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# Spatial and seasonal variations of leaf area index (LAI) in subtropical secondary forests related to floristic composition and stand characters

**Wenjuan Zhu[1,2], Wenhua Xiang[1,2,3*], Qiong Pan[4,1], Yelin Zeng[1], Shuai Ouyang[1,2,3], Pifeng Lei[1,2,3], Xiangwen Deng[1,2,3], Xi Fang [1.2,3], Changhui Peng[5,1]**

1 Faculty of Life Science and Technology, Central South University of Forestry and Technology, Changsha 410004, Hunan Province, China

2 Huitong National Field Station for Scientific Observation and Research of Chinese Fir Plantation Ecosystem in Hunan Province, Huitong 438107, China

3 National Engineering Laboratory of Applied Technology for Forestry & Ecology in Southern China, Changsha 410004, China

4 Changsha Environmental Protection College, Changsha 410004, China

5 Institute of Environment Sciences, Department of Biological Sciences, University of Quebec at Montreal, Montreal, QCH3C 3P8, Canada

* *Correspondence to*: Wenhua Xiang, Email: xiangwh2005@163.com, Tel.: +86 0731 85623483

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**Abstract.** Leaf area index (LAI) is an important parameter related to carbon, water and energy exchange between canopy and atmosphere, and is widely applied in the process models to simulate production and hydrological cycle in forest ecosystems. However, fine-scale spatial heterogeneity of LAI and its controlling factors have not been fully understood in Chinese subtropical forests. We used hemispherical photography to measure LAI values in three subtropical forests (i.e. *Pinus massoniana* - *Lithocarpus glaber* coniferous and evergreen broadleaved mixed forests, *Choerospondias axillaris* deciduous broadleaved forests, and *L. glaber* - *Cyclobalanopsis glauca* evergreen broadleaved forests) during period from April, 2014 to January, 2015. Spatial heterogeneity of LAI and its controlling factors were analysed by using geostatistics method the generalised additive models (GAMs), respectively. Our results showed that LAI values differed greatly in the three forests and their seasonal variations were consistent with plant phenology. LAI values exhibited strong spatial autocorrelation for three forests measured in January and for the *L. glaber* - *C. glauca* forest in April, July and October. Obvious patch distribution pattern of LAI values occurred in three forests during the non-growing period and this pattern gradually dwindled in the growing season. Stand basal area, crown coverage, crown width, proportion of deciduous species on basal area basis and forest types affected the spatial variations in LAI values in January, while species richness, crown coverage, stem number and forest types affected the spatial variations in LAI values in July. Floristic composition, spatial heterogeneity and seasonal variations should be considered for sampling strategy in indirect LAI measurement and application of LAI to simulate functional processes in subtropical forests.

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**Keywords:** Leaf area index; Spatial heterogeneity; Deciduous species; Generalised additive models (GAMs)

## 1 Introduction

Many fundamental ecological processes in forest ecosystems, such as carbon (C) flux as well as water and energy exchanges, take place between canopy layer and the atmosphere (Brut et al., 2009; GCOS, 2006; Alonzo et al., 2015; Liu et al., 2015b). At finer scale, leaves within canopy are the primary organ to perform a series of physiological activities (i.e. photosynthesis, respiration and evapotranspiration) (Aragão et al., 2005) and physical reactions (i.e. rainfall and radiation interception) (Smith, 1981; Crockford & Richardson, 2000; Aston, 1979). Therefore, the amount of leaves in a forest is the determinant of aboveground ecological processes and ecosystem functions. Leaf area index (LAI), defined as total one-sided leaf area per unit ground surface area (Biudes et al., 2014), is widely used parameter (Kross et al., 2015) to quantitatively describe the vegetation canopy structure (Woodgate et al., 2015), to simulate ecological process models (Sprintsin et al., 2007; Facchi et al., 2010; Brooks et al., 2006; Gonsamo & Chen, 2014) and to reveal tree growth and productivity in forests at stand scale and landscape level (Liu et al., 2015b; Lee et al., 2004). In addition, LAI is listed as one of the essential variables for observation of global climate (Mason et al., 2003; Manninen et al., 2009) and for remote sensing data validation (Asner et al., 2003; Clark et al., 2008). Thus, accurate estimations of LAI value are important to understand ecological processes in forest ecosystems.

