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Relative contributions of biotic and abiotic factors to the spatial variation of litter stock in a mature subtropical forest

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Abstract

Aims

Dead plant material (i.e. litter) is the major source of soil organic matter and thus plays a fundamental role in regulating soil carbon cycling in global forest ecosystems. The storage of litter is jointly determined by its production from plants and decomposition in a given environment. However, only few studies have explored the relative importance of environmental (i.e. abiotic) and plant (i.e. biotic) factors in driving the spatial variation of litter mass. The objective of this study is to quantify the relative contributions of biotic and abiotic factors in affecting the spatial variation of aboveground litter stock in a mature subtropical forest.

Methods

The aboveground litter mass was sampled in 187 grids of a 20-hm forest dynamics plot in a subtropical broad-leave forest in eastern China. The contributions of environmental variables, topographical and species variables on litter stocks were quantified by the boosted regression tree analysis.

Important Findings

The mean aboveground litter stock was 367.5 g m^{-2} in the Tiantong dynamics forest plot across all the 187 grids. The litter stock ranged from 109.2 to 831.3 g m^{-2} and showed a large spatial variation with the coefficient of variance as 40.8%. The boosted regression tree analysis showed that slope elevation and soil moisture were the most influential variables on the spatial variation of litter stock. The relatively influence of abiotic factors (environmental and topographical factors) was 71.4%, which is larger than biotic factors (28.6%). Overall, these findings suggest that abiotic factors play a more important role than plants in driving the spatial variation of aboveground litter stock in the subtropical forest. Given that the global carbon-cycle models have been aiming to refine from the hundred kilometers to sub-kilometer scale, this study highlights the urgency of a better understanding of the spatial variation of litter stock on the fine scale.

Keywords: litter stock, spatial variability, subtropical forest, topography

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INTRODUCTION

Litter plays a fundamental role and is a key pathway in the carbon cycling in global forest ecosystems (Jacob *et al.* 2010; Keiser 2017). The litter carbon pool accumulates from living plants and further forms the horizon layer of the soil organic matters, which contains about 18% organic carbon of the soil reservoir (Bleam 2016). As a continuous source of soil organic carbon pool, the fluctuation of litter mass could significantly affect the soil organic carbon dynamics. For example, a doubling input of litterfall will cause a 31% increase in the soil carbon stock in a wet tropical forest in Costa Rica (Leff *et al.* 2012). Recently, the dynamic of soil carbon stock has been recognized as one of the largest uncertain components in the Earth System Models (Luo *et al.* 2016). However, the ecological mechanisms underline the dynamic of litter carbon stock vary widely among these models (Burke *et al.* 2003; Del Grosso *et al.* 2005). Thus, a better understanding of the spatial variability of aboveground litter stock and its controlling factors will strength the predictive ability of these models (Bonan *et al.* 2013; Bruckner 1999; Richards 1973).

The aboveground litter stock varies with the climate, topographic factors, and species composition (Hall *et al.* 2006; Lal 2005; Matthews 1997). However, the relative importance of abiotic (e.g. microclimate and topography) and biotic (e.g. forest composition, stand diversity etc.) in the spatial variations of aboveground litter stock is still unclear. There are strong interactions between abiotic variables and biotic characteristics in the aboveground litter-soil system. For example, climate is regarded as a direct influence on aboveground litter stock by regulating the decomposition rates (Aerts 1997; Conant *et al.* 2011), which could explain 46% of the spatial variability of aboveground litter stock at the global scale (Aerts 1997). High temperature and precipitation can accelerate the plant-soil feedbacks and further increase decomposition rates in tropical forests (Raich *et al.* 2006; Taylor *et al.* 2017; Wieder *et al.* 2009; Zhu *et al.* 2017). The faster decay of litter in tropical forests could largely due to the higher temperature which is known as the dominant control of decomposition rates (Alster *et al.* 2016). In forest ecosystems, topographical factors strongly influence litter stock via affecting the spatial distribution of plant species and aboveground biomass (McEwan *et al.* 2011). For example, Salinas *et al.* (2011) have noted a 10% decrease in decomposition rates of leaf litter across an elevation gradient from 210 m to 2720 m at the decadal scale.

Besides the well-studied control of climate and topographical factors on litter decomposition rates, the composition of plant species also markedly affects the litter stock (Aubert *et al.* 2010; Cornwell *et al.* 2008). Wieder *et al.* (2009) have observed a substantial variation in decomposition rate of leaf litter (0.86 ± 0.07 year^{-1} to $3.24 \pm$ year^{-1}) among 11 tropical species in Costa Rica. A similar 4-fold range (0.37 year^{-1} to 1.58 year^{-1}) for the leaf decay rate has been found among 15 Peruvian tropical species (Salinas *et al.* 2011). The large-scale analyses have demonstrated that the decomposition rate of litter is faster in tropical than boreal and temperate forests (Raich *et al.* 2006; Strickland *et al.* 2015; Zhang *et al.* 2008; Zhu *et al.* 2017). Biologically, species composition affects the spatial distribution of the litter mass due to the different chemical properties (such as soil pH and nutrient content) which are caused by the different recycling rates of litter input among plant species at both local and fine scales (Adair *et al.* 2008; Gholz *et al.* 2000; Xia *et al.* 2015). For example, a higher accumulating rate of litter mass with a lower beech diversity has been found in the central European forests (Keiser 2017). In contrast, a study in the tropical region has reported that the mixed forests have faster litter decomposition rates than monocultures, leading to a less accumulated litter mass even with a larger amount of litter production (Guo *et al.* 1999).

