

# TEMPORAL AND SPATIAL PATTERNS IN ABOVEGROUND BIOMASS WITHIN DIFFERENT HABITATS IN A SUB-TROPICAL FOREST

Ma L<sup>1</sup>, Shen CY<sup>2, 3</sup>, Fu SL<sup>1</sup>, Lian JY<sup>4</sup> & Ye WH<sup>4</sup>, \*

<sup>1</sup>Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions, College of Environment and Planning, Henan University, Kaifeng, 475004, P. R. China

<sup>2</sup>School of Environmental Science and Engineering of Sun Yat-sen University, No. 135, Xingang Xi Road, Guangzhou, 510275, P. R. China

<sup>3</sup>Guangdong Provincial Key Laboratory of Environmental Pollution Control and Remediation Technology, South China Botanical Garden, Chinese Academy of Sciences, Xingke Road 723, Guangzhou, 510650, P. R. China

<sup>4</sup>Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Xingke Road 723, Guangzhou, 510650, P. R. China

\*sysugds@163.com

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In order to explore the variation in aboveground biomass among five topographically-defined habitats in old-growth forest, we measured aboveground biomass within a 20 ha permanent plot in Southern China. Aboveground biomass was estimated by using allometric regression equations. In the present study, there was no significant difference between the average aboveground biomass in 2005 ( $153.7 \pm 58.7 \text{ mg ha}^{-1}$ ) and in 2010 ( $152.3 \pm 60.8 \text{ mg ha}^{-1}$ ). Biomass also varied substantially among habitats, from  $138.9 \text{ Mg ha}^{-1}$  in the higher slope and lower valley habitat to  $200.1 \text{ mg ha}^{-1}$  in the mountain ridge habitat in 2005, and from  $132.1 \text{ mg ha}^{-1}$  in the lower slope to  $198.8 \text{ mg ha}^{-1}$  in the mountain ridge in 2010. Medium trees were the largest contributor (48%) to the total aboveground biomass within all habitats. Variability in species contributions to total habitat biomass were suggestive of species habitat preferences. This study provides a detailed overview of aboveground biomass patterns among old-growth forest habitats and highlights the importance of incorporating community characteristics and environmental variables (i.e. topography) into forest ecosystem carbon studies. The results will further our understanding of the contributions of old-growth forests to global carbon cycles and provide valuable information to improve conservation planning strategies.

Keywords: Allometric equation, environment variables, habitat, old-growth forest

## INTRODUCTION

Forests represent a major reservoir of global carbon, and play a major role in regional and global carbon cycles because they act as carbon sinks during succession and as carbon sources when destroyed or degraded by human or natural disturbances (Luyssaert et al. 2008, Marin-Spiotta & Sharma 2013). Estimates suggest that about half of the organic carbon contained in terrestrial ecosystems is stored within forests (Wagner et al. 2015). Therefore, even a slight change in the global forest carbon pool could have profound impacts on the global carbon balance (Malhi et al. 2006, Zhao et al. 2014). An accurate estimate of the magnitude of forest carbon stocks within different climate regions is therefore essential for understanding global and regional carbon budgets. As a result, there have been increased

efforts during the past several decades to quantify forest ecosystem carbon stocks (Baraloto et al. 2011, Lindsell & Klop 2013, Liu et al. 2014). However, most of these previous studies were based on measurements over extremely small areas, and thus are subject to large sampling errors and may fail to adequately characterise the actual aboveground biomass of the study sites (Lin et al. 2012). In addition, limited data from sub-tropical forests in China and limited understanding of fine-scale variation among habitats hinder our understanding of the carbon cycle. Therefore, studies across larger sampling areas are needed to obtain more accurate sub-tropical old-growth forest biomass quantifications. It is critical to supplement our knowledge of changes in aboveground biomass

under natural conditions, with information from actual measurements derived by plot-based studies.

Forest aboveground biomass and its distribution among different forest ecosystems is, to some extent, affected by external factors (Ruiz-Benito et al. 2014, Borah et al. 2015). The ability of a forest to sequester carbon is affected by the species diversity (Zhang et al. 2015, 2016); climate (e.g., temperature and precipitation); topography (e.g., elevation and aspect); human activities (e.g., afforestation and harvesting); and natural disturbances (e.g., fire and pest outbreaks) (Seidl et al. 2014, Ma et al. 2015, Dar & Sundarapandian 2015). Thus, aboveground biomass dynamics tend to dominate influences on short-term fluctuations in forest ecosystem carbon storage, and therefore, are appropriately the primary focus of research on forest carbon pools. However, important issues, such as (1) within-site variability in aboveground biomass, especially with respect to local variation in habitat, and (2) species contribution, either similarly or differently, to the aboveground biomass in the old-growth subtropical forest in southern China, remain undiscovered. It is evident that more data are required to better understand old-growth forest productivity and carbon storage potential, particularly because different forest ecosystems have inherently different productivity dynamics, suggesting a common trend between different forest ecosystems might not exist.