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58 At present, various direct and indirect methods have been developed to measure LAI in forests.
59 Direct estimation methods including leaf harvest (Clark et al., 2008), allometric equations and litter
60 collection (Ryu et al., 2010; Liu et al., 2015a) are recognised as the most accurate method. However,
61 leaf harvest and allometric equations methods need time-consuming, labour-intensive and destructive
62 sampling process, while litter collection is more feasible for temperate deciduous forests. Obviously, the
63 direct method is less applicable for large-scale and long-term LAI monitoring (Bequet et al., 2012;
64 Biudes et al., 2014). Indirect methods include plant canopy analyser (Licor LAI-2000), hemispherical or
65 fisheye photography (Macfarlane et al., 2007) and remote sensing (Biudes et al., 2014). The indirect
66 methods retrieve LAI value from light transmittance through canopies or from canopy image analysis.
67 For large scale LAI estimates, remote sensing is the effective method but requires validation with the
68 ground-based LAI data. It is still a challenge for LAI estimates on the ground at small scales due to the
69 problems of sampling strategies associated with accepted level of accuracy, time and cost consideration
70 (Richardson et al., 2009). Hemispherical photography is a relatively simple and easily operated method
71 among many indirect methods to retrieve LAI value at small scales (Demarez et al., 2008). Correction
72 of the effects of woody materials, clumping and zenith angels or exposure is critical for improving the
73 accuracy of LAI estimation (Liu et al., 2015b). Analysis software development and portable and timely
74 characteristics allow hemispherical photography to measure spatial heterogeneity and seasonal
75 variations of LAI in forests.

76 Forest canopy structure is highly complicate so LAI values show great temporal and spatial variations

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77 at scales ranging from stand to global scale. For example, LAI values in the 7.9 ha plot of an old humid
78 temperate forest tended to increase spatially as elevation increased and showed a temporal variation
79 with plant phenology (Naithani et al., 2013). The spatial patterns of LAI values at stand scale were
80 significantly influenced by spatial distribution of tree species, which was dependent on topography and
81 soil types (Naithani et al., 2013). Coefficient of variations (CV) in LAI decreased as the scale increased
82 and LAI values did not have any relationship with biome type and climate patterns, but were influenced
83 by land use and land cover, terrain features, and soil properties at stand scale (Aragão et al., 2005). The
84 CV of LAI of three species (i.e. beech, oak and pine) had different degree spatial variations in 1 ha plot
85 at stand level (Bequet et al., 2012). LAI values in sagebrush displayed strong spatial patterns with the
86 time after disturbance and increased with stand age and total plant cover (Ewers & Pendall, 2007). The
87 LAI values derived from MODIS data (Huang et al., 2008; Myneni et al., 2002) revealed strong spatial
88 variations at global scale and the variations were correlated with latitude (Tian et al., 2004). At global
89 scale, temperature is the limiting factor for LAI under cool conditions while water plays a predominant
90 role under other conditions, and this pattern differed among plant functional types (Iio et al., 2014). The
91 factors that govern the spatial variations in LAI values at stand level include forest types, stand structure
92 (Bequet et al., 2012), climate (Shao & Zeng, 2011), topography, soil moisture condition (Breshears &
93 Barnes, 1999), and human disturbance and management activities (Huang & Ji, 2010). Although effects
94 of topography, soil properties (Naithani et al., 2013; Aragão et al., 2005) and stand character (Bequet et
95 al., 2012; Yao et al., 2015) on LAI values have been investigated in detail, how forest types, tree species

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96 diversity and stand structure affect spatial heterogeneity and seasonal variations of LAI has not been
97 fully understood.

98 Chinese subtropical forests contain a diversity of tree species with complex canopy structure and
99 mostly grow on heterogeneous topography and soil condition. As a result, LAI in subtropical forests
100 may exhibit greatly spatial and seasonal variations, which is worthy of further investigation. However,
101 LAI data of subtropical forests are relative deficiency in the global database (see Asner et al., 2003). In
102 this study, we selected three different forests (i.e. *Pinus massoniana* - *Lithocarpus glaber* coniferous
103 and evergreen broadleaved mixed forests, *Choerospondias axillaris* deciduous broadleaved forests, and
104 *L. glaber* - *Cyclobalanopsis glauca* evergreen broadleaved forests), LAI values were measured by using
105 hemispherical photography. Spatial heterogeneity of LAI was investigated through geostatistics analysis
106 method. The generalised additive models (GAMs) were used to examine how tree species diversity and
107 stand characters affect LAI variations in the three forests. Specifically, the objectives of this study were:
108 (1) to examine differences and seasonal variations in LAI among three forests in subtropical China; (2)
109 to analyse spatial heterogeneity of LAI values within a specific forest; and (3) to identify how forest
110 types, species diversity and stand characters control the spatial heterogeneity and seasonal variations of
111 LAI values in three forests.