The mature forests provide an opportunity to evaluate the relative influence of biotic and abiotic factors in controlling the spatial variation of aboveground litter stock. On the global scale, most forests are aging in the current era (Curtis and Gough 2018). Relative to young forests, the mature forests have more buffering of microclimates and thus maintain a quasi-equilibrium state of carbon storage (Chen *et al.* 1993; Curtis *et al.* 2018). While the rate of net primary productivity decreases to zero from mature to old forests, the litter carbon stock could approach to a stable state (Pregitzer *et al.* 2004; Ryan *et al.* 1997). Thus, quantifying the relative contributions of biotic and abiotic factors to the spatial variation of aboveground litter stock in mature forests becomes increasingly important.

This study was conducted in a mature and mixed subtropical broad-leaves forest in the eastern China. It focuses on detecting the spatial pattern of aboveground litter stock and its controlling processes on the fine scale of about 20×25 m^2. The aboveground litter pool in this study is defined as the fallen litterfall and decomposing organ residue lying loose above the mineral soil with the exclusion of both fine (>0.5 cm in diameter; Woodall and Monleon 2008) and coarse (>7 cm; Vogt *et al.* 1986) debris. The boosted regression tree analysis was applied to evaluate the explanation of environmental and plant factors to the spatial variations of litter mass. The objective of this study is to explore how the spatial distribution of the aboveground litter stocks were influenced by the abiotic and biotic factors on the fine spatial scale.

MATERIALS AND METHODS

Study site

This study was performed in a 20-hm forest dynamics plot in the Tiantong Forest Park, Zhejiang Province, China (121.78° E, 29.80° N; Fig. 1). The 20-hm forest plot was established in the year 2010, and all woody stems with diameter ≥1cm at breast height (DBH) at 130 cm have been measured with an interval of 5 years. The stand age of this forest is around 60 years. It is characterized as an undisturbed and typical low-elevation moist broad-leaved subtropical forest in the eastern China (Song 1995, 1988; Yang *et al.* 2010). The plant

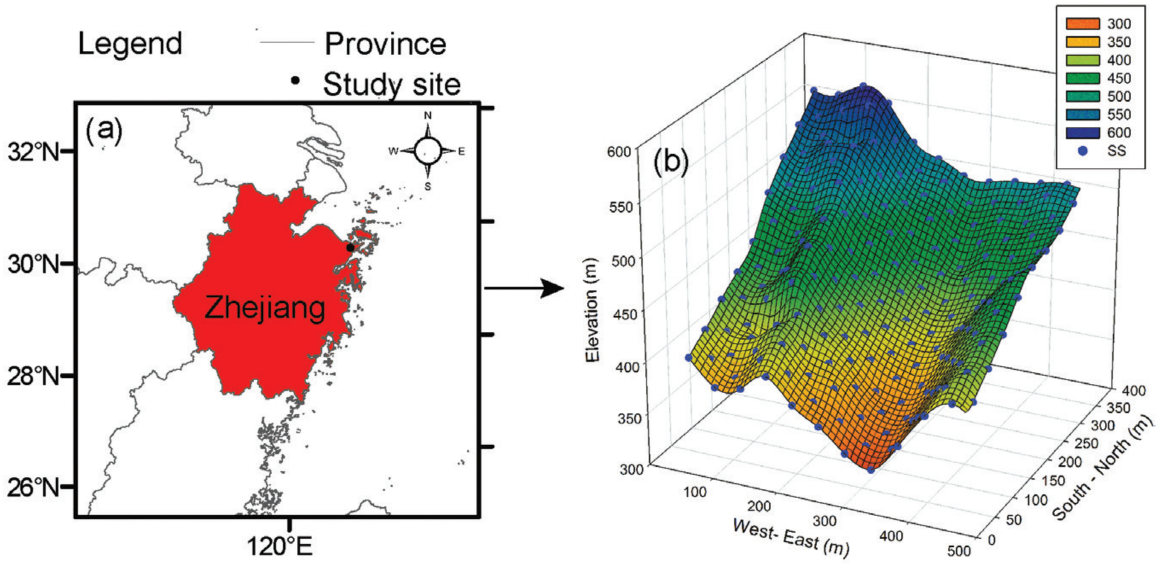

Figure 1: the location of the 20-hm forest dynamics plot in the Tiantong Forest Park (**a**); the distribution of sampling sites (**b**).

community is dominated by species of *Theaceae*, *Lauraceae* and *Fagaceae*. Important tree species in the plot includes *Schima superba*, *Castanopsis Fargesii*, *Choerospondias axiliaris* and *Machilus thunbergii*. The soil is acid yellow-red soil and developed from Mesozoic sedimentary rocks parent materials, with the pH ranges from 4.5 to 5.1 (Song 1988).

As shown in Fig. 1c, the forest plot was systematically divided into 187 grids with each occupies an area of 20 × 25 m^2. Three replications of aboveground litter were collected in each grid with a sampling size of 50 cm × 50 cm. The litter samples were collected in May 2016. The samples of the litter were dried in the oven for 48 h at 65°C and the dried weight was then measured.

The vegetation in the Tiantong forest dynamics plot is subtropical broad-leaved forest, which contains both evergreen and deciduous species. All the grids were divided into the two habitats (i.e. evergreen and deciduous) based on the importance value which is defined as (relative abundance + relative basal area)/2 (Yang *et al.* 2011). The relative abundance was calculated as the number of independent individuals. The plant community of the forest plot was fully surveyed in 2010, and there are totally 94 605 living stems belonging to 152 species recorded (Yang *et al.* 2016). Among the 187 grids, 151 grids were dominated by evergreen species while the other 36 grids were dominated by deciduous species (Yang *et al.* 2011).

Climate data and geographical information

The soil temperature was detected every half hour with temperature data loggers (iButton, DS1922, Wdsen electronic technology Co., Shanghai, China), which were installed horizontally at the depth of 10 cm in all the 187 grids. Soil moisture in each grid was manually measured every 3 weeks with a portable soil moisture detector (TZS, Zhejiang, China). The monthly soil moisture value was calculated for the 0–10 cm soil layer by averaging the three replications of measurement. The monthly air temperature and precipitation data were collected from China Meteorological Data Service Center (http://www.cma.gov.cn/2011qxfw/2011qsjgx/).