Commonly, quantification of old-growth forest carbon levels can be expected to provide a reasonable estimate of the upper limit of carbon storage for similar forest types. Old-growth forests are conventionally considered to be the climax ecosystem, which means that forests in similar climate and disturbance regimes achieve the old-growth stage at similar stand ages (Liu et al. 2014). The ecological basis for using old-growth forests to study patterns of carbon accumulation is the hypothesis that old-growth forests have a relatively high carbon density. The few remaining old-growth forests in this region offer an opportunity to empirically estimate upper limits of carbon storage. In addition, carbon stocks in intact old-growth forests may be increasingly affected by global environmental changes (Luyssaert et al. 2008, Liu et al. 2014). In this study, spatial and temporal patterns were examined in aboveground biomass within different habitats within a 20-ha permanent plot

in South China. Our objectives were as follows: (1) to document the temporal and spatial patterns in aboveground biomass throughout the study plot, (2) to characterise the variation in aboveground biomass among different habitats within the study plot and compare aboveground biomass measurements between two sample years separated by five years and (3) to test the relative aboveground biomass contributions of individual species, and determinants of aboveground biomass dynamics across a five year time period.

## MATERIALS AND METHODS

### Study site

This study was carried out in a sub-tropical broadleaved evergreen forest in Dinghushan Nature Reserve, located between 23° 09' to 23° 11' N and 112° 30' to 112° 33' E, in Guangdong Province, China. This reserve, which was established in 1956, was the first nature reserve to be established in China, and has significantly contributed to the conservation of forest ecosystems over the past 60 years (Zhou et al. 2006, Li et al. 2009). The reserve covers an area of 1,155 ha, with an elevation range of 14 to 1,000 m, including low mountain and hilly landscape habitats. The zonal vegetation is low sub-tropical evergreen broadleaved forest, with forests that are more than 400 years old. The mean annual temperature and precipitation are 21.1 °C and 1,927 mm, respectively, and mean relative humidity is 85%. The soil is composed mainly of lateritic red and mountain yellow brown soil (Ma et al. 2016).

### Field methods

In 2005, a 20-ha (500 × 400 m) forest plot (DHS plot) within the Nature Reserve was established and surveyed as described below. This plot was subdivided into 500 20 × 20 m subplots. The 20-ha study plot was located in the core zone of the reserve in order to avoid human disturbances. The elevation of the plot ranged from 230 to 470 m with a mean elevation of 340 m. All free-standing trees measuring at least 1 cm diameter at breast height (DBH), 1.3 m aboveground, were tagged, measured and identified to species level, and their geographic coordinates were recorded following a standard field protocol (Wang et al. 2009). A second survey of the study plot following the first census was carried out between

September and December 2010. In addition to the measurements and observations made in 2005, the status of tagged trees (live or dead) was recorded and recruits were noted during the 2010 survey. A total of 71,457 individuals making up 195 species were recorded during the 2005 survey. In 2010, 60,067 individuals belonging to 177 species were observed. The 2005 and 2010 data showed that the three dominant tree species, based on importance values (IV) were *Castanopsis chinensis*, *Schima superba* and *Engelhardtia roxburghiana* (Ma et al. 2014).

### Aboveground biomass estimates

The aboveground biomass was estimated using a previously published allometric equation developed for mixed forests in the Dinghushan Nature Reserve (Wen et al. 1997), and their plots had almost the same species composition and community structure. Standard trees with different DBH classes for key species were selected. Based on the measurements for standard trees, they estimated the dry weight of biomass by allometric regression equations (Wen et al. 1997).

$$AGB = a \times DBH^b \quad (1)$$

where, a and b = statistical parameters (Table 1). Aboveground biomass refers to the sum of the dry weight of trunks, branches, leaves and roots. This model has been successfully applied to estimate tree biomass in a sub-tropical forest located in the Nature Reserve (Liu S et al. 2007).

### Habitat classification in the study site

Three topographic attributes (elevation, slope and convexity) were calculated for each 20 × 20 m subplot according to the methods described by Harms et al. (2001). Elevation was measured at the corners of each subplot. Elevation values for these subplots were interpolated into the 20

× 20 m subplots. Slope and convexity values were then calculated for each subplot. In a previous study of species-topography associations within DHS plot, Wang et al. (2009) used a multivariate regression tree to interpolate the 20 × 20 m subplot to one of the five habitats. Each habitat classification was based on measurements of a predetermined set of topographic conditions. The habitat classifications included five different habitats: higher slope (HS), mountain ridge (MR), higher valley (HV), lower slope (LS) and lower valley (LV) habitat (Figure 1). Tree species composition, tree density (stems ha<sup>-1</sup>) and number of stems within different DBH ranges were used to describe forest community characteristics within these five habitats.