112

113 # 2 Materials and methods

114 ## 2.1 Study site description

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115 The study was carried out at the Dashanchong Forest Farm (latitude 28°23′58″ - 28°24′ 58″ N,
116 longitude 113°17′46″ - 113°19′08″ E), Changsha County, Hunan Province, China. The Farm
117 experiences a humid mid-subtropical monsoon climate. Mean annual air temperature was between
118 16.6 ℃ to 17.6 ℃, with a mean monthly minimum temperature of -11 ℃ in January and maximum
119 temperature of 40 ℃ in July. Mean annual precipitation ranged from 1412 mm to 1559 mm, mostly
120 occurring between April and August. The topography is characterized by a typical low hilly landscape
121 with an altitude between 55 m to 260 m above sea level. Soil type is designated as well-drained clay
122 loam red soil developed on slate and shale rock, classified as Alliti-Udic Ferrosols, corresponding to
123 Acrisol in the World Reference Base for Soil Resource (IUSS Working Group WRB, 2006). Evergreen
124 broadleaved forest is the climax vegetation of the region. As a result of human disturbance and
125 management activities, the Farm possesses a range of secondary forests dominated by different tree
126 species, including *P. massoniana* - *L. glaber* coniferous and evergreen broadleaved mixed forests, *C.*
127 *axillaris* deciduous broadleaved forests, and *L. glaber* - *C. glauca* evergreen broadleaved forests (Xiang
128 et al., 2015).
129
130 **2.2 Stand characteristics determination**
131 We established a permanent plot for each of three forests (i.e. 90 m × 190 m plot for *P. massoniana* -
132 *L. glaber* mixed forests, 100 m × 100 m plot for *C. axillaris* deciduous forests, and 100 m × 100 m plot
133 for *L. glaber* - *C. glauca* evergreen broadleaved forests). Each plot was divided into 10 m × 10 m

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subplots, where tree species, diameter at breast height (DBH, cm), tree height (H, m), height under the lowest live branch (m) and crown width (m) were measured for the individual stem with DBH larger than 1 cm. Stand characteristics for the trees with DBH larger than 4 cm of the three forests were presented in Table S1.

To identify the factors that control spatial heterogeneity of LAI values in the forests, we selected individual trees with H larger than average height of each stand (see Table S1) and calculated their stem number, average DBH, H, total basal area at breast height (BA), crown width, crown coverage, biodiversity index, the proportion of BA of three functional group (coniferous, deciduous and evergreen broadleaved species) to total stand BA within a subplot. Biodiversity index (BDI) was determined by Shannon-Wiener index as the formula:

$$BDI=-\sum P_i \ln P_i \quad (1)$$

where $P_i$ is important value of *i*th species and is calculated by dividing the sum of relative abundance degree (*A*r) and relative dominance degree (*D*r) of *i*th species within a subplot by two.

## 2.3 Sampling design for LAI measurement

At the centre of each subplot of the three forests, hemipherical photographs were taken using a LAI measuring instrument (SY-S01A) throughout four measurement seasons, i.e. in April (spring), July (summer) and October (autumn) in 2014 and January (winter) in 2015. The operation was carried out below canopy with the fisheye lens 1.0 m above the ground (Manninen et al., 2009). We took the

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153 photographs in the morning, dusk or cloudy to minimize influence of direct sunshine (Rich, 1990;
154 Bequet et al., 2012). The images were processed and effective LAI values ($L_e$) were recorded by the
155 plant canopy analysis system of the LAI measuring instrument. To obtain accurate LAI ($L$), the
156 correction was made to $L_e$ based on previous theory (Chen, 1996):

157 $$L = \frac{(1-\alpha)L_e\gamma_E}{\Omega_E} \quad (2)$$

158 where $\alpha$ is the ratio of woody to total area and reflects the contribution of woody materials to $L_e$. $\Omega_E$ is
159 the clumping index that quantifies the effect of foliage clumping beyond shoots level. $\gamma_E$ is the needle to
160 shoot area ratio and quantifies the effect of foliage clumping within shoots.

161 Photoshop Software (Adobe Photoshop CS5, Adobe Systems Incorporated, North America) was used
162 to calculate $\alpha$. After total pixel number of $L_e$ image was determined, the Clone Stamp Tool in the
163 software was used to replace the woody materials with surrounding of non-woody materials and to
164 obtain the pixel number and recorded as LAI of leaves ($LAI_{leaf}$). The value of $\alpha$ was calculated
165 accordingly:

166 $$\alpha = (L_e - LAI_{leaf})/L_e \quad (3)$$

167 The logarithm averaging method proposed by Lang and Xiang (1986) was applied to calculate $\Omega_E$:

168 $$\Omega(\theta) = \frac{\ln[P(\bar{\theta})]}{\ln[P(\bar{\theta})]} = \frac{n\ln[P(\bar{\theta})]}{\sum_{k=1}^{n}\ln(P_k(\theta)]} \quad (4)$$

169 where $P(\theta)$ is the average gap fraction (expressed without the bar in the text), $\ln[P(\theta)]$ is the logarithm
170 average of the gap fraction, $P_k(\theta)$ is the gap fraction of segment $k$. For deciduous and evergreen

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broadleaved species, $\gamma_E$=1.0, but for coniferous species, $\gamma_E$ is always greater than 1.0, but we ignored the effect of needle to shoot area on LAI in this study.

