



# Vegetation carbon stocks driven by canopy density and forest age in subtropical forest ecosystems

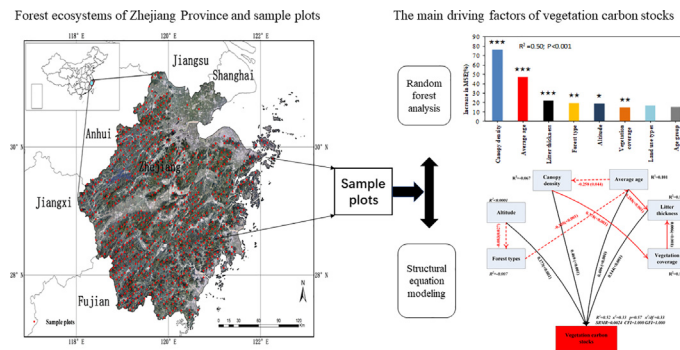
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## HIGHLIGHTS

- Random Forest analysis combined with SEM to evaluate the abiotic and biotic driving factors effects on vegetation carbon stocks.
- Canopy density and forest age were the most crucial driving factors.
- Provides new insights into the potential response of subtropical forest ecosystems carbon sequestration to climate change.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Subtropical forests play an important role in global carbon cycle and in mitigating climate change. Knowledge on the abiotic and biotic driving factors that affect vegetation carbon stocks in subtropical forest ecosystems is needed to take full advantage of the carbon sequestration potential. We used a large-scale database from national forest continuous inventory in Zhejiang Province, and combined the Random Forest analysis (RF) and structural equation modeling (SEM) to quantify the contribution of biotic and abiotic driving factors on vegetation carbon stocks, and to evaluate the direct and indirect effects of the main driving factors. The RF model explained 50% of the variation in vegetation carbon stocks; canopy density accounted for 17.9%, and forest age accounted for 7.0%. Moreover, the SEM explained 52% of the variation in vegetation carbon stocks; the value of standardized total effects of canopy density and forest age were 0.469 and 0.327, respectively, suggesting that they were the most crucial driving factors of vegetation carbon stocks. Since the forests in our study were relatively young, the forests had a large potential for carbon sequestration. Overall, our study provided new insights into the sensitivity and potential response of subtropical forest ecosystems carbon cycle to climate change.

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## 1. Introduction

Human activities, such as combustion of fossil fuels and deforestation, increase the concentration of atmospheric carbon dioxide (CO<sub>2</sub>) that is one of the main causes of global climate change (IPCC, 2014). A large body of research indicates that forest ecosystems play an important role in the global carbon cycle. The capacity of forests for sequestering additional atmospheric CO<sub>2</sub> is one possible way to mitigate climate warming (Luyssaert et al., 2007; Pan et al., 2011; Xu et al., 2016). National carbon budgets have been calculated and carbon stocks estimated in regional forests (Canadell and Raupach, 2008; Chave et al., 2003; Chheng et al., 2016; Phillips et al., 2016), including tropical, subtropical, temperate, boreal, and bamboo forests (Chave et al., 2003; Houghton, 2005; Mao et al., 2016; Xu et al., 2011; Yen, 2016; Zhang et al., 2007; Zheng et al., 2008; Zhou et al., 2011). The subtropical forests are widely distributed and frequently disturbed by human activities. The total net ecosystem productivity (NEP) of East Asian monsoon subtropical forests was estimated to be  $0.72 \pm 0.08 \text{ Pg C yr}^{-1}$ , which accounts for 8% of the global forest NEP. The average NEP value of subtropical forests is higher than those of Asian tropical forests, temperate forests, and forests at the same latitudes in Europe, Africa and North America (Yu et al., 2014). However, the effects of abiotic and biotic factors on vegetation carbon sequestration in large regional forest ecosystems are rarely studied. Thus, studying the driving factors of carbon sequestration in subtropical forests will significantly improve our knowledge of the terrestrial carbon cycle.

Previous studies have shown that the carbon sequestration ability of forest ecosystems is interactively driven by abiotic and biotic factors such as forest origin, forest age, forest type, geography, and soil environment. For instance, carbon stocks increased from 1.70 Mg C ha<sup>-1</sup> in grasslands, 4.15 Mg C ha<sup>-1</sup> in shrublands, 22.3 Mg C ha<sup>-1</sup> in shrub forests, and 70.3 Mg C ha<sup>-1</sup> in secondary forests to 142.2 Mg C ha<sup>-1</sup> in primary forests in a chronosequence of natural vegetation in karst regions (Liu et al., 2016). In different ecological service forest types of Zhejiang Province, the mean biomass values were significantly different among evergreen broad-leaved forest, coniferous and broad-leaved mixed forest, pine forest, and Chinese fir forest (Zhang et al., 2007). Forest age is also a critical factor determining ecosystem carbon storage and fluxes. The rate of carbon storage changes declined with stand age and approached equilibrium during the later stage of stand development (Yang et al., 2011). Gray et al. (2016) suggested that the old and large trees are important carbon stocks, but play a minor role in additional carbon accumulation in Pacific Northwest forests. Wang et al. (2017) found that forest age was a dominant factor that modulated carbon turnover times, especially for vegetation. In a *Zanthoxylum bungeanum* plantation, the total forest ecosystem carbon storage increased with plantation age (Cheng et al., 2015). Research on the relationships between net primary productivity and stand age for several forest types confirmed the importance of forest age in estimating regional and global terrestrial carbon budgets (Wang et al., 2011). Besides forest type and forest age, vegetation coverage strongly determines the forest structure and plant growth, since it may also be important for vegetation biomass accumulation (Grytnes, 2000; Ji et al., 2009). An increased canopy opening increased the potential and variance of height growth (Madsen and Larsen, 1996), thereby increased the forest biomass.