### Statistical analyses

The aboveground biomass of each 20 × 20 m subplot within the different habitats were calculated by summing the estimated biomass of each individual, and then the aboveground biomass density of each subplot (mg ha<sup>-1</sup>) was calculated. In order to compare the aboveground biomass storage within each habitat, the mean value of aboveground biomass density (mg ha<sup>-1</sup>) of each habitat was calculated, as the number of subplots differed within each habitat. The significant effects of habitat on tree biomass density were tested using an ANOVA. *P* values (*p* < 0.05) were considered significant.

In order to test the relationship between the proportion of stems from each species and the proportion of biomass from each species within habitats, we used the Pearson's correlation method. Generalised linear models (GLM) were used to model the determinants of aboveground biomass storage at each subplot as a function of biotic (richness, abundance and number of individuals within different DBH ranges) and abiotic (elevation, convexity and slope) factors. All of these variables within each subplots in this model were statistically independent. Values

**Table 1** Allometric regression equations and the statistics

| DBH-class        | Equations                        | Adjusted R <sup>2</sup> | Standard error of the mean |
|------------------|----------------------------------|-------------------------|----------------------------|
| DBH ≤ 5 cm       | $W = 0.05549 \times D^{2.87776}$ | 0.91164                 | 0.60826                    |
| 5 < DBH ≤ 10 cm  | $W = 0.11701 \times D^{2.36933}$ | 0.88428                 | 2.05700                    |
| 10 < DBH ≤ 20 cm | $W = 0.10769 \times D^{2.34891}$ | 0.77761                 | 4.15734                    |
| DBH > 20 cm      | $W = 0.03541 \times D^{2.65146}$ | 0.97844                 | 36.71034                   |