Each 20 × 25 m^2 grid had three categorizations of topographic information, including elevation, convexity and slope. The elevation of 20-hm quadrats ranges from 304.3 to 602.9 m with the mean value of 441.4 m (Fig. 1c). The topographic feature of 20-hm forest dynamic plot is steeply and rocky with two large gullies from north to south, and the northwestern corner of the whole plot is the highest point. The convexity was calculated as the difference of average elevation which the i-*th* quadrat minus the average elevation of the adjacent 8 quadrats (Valencia *et al.* 2004). The range of convexity is −2.43 to 3.02, with the positive convexity indicates that the altitude of the sample is higher than that of the surrounding sample (Harms *et al.* 2001).

Statistical analysis

The coefficient of variance (100 × SD/Mean, %) was calculated for the variance of litter stock, environmental or topography factors. The litter carbon storage was calculated as the product of carbon bulk density in the litter mass and the grid area. The spatial distribution of the accumulated litter stock and its related variables were mapped with the Kriging method using the ArcGIS software (Version 10.4.1, Environmental System Research Institute, USA 2016).

The topography position index (TPI) was adopted to quantify the influence of topographic factors on aboveground litter stocks (Jenness 2006). The TPI is an index comparing the elevation and slope with adjacent cells. The values of TPI for each plot were calculated from interpolated elevations using 3 × 3 tangle moving windows with the ArcGIS software. The positive TPI values represent that the locations are higher than the average of their surroundings (i.e. Upslope), while the negative values indicate lower locations than their surroundings (i.e. Downslope). The zero values of TPI indicate the flat areas (i.e. Mid-slope). The correlation between aboveground litter stock with microclimate and TPI was also calculated with R (version 3.3.2, R Development Core Team 2017).

The relative influences of different predictors (i.e. environmental, topographic and species variables) on aboveground litter stock and the specific influences of each relationship were accessed by using the boosted regression tree analysis. The variables had been standardized by a Z-score-based method before were used in the boosted regression tree analysis (Friedman 2001). The boosted regression tree analysis was applied to investigate the controlling factors of litter stock by iteratively splitting the data into groups and then create ensembles of regression trees. This method could overcome the over-fitting issue (Lawrence *et al.* 2004). Higher relative influence values for a given variable indicate a stronger influence on controlling the spatial variation of the litter stock. Partial dependency plots were used to interpret the relationships between the predictors and the response variables. The boosted regression tree analysis was applied with the '*gbm*' R package (version 2.9) (Elith *et al.* 2008).

The boosted regression tree analysis fits model according to an interactive bagging process. In each iteration, the fraction of the total dataset (explicitly *bag fraction* in the *gbm* package, the same below) is randomly selected without replacement. The three main parameters needing optimization in the boosted regression tree analysis were the learning rate (*shrinkage*), the depth of each regression tree (*interaction.depth*) and the number of iteration (*ntree*). In this study, the three optimized parameters for *shrinkage*, *interaction.depth* and *ntree* were 0.01, 5 and 3000, respectively. The cross-validation (*cv. folds* = 5) was applied to estimate the predictive power of the models. The dataset (187 grids) was divided into a training set (131 grids) and a test set (56 grids). All variables for predicting the litter stocks include elevation, slope, convexity, number of trees, the dominant species, soil moisture, and soil temperature in each grid.

RESULTS

Environmental factors

Both annual air temperature and precipitation showed seasonal fluctuations. Mean annual precipitation of 2016–2017 was 1027 mm, >70% of which occurred in the wet season (i.e. May to July). Mean annual air temperatures over 2008–2017 was 16.5°C, with the lowest and highest monthly mean temperatures as 4°C and 30°C in January and in July, respectively. The annual mean air temperature was 17.8°C over 2016–2017 (Fig. 2). Mean monthly soil moisture at the depth of 0–10 cm showed a slight fluctuation during the whole year. However, the coefficient of variances of soil moisture among different months range from 19.6% to 64.8% among the 187 grids (Table 1, Fig. 2). The soil temperature was the highest in August as 24.8 ± 1.4°C and the lowest in February as 7.3 ± 1.2°C (Fig. 2a). In contrast, the soil moisture was the highest in April as 26.2 ± 6.5% and the lowest in August as 10.8 ± 3.9% (Fig. 2).

The aboveground litter stock

The mean aboveground litter stock was 367.5 g m^{-2} (Table 1, Fig. 3) at the Tiantong dynamics forest plot among all 187 sites. The litter stocks ranged from 109.2 to 831.3 g m^{-2}, with a large spatial variance with the coefficient of variance as 40.8%. The mean litter stock was lower in the mid-slope grids (331.3 ± 170.0 g m^{-2}) than that in the upslope (384.1 ± 152.0 g m^{-2}) and downslope (363.9 ± 118.0 g m^{-2}) grids (Table 1).

Effects of abiotic and biotic factors on litter stock

The dataset (187 grids) was divided into a training set (131 grids; 70% of the total grids) and a validation set (56 grids; 30% grids). The boosted regression tree analysis predicts reasonably well with R^2 = 0.69, and *RMSE* = 4.69 g m^{-2} based on the training dataset. The trained model performs well with the validation dataset, with the R^2 and *RMSE* as 0.65 and 4.82 g m^{-2}, respectively (Fig. 4b). The results from the boosted regression tree analysis showed that slope and elevation were the two most influential abiotic variables (Fig. 4a). The relative influences of litter stocks were 48.2, 28.6 and 23.2% from topographical, species and environment variables across the 187 grids (Fig. 4a). Although each variable was accounted for small variance of litter stocks, the abiotic variables (i.e. topographical and environmental variables) account for 71.4% of the overall influence of all variables (Fig. 4a). Both the number of trees and soil moisture varied along the three topographical gradients (Table 2). The numbers of trees at downslope and upslope were higher than mid-slope grids; The number of trees decreased in the order of downslope grids (303.7 ± 112.4) > upslope grids (230.7 ± 71.2) > mid-slope grids (197.1 ± 91.8).

