. soil C: N ratio and soil texture coarseness were positively correlated to stem density in a study by Slik et al. (2010). However, forests on fertile soil may be more dynamic; tree mortality rate was high and lead to low biomass when the mortality rate was faster than growth rate (Russo et al., 2005). In addition, ter Steege et al. (2003) found that more productive forests always had relatively higher stem density. Therefore, future work is needed to explore the effect of soil factors on stem density and forest biomass.

Community average wood specific gravity (weight by basal area) explained part of the variation in the distribution of forest biomass and large tree density and showed positive correlations in both distributions. The community average wood specific gravity was also positively related to VDCN ($R^2 = 0.07$, $p < 0.001$) and convexity ($R^2 = 0.035$, $p < 0.001$). The results suggest that ridge quadrats with many large trees had higher community average wood specific gravity. Slik et al. (2013) speculated that this variance may due to species with wind-dispersed seed which needed large statures to dispersal seeds. In the BDGS plot, the dominant wind dispersal species were mostly *Acer*. However, it was still unclear how these wind-dispersed species influence biomass, so future work is needed to reveal the mechanism. In addition, wood specific gravity owing to its wide range also affected forest biomass and large tree density distributions (Chave et al., 2009). It should be noted that wood specific gravity is an important variable of AGB models to estimate forest biomass, but the portion of variation explained by wood specific gravity is minimal, so the effect of this potential artifact may be limited.

Although species richness did not explain much variation in either forest biomass or large tree density in this study, it may still be an important issue in biodiversity and forest ecosystem function. A growing question in the literature is whether forests with high diversity are greater sinks sequestering more carbon. Ruiz-Jaen and Potvin (2011) found that biodiversity can substitute for allometry models to estimate forest biomass, and the proportion of large trees and forest biomass increases as species richness increases. In a recent study, species richness significantly predicted above-ground biomass in two forest plots (McEwan et al., 2011), which implies that complementarity among tree species for resource use may affect total accumulated forest biomass. In addition, discovering the relationship between tree species diversity and biomass is helpful for understanding biodiversity and ecosystem function (e.g. productivity), although the relationship between diversity and biomass is controversial (Vance-Chalcraft et al., 2010). The controversy in part from a pervasive unimodal pattern (Huston and DeAngelis, 1994) that a meta-analysis revealed was suitable in all conditions (Mittelbach et al., 2001). Confounding results suggest that more research is needed to explore the role of biodiversity regulating forest carbon storage.

5. Application for forest carbon management

This study suggested that an efficient way to improve forest carbon balance could be to preserve large trees from logging (Sist et al., 2014). As previously discussed, large trees play an important role in forest community structure and ecosystem nutrient cycling (Lutz et al., 2012). If these large trees were logged, a large amount of carbon would be released to the atmosphere. In general, small young trees may absorb more carbon than large older trees due to their more vigorous growth. However, a recent study showed that most species mass growth rate and carbon accumulation rate in tropical forest increased continuously with tree size (Stephenson et al., 2014). This indicates that large trees also fix carbon compared to small young trees. Large trees not only acted as carbon reservoirs but also actively carbon sinks in forest, and thus deserve more attention and protection. Thus, we need to understand old-growth forest processes and how they contribute to the regional forest carbon cycle.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.08.010.

References

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.-R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Glob. Change Biol. 21 (2), 528–549. http://dx.doi.org/10.1111/gcb.12712.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob. Change Biol. 10 (5), 545–562.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Nallartt, D., Mesones, I., Rios, M., Valderram, E., Fine, P.V., 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Glob. Change Biol. 17 (8), 2677–2688.

Barredo, J.I., San-Miguel-Ayanz, J., Caudullo, G., Busetto, L., 2012. A European map of living forest biomass and carbon stock. Reference Report by the Joint Research Centre of the European Commission. EUR–Scientific and Technical Research, 25730.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73 (3), 1045–1055.

Brandt, J.S., Kuemmerle, T., Li, H., Ren, G., Zhu, J., Radeloff, V.C., 2012. Using Landsat imagery to map forest change in southwest China in response to the national logging ban and ecotourism development. Remote Sens. Environ. 121, 358–369.

Brown, S., Schroeder, P., Birdsey, R., 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. For. Ecol. Manage. 96 (1), 37–47.