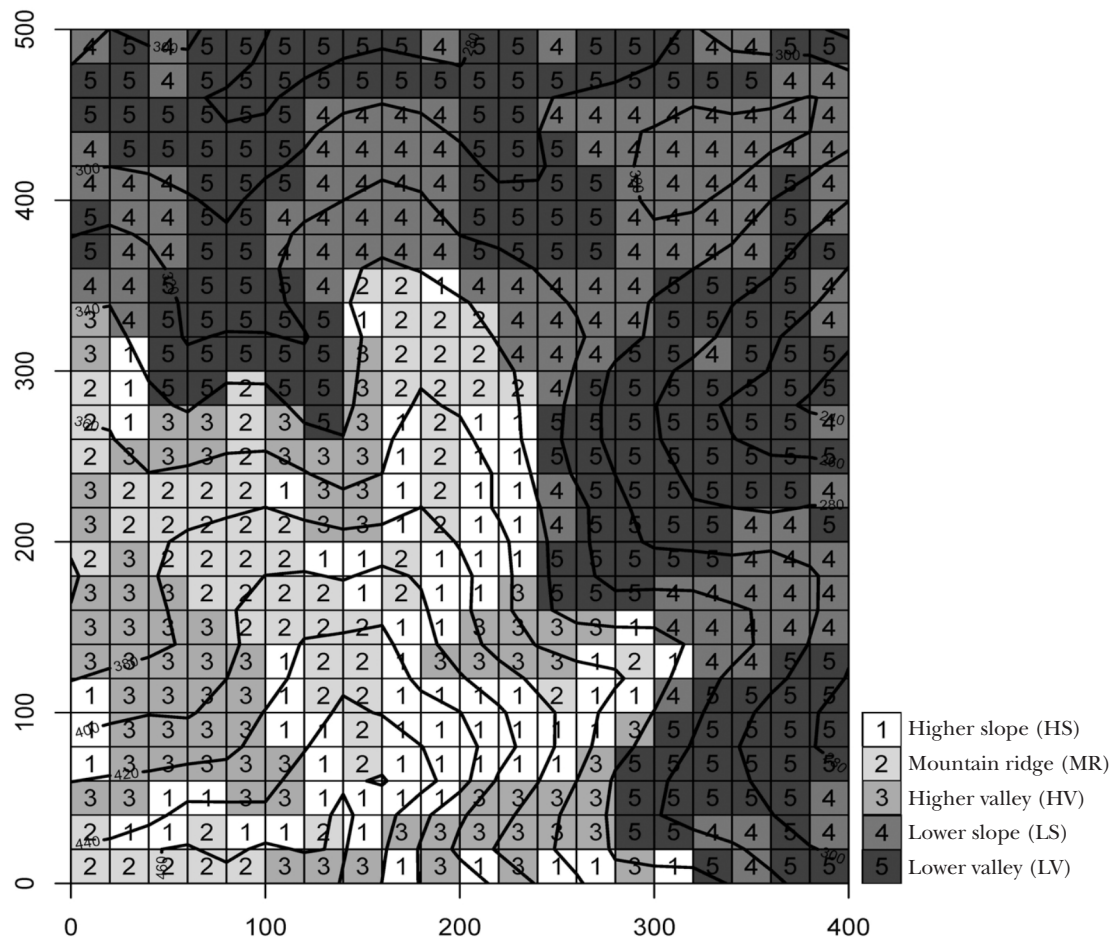


Figure 1 Spatial pattern of five habitats and contour within 20 ha study site

of all explanatory variables were standardised by subtracting the mean values of the variables and dividing by 1 deviation. This allows for a direct comparison of the relative importance of explanatory variables. Values were estimated coefficients in the models of the effects of variables on aboveground biomass. Positive and negative values indicated that variables had positive and negative effects on aboveground biomass. Arithmetic means  $\pm$  standard errors are presented throughout the paper. All analyses were performed within the R (3.1.2) statistical environment (R Core Team 2009).

**RESULTS**

**Patterns of aboveground biomass and its driving forces in DHS plot**

Tree biomass ranged from 127.9 mg ha<sup>-1</sup> to 335.3 mg ha<sup>-1</sup>, with a mean value of 153.7  $\pm$  58.7 mg ha<sup>-1</sup> in 2005 based on site estimation. In 2010, tree biomass ranged from 122.3 mg ha<sup>-1</sup>

to 330.2 mg ha<sup>-1</sup> in all 20  $\times$  20 m subplots, with a mean value of 152.3  $\pm$  60.8 mg ha<sup>-1</sup>. On average, total live tree biomass decreased by 1.4 mg ha<sup>-1</sup> during the five years between surveys, although there was no significant difference between the two censuses (Table 2). The total average aboveground biomass of recruits was 0.8 mg ha<sup>-1</sup> while tree growth contributed 1.1 mg ha<sup>-1</sup>. Aboveground biomass was significantly greater ( $p < 0.05$ ) in medium diameter classes (10–40 cm) (48%) than other DBH ranges within the habitats. The smaller (< 10 cm DBH) (25%) and larger stem class (> 50 cm DBH) (27%) contributed the least to aboveground biomass due to lower mean DBH and fewer individuals, respectively (Figure 2).

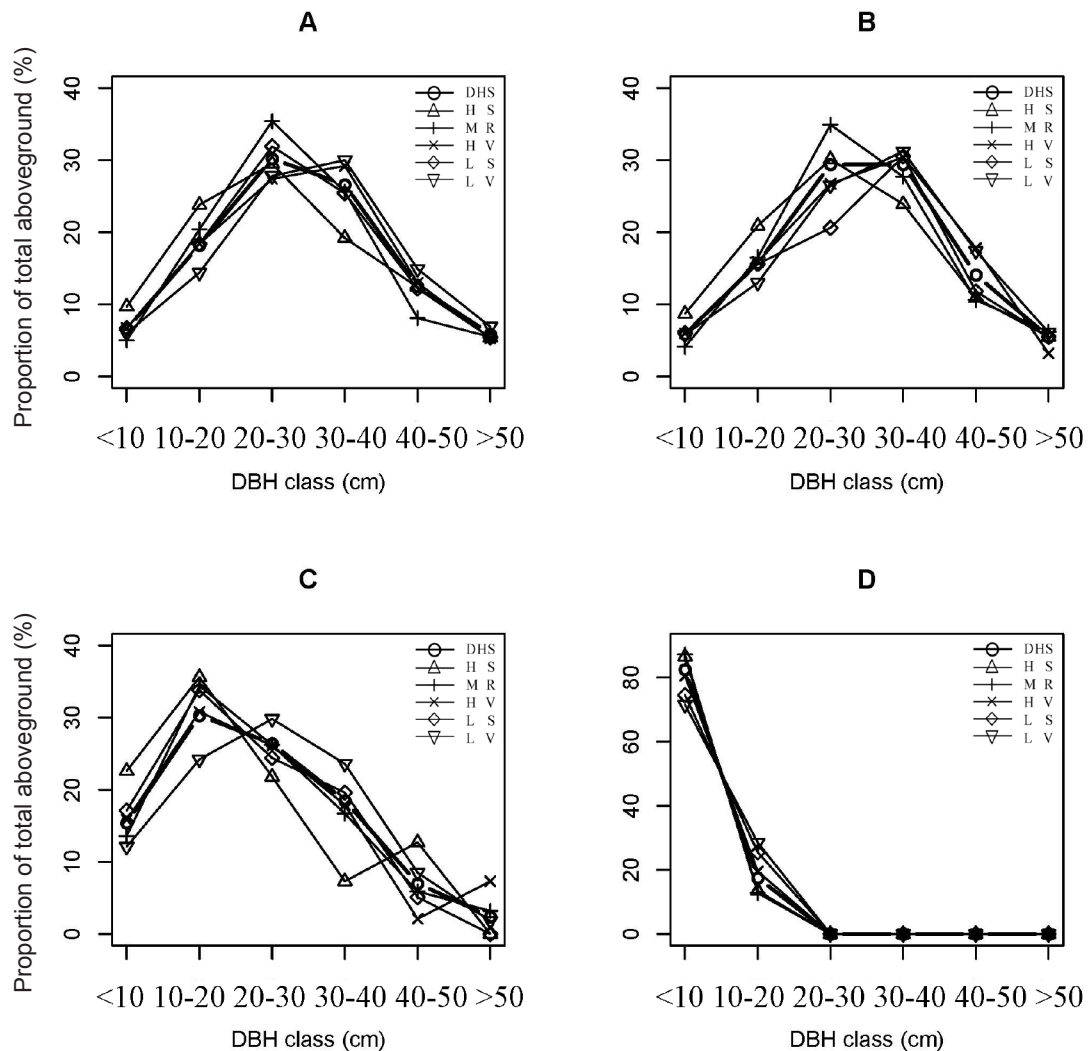
The effects of species richness, stand structure (number of individuals within different DBH ranges) and abiotic variables on aboveground biomass were included in the model for all subplots. The number of larger trees (DBH > 20 cm) was the most important factor for determining aboveground biomass, followed by