Slope, elevation and soil moisture were the most influential factors to predict the litter stocks (relative influence = 19.6%, 16.7% and 12.8%, respectively), but others appear to play a role (Fig. 5). The relationship between litter stock and slope is generally positive but highly variable. The litter stocks are higher in slope between 30° to 35° or larger than 42° (Fig. 5a). The interaction between elevation and litter stock is complicated. The litter stocks are higher in elevation ranges from 360 to 410 m (Fig. 5b). A positive relationship between litter stocks and soil moisture with an increase between 21% to approximately 23% (Fig. 5c). A slightly positive relationship also existed between litter stocks and convexity where the convexity ranges from −1 to 0.5 (Fig. 5d). The positive

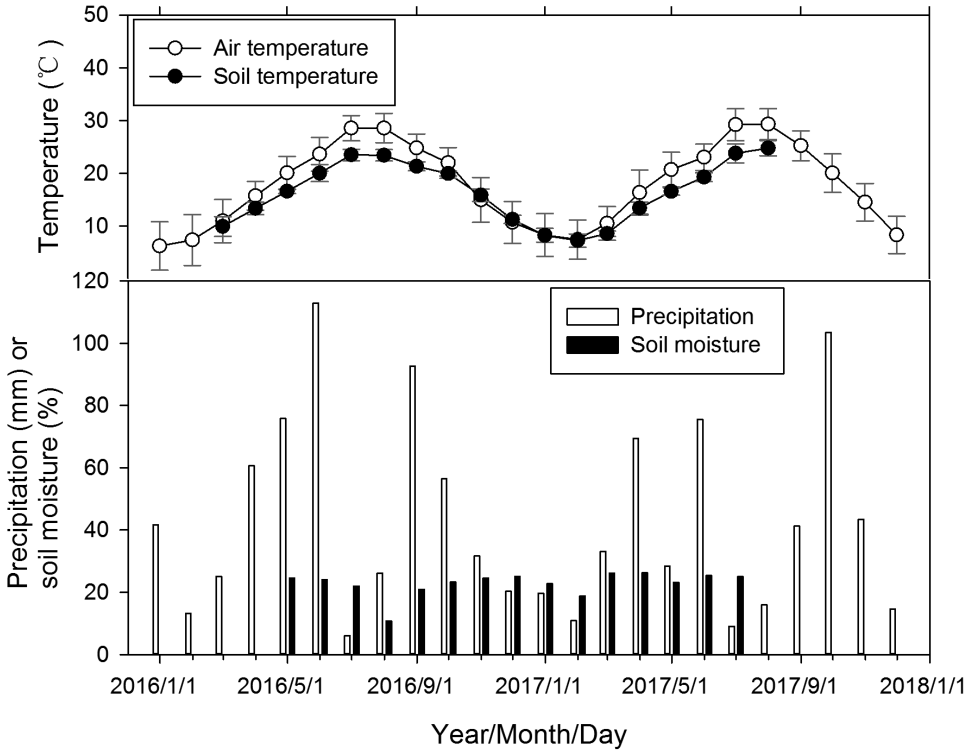

Figure 2: the mean annual air temperature and monthly soil temperature (**a**); mean annual precipitation and soil moisture (**b**).

Table 1: statistics of climatic and topographic factors

Variables	Units	Mean (SD)	Range (Min, Max)	COV (%)
Elevation	m	441.40 (53.60)	(324.30, 571.14)	12.14
Litter (Biomass)	g m^{-2}	367.50 (149.91)	(109.24, 831.28)	40.79
Number of trees	/	262.62 (109.91)	(27, 635)	41.85
Slope	/	35.51 (5.28)	(18.81, 46.43)	14.86
Soil moisture	%	22.85 (2.28)	(17.03, 30.06)	7.53
Soil temperature	°C	16.46 (1.24)	(12.39, 22.17)	10.00
Annual air temperature	°C	17.78 (0.69)	(6.22, 29.30)	3.86
Annual precipitation	mm	1027 (/)	/	/
Convexity	/	−0.05 (0.94)	(−2.43, 3.02)	/
TPI	/	−0.01 (0.19)	(−1.11, 0.69)	/

SD and COV indicate standard deviation and coefficient of variance, respectively. The '/' indicates the missing information.

relationship between sum area and litter stocks shown in sum area below 8000 m^{-2}. The slightly negative relationship existed where sum area ranges from 8000 to 12 000 m^{-2}. The relationship between soil temperature and litter stocks is weak when temperatures range from 15.0°C to 17.5°C.

The boosted regression tree analysis was able to assess the relative influence of each predictor for the impacts of other variables. The effect of slope on litter stocks was stronger at higher elevation (410–550 m; Fig. 6a). The interaction between slope and soil moisture suggests that the slope have more effects on litter stocks at all gradients where the soil moisture higher than 21% (Fig. 6b). The effect of soil moisture on litter stocks is high and stronger where the elevation is higher than 360 m (Fig. 6c). The deciduous species dominant habitats have larger spatial variance and litter stocks, while the evergreen species shown a small spatial variance and litter stocks (Fig. 6d). Also, the deciduous species distributed in the areas of the higher elevation and lower slope, while the evergreen species distributed in the areas of lower elevation and higher slope (Fig. 6e and f). Thus, we integrated the slope, elevation and convexity into TPI to evaluate the spatial variance of litter stocks within two habitats.