The abiotic factors that affect forest carbon sequestration include altitude, slope, slope position, soil environment, and climate. Particularly, altitude, slope and aspect influence stand microclimate, which has both direct and indirect effects on aboveground biomass in forest ecosystems (Fotis et al., 2017). Environmental factors affect species distributions and abundances (Boerner, 2006; Fotis et al., 2017; Murphy et al., 2015), which in turn affect both physical and biological stand attributes, for example tree size distribution, leaf arrangement, and leaf physiological traits (Fahey et al., 2015; Fotis et al., 2017; Jucker et al., 2015). There may also have a direct effect on aboveground biomass by affecting soil moisture availability (Boerner, 2006); in wetter areas the aboveground

biomass is commonly higher (Desta et al., 2004; Sharma et al., 2011). Zhang and Chen (2015) reported that nutrient availability may affect aboveground biomass by affecting stand structure. Altitude affects plant growth and productivity primarily through temperature effects (L. Xu et al., 2017), while slope through solar radiation, wind velocity and soil types (Moelsund et al., 2013). Fan et al. (2012) reported that the carbon stocks of Moso bamboo forests were significantly affected by slope aspect and slope position.

Some of the relationships between abiotic/biotic factors and aboveground biomass or productivity have been studied, yet the main driving factors and their contributions in subtropical forest ecosystems carbon sequestration are still uncertain. In this study, we collected data from 701 forest plots from subtropical forests in Zhejiang, China. We used Random Forest analysis to identify the main driving factors of vegetation carbon stocks, and then used structural equation modeling (SEM) to evaluate the direct and indirect effects of the main driving factors on vegetation carbon stocks. Both approaches provide complementary insights on the patterns that drive vegetation carbon stocks at a large scale. The main objectives of this study were to (1) quantify the contribution of each driving factor, (2) reveal the main driving factors of vegetation carbon stocks, and (3) evaluate the direct and indirect effects of the main driving factors on vegetation carbon stocks.

## 2. Materials and methods

### 2.1. Description of study area

The study area in Zhejiang Province (118°1′–123°10′ E, 27°6′–31°11′ N), on the southeast coast of China, covers approximately 105,500 km<sup>2</sup> (Fig. 1). The terrain varies from mountains with an average altitude of 800 m in the southwest, to hills in the central areas and alluvial plains in the northeast (Mao et al., 2017). The area has a subtropical monsoon climate with annual average precipitation of 1319.7 mm and annual average temperature of 15.6 °C. The primary vegetation types are coniferous evergreen, mixed coniferous, deciduous broad-leaved, and bamboo forests (Xu et al., 2018). The primary soil types are yellow and red soils (Chinese Soil Taxonomy), equivalent to Hapludult in the U.S. Department of Agriculture Soil Survey Manual (Soil survey Staff of United States Department of Agriculture (USDA), 1999). By the end of 2010, forests area in Zhejiang Province was 6.02 million ha, including 0.254 billion cm<sup>3</sup> of live stumpage, and accounting 60.63% of the total area (DFZP, 2011).

### 2.2. Sample plots and data collection

We collected data from 701 permanent sample plots that were designed and sampled following the national forest continuous inventory protocols. The east-west interval between adjacent plots was 6 km, the south-north interval was 4 km, and each plot covered an area of 800 m<sup>2</sup>. In each plot, abiotic factors (slope, aspect, slope position, altitude, land use type and soil thickness) and biotic factors of tree (diameter at breast height (DBH), trees height, canopy density, forest type, forest origin, forest age, vegetation coverage, age group, humus layer thickness, litter thickness, vegetation coverage and ratio of C to N in leaf) were recorded from May to September in 2010 (Supplementary file 1). Based on the principles of Chinese vegetation regionalization (Hou et al., 1982) and the national forest continuous inventory protocols, we classified the sampled forests into six forest type groups: deciduous broadleaf forest (DBF), deciduous needle-leaf forest (DNF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF), bamboo forest (Bamboo), and needleleaf and broadleaf mixed forest (NBF). The shrub and herb characteristics (average height, average ground diameter and coverage) were measured from three randomly selected 2 m × 2 m quadrats in each plot.

The aboveground and belowground vegetation biomass in sample plots were estimated using forest biomass model designed by Yuan

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