Ciais, P., Tans, P.P., Trolier, M., White, J.W.C., Francey, R.J., 1995. A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. Science 269 (5227), 1098–1102.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. http://dx.doi.org/10.1111/j.1461-0248.2009.01285.x.

Condit, R., 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer Science & Business Media.

de Castilho, C.V., Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Albertina, P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography. For. Ecol. Manage. 234, 85–96.

de Toledo, J.J., Magnusson, W.E., Castilho, C.V., Nascimento, H.E., 2012. Tree mode of death in Central Amazonia: effects of soil and topography on tree mortality associated with storm disturbances. For. Ecol. Manage. 263, 253–261.

DeWalt, S.J., Chave, J., 2004. Structure and biomass of four lowland Neotropical forests. Biotropica 36 (1), 7–19.

Dray, S., Legendre, P., Blanchet, G., 2009. packfor: Forward Selection with permutation (Canoco p. 46). R package version 0.0-7/r58. See <http://R-Forge. R-project. org/projects/sedar>.

Fang, J., Chen, A., Peng, C., Zhao, S., Ci, L., 2001. Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292 (5525), 2320–2322.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Pati ~ no, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonke, B., Taedoumg, H. E., Tan, S., White, L., Woll, H., Lloyd, J., 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8, 1081–1106. http://dx.doi.org/10.5194/bg-8-1081-2011.

Ferry, B., Morneau, F., Bontemps, J.D., Blanc, L., Freycon, V., 2010. Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. J. Ecol. 98, 106–116.

Holl, K.D., Zahawi, R.A., 2014. Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. For. Ecol. Manage. 319, 36–43.

Huston, M.A., DeAngelis, D.L., 1994. Competition and coexistence: the effects of resource transport and supply rates. Am. Nat., 954–977.

Kindermann, G.E., McCallum, I., Fritz, S., Obersteiner, M., 2008. A global forest growing stock, biomass and carbon map based on FAO statistics. Silva Fenn. 42 (3), 387.

Kirby, K.R., Potvin, C., 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. For. Ecol. Manage. 246 (2), 208–221.

Laliberté, E., Shipley, B., Laliberté, M.E., 2010. Package 'FD': Measuring Functional Diversity (FD) from Multiple Traits, and Other Tools for Functional Ecology.

Larjavaara, M., Muller-Landau, H.C., 2010. Rethinking the value of high wood density. Funct. Ecol. 24 (4), 701–705.

Larsen, D.R., Speckman, P.L., 2004. Multivariate regression trees for analysis of abundance data. Biometrics 60, 543–549.

Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin-de Merona, J.M., Chambers, J.Q., Gascon, C., 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. For. Ecol. Manage. 118 (1), 127–138.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., K, M-N.D., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J. C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., Woll, H., 2009. Increasing carbon storage in intact African tropical forests. Nature 457 (7232), 1003–1006.

Lin, D., Lai, J., Muller-Landau, H.C., Mi, X., Ma, K., 2012. Topographic variation in aboveground biomass in a subtropical evergreen broad-leaved forest in China. PLoS ONE 7 (10), e48244.

Lin, D., Lai, J., Mi, X., Ren, H., Ma, K., 2013. Spatial variation in community structure of a subtropical evergreen broad-leaved forest: implications for sampling design. Chin. Sci. Bull. 58 (10), 1181–1186.

Luizão, R.C.C., Luizão, F.J., Paiva, R.Q., Monteiro, T.F., Sousa, L.S., Kruijt, B., 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. Glob. Change Biol. 10 (5), 592–600.

Luo, Y., Randerson, J., Abramowitz, G., Bacour, C., Blyth, E.M., Carvalhais, N., Ciais, P., Dalmonech, D., Fisher, J.B., Fisher, R.A., Friedlingstein, P., Hibbard, K., Hoffman, F., Huntzinger, D.N., Jones, C.D., Lawrence, D., Li, D., Mahecha, M., Niu, S., Norby, R., Piao, S., Qi, X., Peylin, P., Prentice, C., Riley, W.J., Reichstein, M., Wang, Y.P., Xia, J., Zaehle, S., Zhou, X., 2012. A framework of benchmarking land models. Biogeosciences 9, 3857–3874.

Lutz, J.A., Larson, A.J., Swanson, M.E., Freund, J.A., 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS ONE 7 (5), e36131.