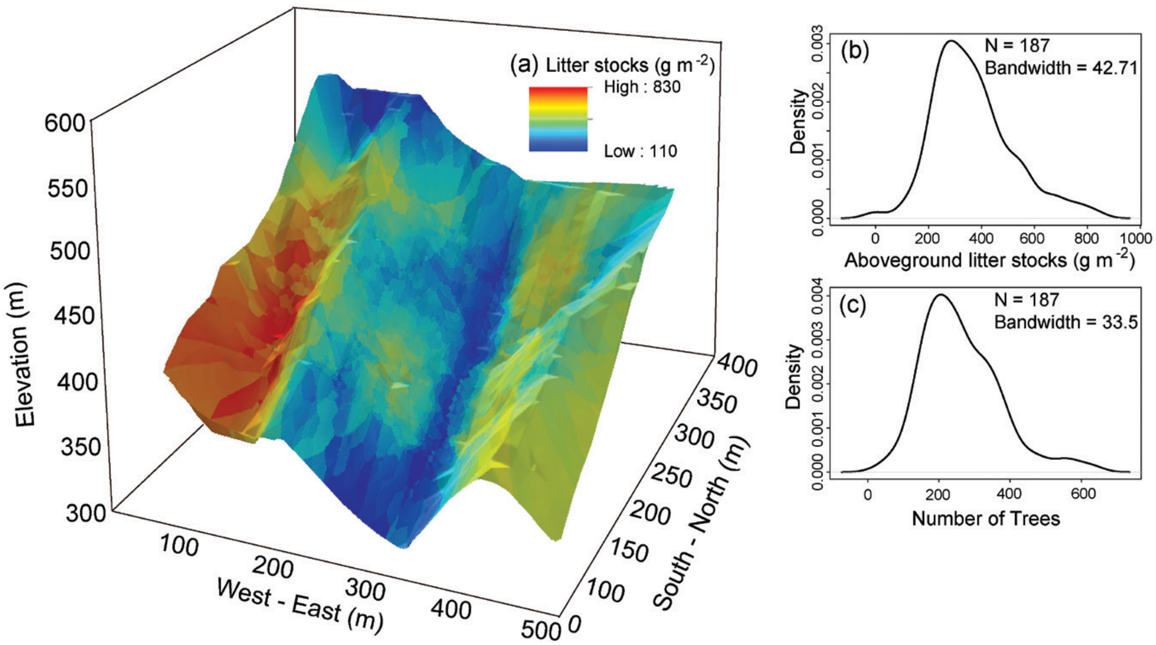

Figure 3: spatial distribution of aboveground litter stocks in the 20-hm forest dynamics plot (**a**). The density distribution of aboveground litter stocks (**b**) and the number of trees (**c**).

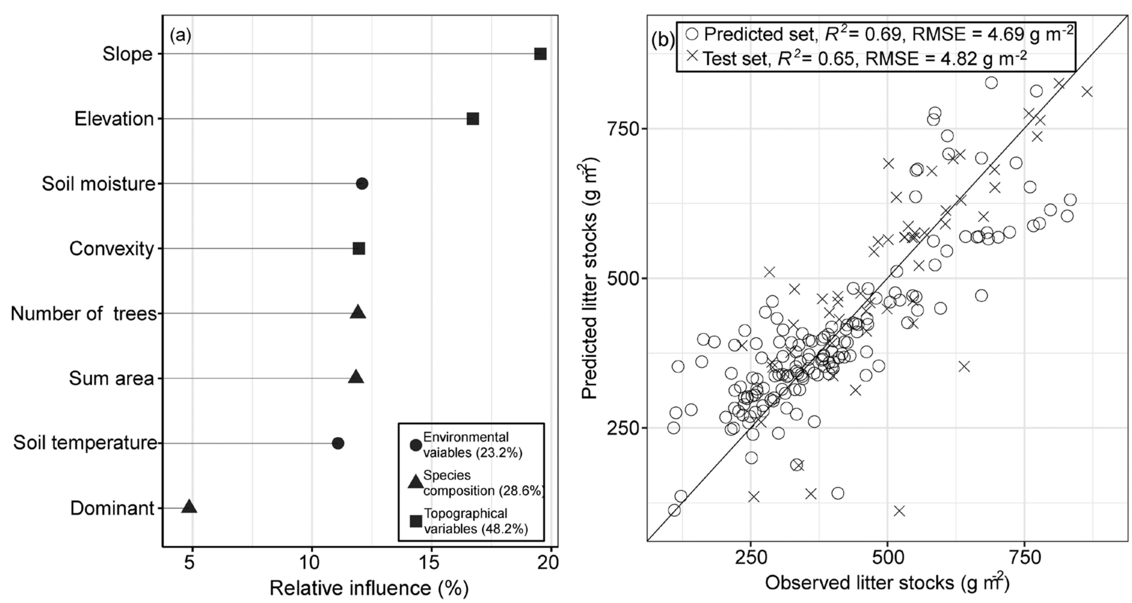

Figure 4: the relative influence (%) of predictor variables (environmental, topographic factors and species composition) for the boosted regression tree analysis (**a**). The observed and predicted litter stocks for the prediction set (open circle symbol) and test set (cross symbol) by boosted regression tree analysis (**b**). The black line is 1:1 line in panel (**b**).