**Table 2** Mean aboveground biomass ( $\text{Mg ha}^{-1}$ ) of live stems (2005 and 2010), dead wood (including mortality rate) and recruits (including recruitment rate) within five different sized habitats

|              | 2005         | 2010         | Dead wood | Recruits  | M rate %  | R rate %  |
|--------------|--------------|--------------|-----------|-----------|-----------|-----------|
| DHS (20 ha)  | 153.7 ± 58.7 | 152.3 ± 60.8 | 3.3 ± 1.1 | 0.8 ± 0.5 | 2.8 ± 1.2 | 2.4 ± 0.8 |
| HS (2.92 ha) | 138.9 ± 9.5  | 135.5 ± 10.1 | 3.1 ± 0.3 | 0.7 ± 0.1 | 6.1 ± 0.3 | 1.9 ± 0.1 |
| MR (2.48 ha) | 200.1 ± 14.6 | 198.8 ± 15.2 | 2.9 ± 0.2 | 0.4 ± 0.1 | 6.0 ± 0.2 | 4.1 ± 0.3 |
| HV (3.08 ha) | 150.7 ± 12.4 | 146.6 ± 12.6 | 3.7 ± 0.2 | 0.8 ± 0.1 | 6.5 ± 0.3 | 3.1 ± 0.2 |
| LS (4.60 ha) | 162.2 ± 12.8 | 161.7 ± 13.1 | 3.3 ± 0.3 | 1.1 ± 0.1 | 5.1 ± 0.2 | 1.8 ± 0.1 |
| LV (6.92 ha) | 138.9 ± 9.4  | 132.1 ± 9.8  | 3.4 ± 0.1 | 0.8 ± 0.1 | 6.1 ± 0.2 | 2.1 ± 0.1 |

DHS = 20 ha study plot within the Dinghushan Nature Reserve, HS = higher slope, MR = mountain ridge, HV = higher valley, LS = lower slope, LV = lower valley, M rate = mortality rate during the five-year period, R rate = recruitment rate during the five-year period



**Figure 2** Contribution of trees within different DBH ranges to aboveground biomass in five habitats, A = 2005, B = 2010, C = dead wood, D = recruits, DHS = Dinghushan 20 ha study plot, HS = higher slope, MR = mountain ridge, HV = higher valley, LS = lower slope, LV = lower valley

richness, elevation and slope in aboveground biomass storage in 2005 and 2010. Community characteristics (variables of richness and number of individuals within different DBH ranges) had positive effects on aboveground biomass while variables including elevation and slope had negative effects on aboveground biomass storage in 2005 and 2010 (Table 3).

**Community characteristics and aboveground biomass within the five habitat types**

The five habitats differed in forest community characteristics and aboveground biomass (Table 2 & 4). The LV and HS habitats had lowest tree density and slightly below average aboveground biomass in 2005 and 2010. The MR habitat had the largest ( $p < 0.05$ ) mean aboveground biomass. HV and LS had intermediate stem density, and somewhat below or above average aboveground biomass. HS contrasted sharply in forest structure from all other habitats with the highest stem density and the lowest aboveground biomass, reflecting a high density of small trees. In addition, aboveground biomass within LV habitats decreased more than the other four habitats' aboveground biomass during the five year period between surveys (Table 2). Aboveground biomass of dead wood was highest in the HV habitat ( $p < 0.05$ ), followed by LV and then LS habitats. Aboveground biomass of recruits was very low among all five habitats, due to a low number of stems and individuals with small DBH.