Marshall, A.R., Willcock, S., Platts, P.J., Lovett, J.C., Balmford, A., Burgess, N.D., Latham, J.E., Munishi, P.K.T., Salter, R., Shirima, D.D., Lewis, S.L., 2012. Measuring and modelling above-ground carbon and tree allometry along a tropical elevation gradient. Biol. Conserv. 154, 20–33.

McEwan, R.W., Lin, Y.C., Sun, I., Hsieh, C.F., Su, S.H., Chang, L.W., Song, M.G.-Z., Wang, H.H., Hwong, J.L., Lin, K.C., Yang, K.C., Chiang, J.M., 2011. Topographic and biotic regulation of aboveground carbon storage in subtropical broad-leaved forests of Taiwan. For. Ecol. Manage. 262 (9), 1817–1825.

McIntyre, P.J., Thorne, J.H., Dolanc, C.R., Flint, A.L., Flint, L.E., Kelly, M., Ackerly, D.D., 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. Proc. Nat. Acad. Sci., 201410186

Meyer, V., Saatchi, S.S., Chave, J., Dalling, J.W., Bohlman, S., Fricker, G.A., Robinson, C., Neumann, M., Hubbell, S., 2013. Detecting tropical forest biomass dynamics from repeated airborne Lidar measurements. Biogeosciences 10 (8), 5421–5438.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82 (9), 2381–2396.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M.A.S.S., 2007. The vegan package. Community ecology package 10.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333 (6045), 988–993.

Paoli, G.D., Curran, L.M., Slik, J.W.F., 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. Oecologia 155 (2), 287–299.

Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C.V., Nimal Gunatilleke, I.A.U., Wiegand, K., Huth, A., 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. J. Ecol. 101, 149–160. http://dx.doi.org/10.1111/1365-2745.12017.

Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol. 189 (4), 978–987.

Russo, S.E., Davies, S.J., King, D.A., Tan, S., 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. J. Ecol. 93, 879–889.

Sist, P., Mazzei, L., Blanc, L., Rutishauser, E., 2014. Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. For. Ecol. Manage. 318, 103–109.

Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., van Valkenburg, J.L.C.H., 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Global Ecol. Biogeogr. 19, 50–60. http://dx.doi.org/10.1111/j.1466-8238.2009.00489.x.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G., Zweifel, N., 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Global Ecol. Biogeogr. 22 (12), 1261–1271.

Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J., Thompson, J., 2009. Above-ground forest biomass is not consistently related to wood density in tropical forests. Global Ecol. Biogeogr. 18 (5), 617–625.

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507 (7490), 90–93.

Team, R.C., 2012. R: A Language and Environment for Statistical Computing.

Tarboton, D.G., 1997. A new method for the determination of flow directions and upslope areas in grid digital elevation models. Water Resour. Res. 33 (2), 309–319.

ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., de Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N., Mogollón, H., Morawetz, W., 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. Biodivers. Conserv. 12, 2255–2277.

Vance-Chalcraft, H.D., Willig, M.R., Cox, S.B., Lugo, A.E., Scatena, F.N., 2010. Relationship between aboveground biomass and multiple measures of biodiversity in subtropical forest of Puerto Rico. Biotropica 42 (3), 290–299.

Wang, Q., Bao, D., Guo, Y., Lu, J., Lu, Z., Xu, Y., Zhang, K., Liu, H., Meng, H., Jiang, M., Qiao, X., Huang, H., 2014a. Species associations in a species-rich subtropical

forest were not well-explained by stochastic geometry of biodiversity. PLoS ONE 9 (5), e97300.

Wang, Q., Xu, Y., Lu, Z., Bao, D., Guo, Y., Lu, J., Zhang, K., Liu, H., Meng, H., Qiao, X., Huang, H., Jiang, M., 2014b. Disentangling the effects of topography and space on the distributions of dominant species in a subtropical forest. Chin. Sci. Bull., 1–10.

Xu, Y., Zhang, J., Franklin, S.B., Liang, J., Ding, P., Luo, Y., Lu, Z., Bao, D., Jiang, M., accepted for publication. Improving allometry models to estimate the above- and below-ground biomass of subtropical forest, China. Ecosphere.

Yu, G., Chen, Z., Piao, S., Peng, C., Ciais, P., Wang, Q., Li, X., Zhu, X., 2014. High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. Proc. Nat. Acad. Sci. 111 (13), 4910–4915.