Among two forest habitats (dominated by evergreen broad-leaves species and deciduous broad-leaves species) (Fig. 7a and b), deciduous species dominant habitats have higher litter stocks in downslope grids (481.6 ± 169.6 g m^{-2}) and upslope grids (409.5 ± 201.5 g·m^{-2}) than mid-slope grids (208.4 ± 103.7 g m^{-2}), while the litter stocks in evergreen species dominant habitats were 382.2 ± 161.4 g m^{-2}, 270.8 ± 54.0 g m^{-2} and 350.0 ± 112.1 g m^{-2} for downslope grids, mid-slope grids and upslope grids. The number of trees in deciduous species dominant habitats were 254.7 ±114.9, 147.1 ±77.3, and 260.7 ± 74.5 for downslope grids, mid-slope grids and upslope grids, respectively. The number of trees in evergreen

Table 2: the detailed information about litter stocks, soil moisture, soil temperature and number of trees across the topographical gradient (mean ± SD)

TPI	Litter stocks (g m^{-2})	Soil moisture (%)	Soil temperature (°C)	Number of trees
Upslope	363.9 ± 118.0	21.4 ± 1.7	16.2 ± 1.6	230.7 ± 71.2
Mid-slope	331.3 ± 170.0	22.3 ± 1.8	16.4 ± 1.2	197.1 ± 91.8
Downslope	384.1 ± 152.0	23.7 ± 2.3	16.6 ± 1.1	303.7 ± 112.4

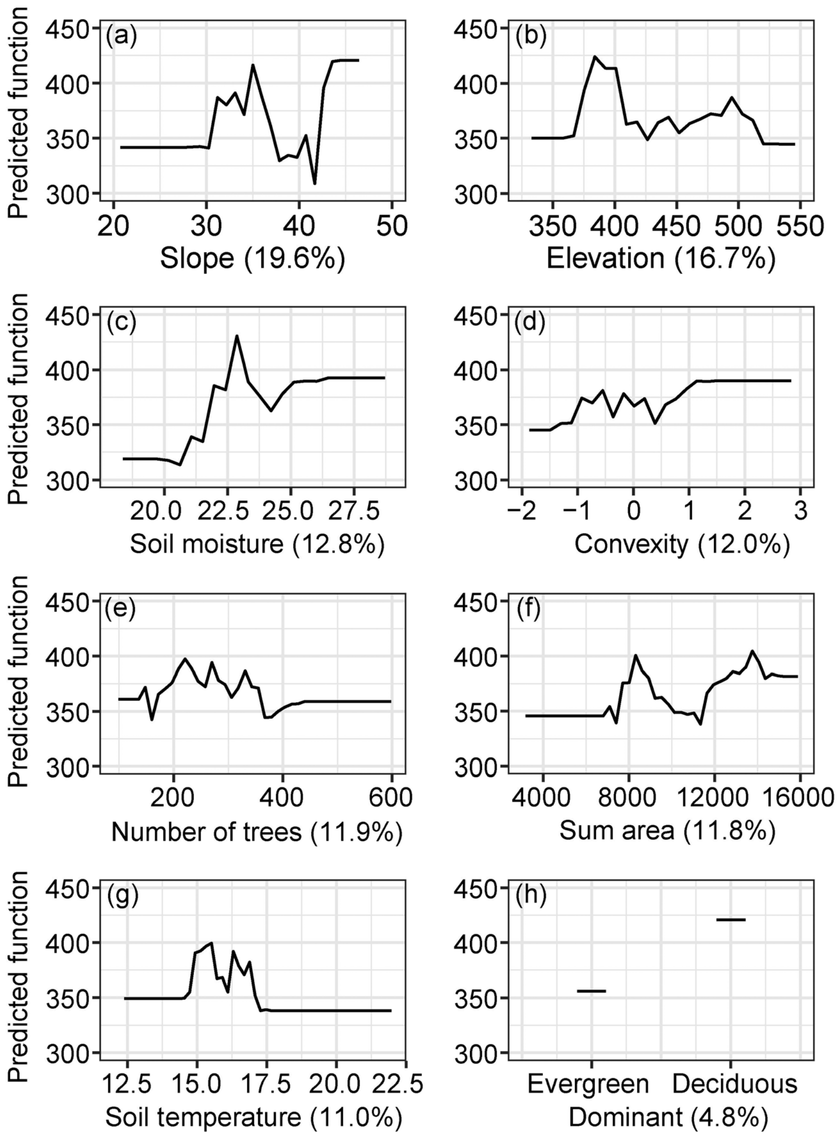

Figure 5: partial dependence of litter stocks for boosted regression tree analysis. The relative contributions are shown in brackets.

species dominant habitats were 304.9 ± 119.3, 244.8 ± 109.4, and 212.4 ± 79.6 for downslope grids, mid-slope grids and upslope grids, respectively.

In deciduous species dominant habitats, the soil moisture at mid-slope grids (21.7 ± 0.9%) was significantly lower than in the upslope grids (22.5 ± 2.0%) and downslope grids (22.2 ± 2.13%). In evergreen species dominant habitats, the soil moisture at downslope grids, mid-slope grids and upslope grids were 24.1 ± 2.5%, 22. 7 ± 1.4%, and 21.7 1.9%, respectively. The lowest soil temperature shown at upslope