**Relative species' contributions to aboveground biomass**

Influences on aboveground biomass was found to be dominated by three species (*C. chinensis*, *S. superba* and *E. roxburghiana*) in the five habitat types. These three tree species cumulatively made up 67.0% of the aboveground biomass in 2005 and 63.3% in 2010 (Table 5). However, these three dominant species made up only 7.8% of all recorded individuals in 2005 and 7.9% of all recorded individuals in 2010. The 10 species with the greatest AGB cumulatively contributed from 81.6% to 93.0% of the total aboveground biomass in 2005 and 2010, depending on habitat type. The three tree species (*C. chinensis*, *S. superba*, and *E. roxburghiana*) accounted for the largest proportions of dead wood aboveground biomass. The aboveground biomass of *E. roxburghiana* recruits was very small relative to other dominant species due to few recruits during the 5-year period.

**DISCUSSION**

**Aboveground biomass dynamics in the 20 ha study plot**

Biomass is an important quantitative characteristic of forest ecosystems. In the present study, the aboveground biomass and its dynamics were estimated within five habitat types in a 20 ha forest plot located in a sub-tropical forest in Southern China. Aboveground biomass was

**Table 3** Summary of generalised linear models analyses of aboveground biomass storage in 2005 and 2010 (number of stems within different DBH ranges)

| Variables     | 2005                  |             | 2010                  |             |
|---------------|-----------------------|-------------|-----------------------|-------------|
|               | Estimated coefficient | Significant | Estimated coefficient | Significant |
| Elevation     | -0.12                 | *           | -0.15                 | **          |
| Convexity     | 0.05                  | **          | 0.04                  | **          |
| Slope         | -0.06                 | ***         | -0.14                 | ***         |
| Richness      | 0.21                  | ***         | 0.19                  | ***         |
| Abundance     | 0.26                  | **          | 0.11                  | *           |
| DBH: <10 cm   | -0.19                 |             | 0.61                  |             |
| DBH: 10–20 cm | 0.14                  |             | 0.17                  | **          |
| DBH: 20–30 cm | 0.23                  | **          | 0.21                  | *           |
| DBH: 30–40 cm | 0.24                  | *           | 0.11                  | *           |
| DBH: 40–50 cm | 0.18                  | **          | 0.23                  | ***         |
| DBH: >50 cm   | 0.33                  | ***         | 0.27                  | **          |

\*  $0.05 > p > 0.01$ ; \*\*  $0.01 > p > 0.001$ ; \*\*\*  $p \leq 0.001$

153.7 ± 58.7 mg ha<sup>-1</sup> in 2005 and 152.3 ± 60.8 mg ha<sup>-1</sup> in 2010, which is well within or near the range of previously reported aboveground biomasses for sub-tropical forests in Southern China (Liu et al. 2007, Xiao Y et al. 2014). Furthermore, differences in topography, soil condition and forest community characteristics are also likely to contribute to variation in aboveground biomass (Ma et al. 2014, 2016).

### Effects of community characteristics on aboveground biomass

Empirical and theoretical studies generally suggest that community characteristics (e.g., species composition and community structure) are important determinants of variation in carbon storage among regions with the same climate range (Dar & Sundarapandian 2015, Liu et al. 2014, Osuri et al, 2014). In this study, the tree species diversity index (richness and abundance) had significantly positive relationship with aboveground biomass storage in 2005 and 2010 (Table 4). The results showed that higher aboveground biomass of live trees in species-rich rather than species-poor subplots. These results are consistent with previous studies that found species diversity increases carbon storage and tree productivity (Ruiz-Benito et al. 2014). Using large forest inventory datasets in natural systems, studies have shown that mixed-species stands have higher tree productivity and higher wood

volume, respectively, than single-species stands, though studies did not control for the potentially better soil conditions on which mixed stands are often established (Borah et al. 2015). Species composition is an important aspect of forest type, and has great impacts on carbon sequestration in tropical, sub-tropical and boreal forests (Ma et al. 2015). Carbon storage in plants varies largely because of the difference in each species' ability to sequester carbon. This highlights the diversity of old-growth productivity in different forest types and regions, and indicates that a general productivity trend in all forest ecosystems does not exist.