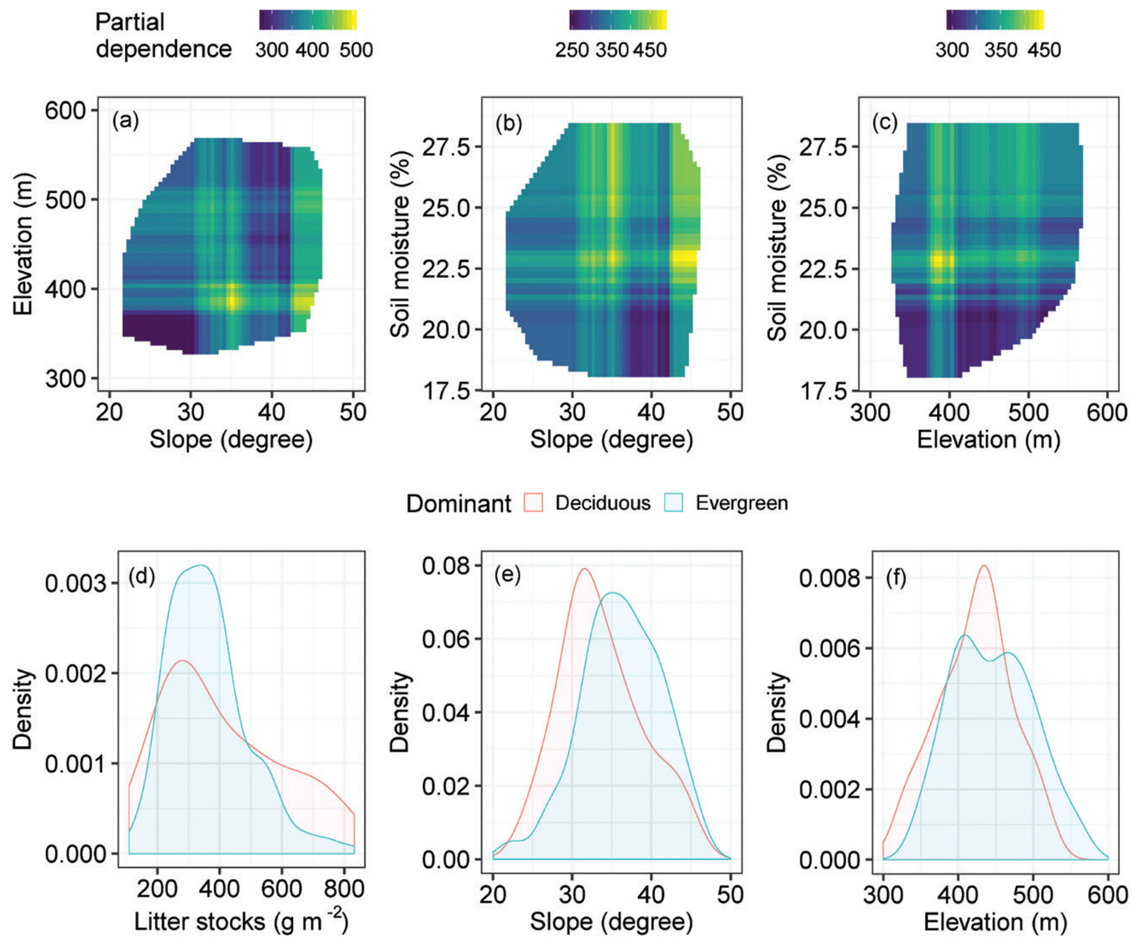

Figure 6: partial dependence plots of litter stocks and the interaction of top three predictors (slope (**a**), elevation (**b**) and soil moisture (**c**)) for boosted regression tree analysis shown in Fig. 4. The density distribution of aboveground litter stocks (**d**), slope (**e**) and elevation (**f**) in two habitats.

grids with value 21.5 ± 1.8% in the evergreen dominant habitats. However, for evergreen species dominant habitats, the mean soil temperature in mid-slope grids (17.10 ± 1.07°C) was slightly higher than the upslope (16.14 ± 1.51°C) and downslope grids (16.59 ± 1.10°C, Fig. 5d).

DISCUSSION

Our results show that abiotic factors, such as slope, elevation and soil moisture, are critical in determining the spatial distribution of the litter stock in the subtropical forest. Compared to an earlier estimate of the average litter stock in the subtropical forests of China (i.e. 6.8 t hm^{-2}; Jia 2016), the average litter stock in our study is lower (i.e. 3.7 t hm^{-2}). The highest litter stock in this region was reported as 12.5 t hm^{-2} in a tropical monsoon forest at Xishuangbanna (Zheng *et al.* 1990), followed by subtropical semi-deciduous forest at Jianfengling (9.8 t hm^{-2}) (Wu *et al.* 1994) and subtropical evergreen forest at Dinghushan (8.5 t hm^{-2}) (Guan *et al.* 2004). Coefficient of variation at our study site was higher than that of Dinghushan (14%). Different from the above three sites, the shorter grown season and distinct seasons made the lower primary production and slower decomposition rate in Tiantong dynamic forest plot. However, it should be noted that the wood debris has not been included in the litter stock in this analysis.

A marked relationship between topographical variables with aboveground litter was detected at both grids in our study (Figs 5 and 6). The topographical variables could affect the horizontal and vertical transitions of nutrients and water (Facelli *et al.* 1991; Tateno *et al.* 2003), and further reform the species composition and microbial activity by regulating the microclimate (Detto *et al.* 2013; Wang *et al.* 2018). Along the topographical gradients, the litter stocks were higher in the downslope (384.1 ± 152.0 g m^{-2}) and upslope (363.9 ± 118.0 g m^{-2}) grids than the mid-slope (331.3 ± 170.0 g m^{-2}) grids (Table 2). While the highest soil moisture shown in downslope grids (23.7 ± 2.3%) and followed by mid-slope (22.3 ± 1.8%) and upslope (21.4 ± 1.7%) grids (Table 2). In fact, the negative effect of increasing annual precipitation on litter decomposition rate has been reported in a wet tropical forest (Schuur 2001). A high correlation between soil moisture and microbial activity has also been reported, e.g. the