### Variation in aboveground biomass among different habitats

Aboveground biomass varied substantially among the five topographic habitat types within the study site. The MR habitat supported the greatest mean aboveground biomass, whereas the greatest aboveground biomass storage was observed in LV and LS habitats because of their larger areas. High local scale variation in aboveground biomass has been documented in other studies, and has been attributed to differences in topography, soil fertility, light conditions, natural disturbances and their interactions (Lin et al. 2012). There are multiple potential mechanisms driving topography influences on forest aboveground biomass (Spracklen & Righelato 2014, Dar &

**Table 4** Community characteristics of the 20 ha Dinghushan Nature Reserve study plot and the five habitats contained within the study plot

|                                                | DHS   | HS    | MR   | HV    | LS    | LV    |
|------------------------------------------------|-------|-------|------|-------|-------|-------|
| Number of plots                                | 500   | 73    | 62   | 77    | 115   | 173   |
| Number of families in 2005                     | 55    | 46    | 38   | 44    | 47    | 48    |
| Number of families in 2010                     | 50    | 43    | 38   | 43    | 45    | 46    |
| Number of genera in 2005                       | 115   | 90    | 71   | 91    | 92    | 99    |
| Number of genera in 2010                       | 106   | 85    | 72   | 86    | 87    | 95    |
| Number of species in 2005                      | 195   | 143   | 101  | 136   | 140   | 157   |
| Number of species in 2010                      | 177   | 126   | 99   | 121   | 129   | 150   |
| Number of stems in 2005                        | 71457 | 14193 | 9431 | 11091 | 17133 | 19609 |
| Stem density in 2005 (stems ha <sup>-1</sup> ) | 3575  | 4875  | 3800 | 3600  | 3750  | 2825  |
| Number of stems in 2010                        | 68067 | 13525 | 9583 | 10343 | 16496 | 18120 |
| Stem density in 2010 (stems ha <sup>-1</sup> ) | 3405  | 3950  | 3450 | 3025  | 3150  | 2325  |

DHS = the 20 ha study plot within the Dinghushan Nature Reserve, HS = higher slope, MR = mountain ridge, HV = higher valley, LS = lower slope, LV = lower valley

**Table 5** Species contribute to total aboveground biomass (%) within 5 different habitats in 2005, 2010, dead wood and recruits in this study

|                                   | 2005                         |      |      |      |      |      |      |      |      |      | 2010 |      |      |      |      | Dead wood |    |     |      |      | Recruits |    |     |      |      |
|-----------------------------------|------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|-----------|----|-----|------|------|----------|----|-----|------|------|
|                                   | HS                           | MR   | HV   | LS   | LV   | HS   | MR   | HV   | LS   | LV   | HS   | MR   | HV   | LS   | LV   | HS        | MR | HV  | LS   | LV   | HS       | MR | HV  | LS   | LV   |
|                                   | <i>Castanopsis chinensis</i> | 35.0 | 36.1 | 32.1 | 33.3 | 34.9 | 32.2 | 39.9 | 33.0 | 37.7 | 28.6 | 7.3  | 15.3 | 14.6 | 15.1 | 32.2      | 3  | 16  | 19.6 | 43.4 | 3.5      | 3  | 16  | 19.6 | 43.4 |
| <i>Schima superba</i>             | 16.4                         | 21.4 | 12.2 | 15.7 | 13.9 | 18.2 | 22.3 | 12.7 | 16.5 | 20.2 | 8.5  | 14.9 | 13.6 | 11.1 | 14.6 | 13        | 25 | 3.6 | 7.8  | 6.7  | 13       | 25 | 3.6 | 7.8  | 6.7  |
| <i>Engelhardtia roxburghiana</i>  | 13.7                         | 16.8 | 12.1 | 17.4 | 21.2 | 12.5 | 13.9 | 12.5 | 15.0 | 12.9 | 15.4 | 30.7 | 8.3  | 27.7 | 24.5 |           |    |     |      |      |          |    |     |      |      |
| <i>Craibiodendron scleranthum</i> | 5.8                          | 7.9  | 9.6  | 4.6  | 1.9  | 4.9  | 6.6  | 9.1  | 3.9  | 1.6  | 8.8  | 13.9 | 10.2 | 7.4  | 2.8  |           |    |     |      |      |          |    |     |      |      |
| <i>Pinus massoniana</i>           | 6.3                          | 6.6  | 6.6  | 2.7  |      |      | 5.7  | 6.6  | 2.2  |      | 6.3  | 4.9  |      |      |      |           |    |     |      |      |          |    |     |      |      |
| <i>Cryptocarya chinensis</i>      | 0.9                          |      | 2.7  | 3.5  | 5.6  |      | 1.0  |      | 6.9  | 5.8  | 4.2  |      | 6.3  | 6.2  | 2.5  |           |    |     |      |      |          |    |     |      |      |
| <i>Machilus chinensis</i>         | 2.3                          |      |      |      | 6.5  |      |      | 2.8  | 4.0  | 6.2  | 1.1  |      |      | 7.5  | 2.5  |           |    |     | 21.0 | 9.8  |          |    |     |      |      |
| <i>Acmena acuminatissima</i>      | 2.4                          |      | 3.6  | 2.1  | 8.3  | 2.0  |      | 4.0  | 2.3  | 8.7  |      |      | 3.1  | 3.3  | 6.1  |           |    | 5.2 |      | 4.0  |          |    |     |      |      |
| <i>Syzygium rehderianum</i>       | 3.9                          |      | 1.4  | 3.1  | 1.5  | 3.8  |      |      | 3.1  | 1.5  | 4.6  |      | 5.6  | 2.7  | 7.0  |           |    |     |      |      |          |    |     |      |      |
| <i>Ilex ficoidea</i>              | 4.6                          |      |      |      |      | 5.1  |      |      |      |      | 3.5  |      |      |      |      |           |    |     |      |      |          |    |     |      |      |



Sundarapandian 2015). Among the potential abiotic factors influencing aboveground biomass, topography was the most variable within the study plot for the present study. The elevation of this plot varies from 230 m to 470 m and contains numerous extremely steep slopes (Wang et al. 2009). The topography of the present study site is, therefore, considerably more complicated than reported in previous studies. For example, elevation differences were less than 40 m in the Changbaishan, Pasoh and BCI plots (Baraloto et al. 2011, Yuan et al. 2013, Liu et al. 2014). In the study site, the three valley habitats (MR, LV and HV) were scattered with many large rocks. Ma et al. (2014) found many dying trees during a five-year study period in this study plot, suggesting that high mortality rate was due to the shallow soil and steep slopes. Changes to abiotic factors due to elevation can have an important influence on plant growth, community structure and ecosystem processes. In a sub-tropical forest in Taiwan, high aboveground biomass was found in topographically flat areas (Tsui et al. 2013). The dead tree biomass was also significantly higher at lower elevations than high elevations, suggesting significant effects of elevation on mortality rate. A previous study of aboveground biomass found steep slopes to be associated with increased tree fall mortality in a lowland rain forest in French Guiana (Pfeifer et al. 2015). However, in the present study, elevation had significant positive effects on the aboveground biomass of recruits. Soil fertility within the two valley habitats of the current study was previously found to be high (Wang et al. 2009). However, this study did not find valley habitat aboveground biomass to be much higher than the aboveground biomass of the other, relatively infertile, habitats. Fertile soil improves stand productivity, leading to more intense competition among trees (Fauset et al. 2015, Lin et al. 2012). Natural disturbances, which can disrupt the carbon cycle of forest ecosystems and cause export carbon from the ecosystem (Seedre et al. 2015), may have influenced patterns of aboveground biomass in the current study site.

### Relative species' contribution to aboveground biomass

As expected, the results clearly revealed that the relative contributions of individual species to total aboveground biomass differed among

habitats (Table 5), resulting in significant species habitat associations, suggestive of species habitat preferences. Specialised ecological strategies (i.e., niche differentiation) of individual species may account for the spatial patterns of species indifferent habitats. For example, most of the recruits that made large contributions to the total aboveground biomass among the five habitats in the present study were light-requiring species. Successful establishment of these recruits may be due to forest gaps resulting from tree deaths, especially deaths of larger individuals (Ma et al. 2016). The complex topographic features of this study site resulted in differential resource availability among the different habitats.

In the present study, we found that relatively few species (*C. chinensis*, *S. superba*, and *E. roxburghiana*) dominated in terms of aboveground biomass, within the studied habitat types. These three dominant tree species contributed to 67% of the cumulative aboveground biomass in 2005 and 63.3% in 2010. In addition to the study sites being dominated by only a few species, these species were the primary contributors to aboveground biomass, which significantly lowered the influence of diversity and species identity on aboveground biomass. The application of the findings to forestry-based carbon projects would translate to the need for special attention on activities that prevent or minimise the loss of these three dominant tree species, to maintain the carbon stock of this 20-ha study site.

## CONCLUSIONS

In the present study, the temporal and spatial variation in aboveground biomass was examined by surveying five different habitats within a 20 ha sub-tropical forest plot across a five-year period. Live tree aboveground biomass decreased by an average of 1.4 mg ha<sup>-1</sup> across all habitat types during the 5-year period. Additionally, three dominant species contributed to more than 60% of the aboveground biomass across all habitat types. Number of larger stems and topography had significant positive and negative effect on aboveground biomass storage, respectively. The MR habitat had the largest mean aboveground biomass storage. The contribution of individual species to the total aboveground biomass within a habitat, differed among habitats, reflecting significant species habitat associations. This study revealed that the variation in community

characteristics among habitat types, within the Dinghushan Nature Reserve study site, distinctly influenced aboveground biomass. These findings further our understanding of the influences on carbon stocks within sub-tropical forests, which will contribute to the development and validation of precise C cycling models.

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