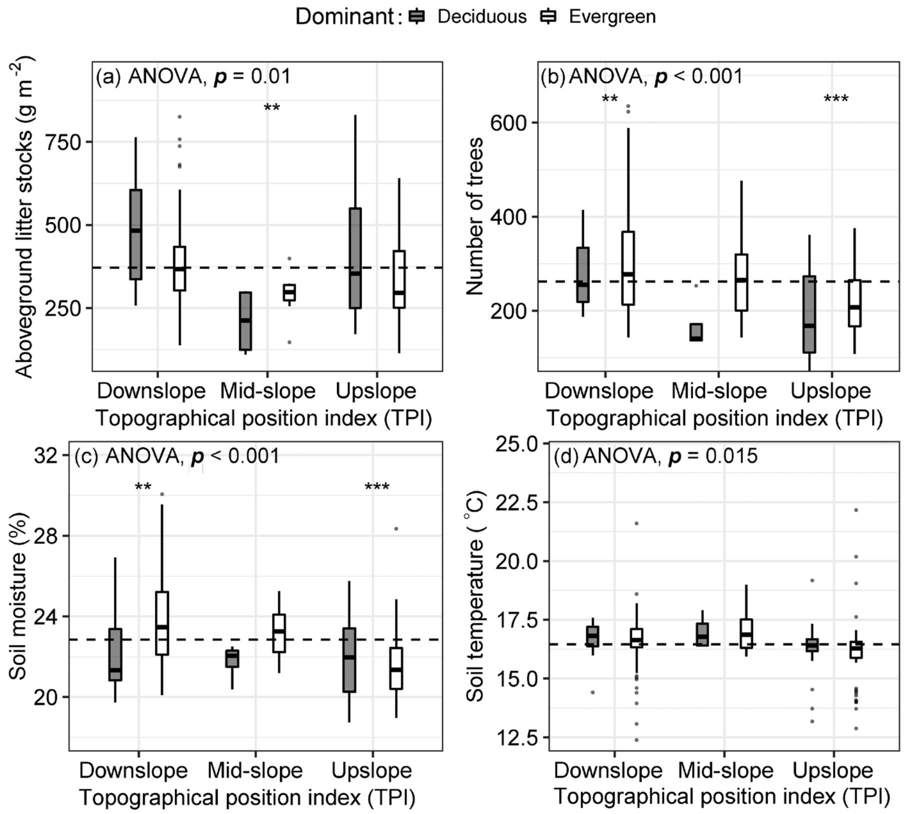

Figure 7: the different variables between downslope, mid-slope and upslope grids. (**a**) The distribution of aboveground litter stocks; (**b**) the number of trees; (**c**) soil moisture; and (**d**) soil temperature in two habitats. The dashed line indicates average value in different variables. ** and *** indicate *P* value as <0.01 and <0.001, respectively.

soil moisture availability accounts for >30% global variance of microbial biomass (Schjønning *et al.* 2003; Serna-Chavez *et al.* 2013). When the soil water excesses the upper limit of organic matter needs, the decomposition of litter also changed with the fluctuation of other variables, such as oxygen availability (Vitousek *et al.* 1994). In our study, the lower correlation between topographical variables and soil moisture may interact to affect the litter stocks via changing the substrate type, oxygen condition and nutrient availability.

The soil moisture also plays a significant role in the spatial variance of litter stocks between habitats occupied by deciduous and evergreen species. For the upslope grids, a higher soil moisture and a lower litter stock shown in deciduous species dominant habitats. For the mid-slope grids, the litter stock and soil moisture are higher in evergreen species dominant habitat. Such effects of soil moisture on litter stock have not been reported in other mixed forests. For example, no high correlation between the observed distribution of evergreen and deciduous stands and environmental variables has been detected in a temperate deciduous forest from Northern Michigan (Fotis *et al.* 2018). Also, similar litter stocks between deciduous (1.37 t hm^{-2}) and evergreen (1.58 t hm^{-2}) forest have been found in eastern India (Mohanraj *et al.* 2011). Considering there are still 31% variance could not be explained, this study leaves the unsolved possibility that other variables we do not mention may contribute the litter stocks, such as water movement (e.g. runoff) in litter layers. Moisture-related variables (e.g. precipitation) have been highlighting the importance of the interaction between climate and organic matters in controlling the storage of soil organic carbon (Guo *et al.* 2006). Considering there is still 31% variance could not be explained, this study suggests that some other variables, such as water movement (e.g. runoff) in the litter layers, may also have contributions to the spatial variation of litter stocks. The positive dependence of litter decomposition rates on the soil water availability has been reported in a wet tropical forest (Leff *et al.* 2012). A positive relationship between litter turnover rate and litter moisture has also been reported in a tropical dry forest, suggesting that the magnitude of individual rainfall events may play an important role in the litter decomposition (Schilling *et al.* 2016).

Decomposition processes in Earth system models remain highly uncertain in the projection of soil C storage and cycling (Denman *et al.* 2007; Matthews 1997). Some models have constrained the litter stock with plant traits data of different forest type, e.g. the Lund-Potsdam-Jena (LPJ) dynamic global vegetation model (DGVM) (Brovkin *et al.* 2012). The

Community Land model (CLM) has been evaluated by the long-term field data from litter traps (Bonan *et al.* 2013). In most of these models, the decomposition of litter is driven by the water and temperature scalars (Bonan *et al.* 2013; Brovkin *et al.* 2012; Sitch *et al.* 2003). It is clear that the contribution of topography to the litter mass dynamics has been overlooked globally. However, it should be noted that the global land models are currently used at much coarser scales, and topography may be only important in mountain areas such as the subtropical forest regions in China. Given that the global carbon-cycle models have been aiming to refine from the 100 kilometers to sub-kilometer scale, this study provides some implications and raises the research importance for a better understanding of the spatial variation of litter mass on the fine scale.

CONCLUSION

Litter has important ecological functions far beyond its commonly recognized role as a transitory bank of organic C (Meentemeyer *et al.* 1982; Netto 1987). In this study, the spatial variability of litter stock is mainly controlled by the abiotic variables in a mature subtropical evergreen broad-leaved forest. The findings highlight the importance of considering the influence of topography on the estimation of litter stock and its spatial variation. Although current Earth system models have considered both plant and environmental factors in estimating the litter accumulation and decomposition, we highly recommend the models to better represent the topography, especially in the subtropical forests.

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