## 2.4 Data analysis

The minimum, maximum, mean value, standard deviation and coefficient of variation (CV) were calculated for the LAI data in the three forests. Two-way analysis of variance (ANOVA) was used to detect effects of forest types and measurement seasons on LAI values. The LAI data in the three forests were tested for normal distribution using the K-S test ($p$<0.05). We used domain method to identify the specific values and replaced them with normally maximal values and if the data did not meet normal distribution, the transformation was applied till the statistical assumption was met. Most values required natural logarithm transformation to meet assumptions of normality. The exception is for *L. glaber* - *C. glauca* in April which was cosine transformed and *L. glaber* - *C. glauca* in November which was artan-transformed.

To investigate spatial heterogeneity of LAI values at four seasons measured in the three forests, semivariance function was calculated as the following formula:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2 \quad (5)$$

where $\gamma(h)$ is semivariance value of lag distance $h$, $N(h)$ is the number of pair data for lag distance $h$, $Z(x_i)$ and $Z(x_i + h)$ represent LAI values at coordinate $x_i$ and $(x_i+h)$ (Rossi et al., 1992). Based on the semivariogram plotting $\gamma(h)$ values against $h$ variable, the appropriate models were fitted and we

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obtained the values of nugget ($C_0$), sill ($C_0+C$), range ($A_0$) (Ewers & Pendall, 2007) and the ratio [$C/(C_0+C)$] that reflected the degree of spatial autocorrelation of LAI values in a forest. Because spatial autocorrelation and semivariogram theory make unbiased optimal estimation for regional variables in a limited area (Bivand et al., 2013), Kriging interpolation method was used to predict unknown LAI values in the forests from the data measured and to produce spatial distribution map of LAI values for the three forests at four seasons.

Because the largest amount of defoliated leaves occurs in January and leaves fully expand in July in subtropical forests, we chose LAI values measured in January and July in three forests as response variable. Stepwise regression was used to select the factors that significantly affect LAI variations. The factors include forest types, species diversity (species richness and biodiversity index) and stand characters (stem number, average DBH, H, BA, crown width, crown coverage, the proportion of two functional groups (deciduous and evergreen broadleaved species) to total stand BA). Stepwise regression showed that BA, crown coverage, crown width, the proportion of deciduous species to total stand BA and forest types significantly influenced LAI values measured in January, whereas species richness, stem number, crown coverage and forest types significantly affected LAI values measured in July (Tables S2). However, residuals of stepwise regression did not meet the requirements of normal distribution and homogeneity (Fig. S1 and Fig. S2). The generalised additive models (GAMs) have the advantages to analyse complex and nonlinear relationships (Guisan et al., 2002; Austin, 2002; Wood, 2006). Therefore, we used GAMs to examine how the factors selected by stepwise regression affect LAI

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values. The function of GAMs is the addition of many smooth functions and each smooth function has an explanatory variable. The variance inflation factor (VIF), the ratio of the variance of regression coefficient for a variable when fitting with all variables to the variance of regression coefficient for the variable if fit on its own, was used to test the multi-collinearity of explanatory variables (James et al., 2013). When the VIF of an explanatory variable is between 0 and 10, the variable was retained to the model; otherwise, we discarded the variable (Shen et al., 2015). The Akaike information criterion (AIC) or generalised cross validation (GCV) was used to determine whether the model was good or bad (Clark, 2013). The factors selected after multi-collinearity test were used for multi-factor analysis. After all the possible models in multi-factor analysis, we determined the optimal model based on the significant influence of all explanatory variables in the model with the smallest AIC or GCV (Dong et al., 2012). Geostatistics analysis was performed with GS+ software (Gamma Design Software). Statistical analysis and GAMs analysis were operated in R programme. The car packages were used to test multi-collinearity and the gam packages were used to select the optimal model.

# 3 Results

## 3.1 Variations of LAI values in three forests

The LAI values varied with forest types and measurement seasons (Table 1). Generally, LAI differed significantly for measurement seasons ($p<0.001$), but LAI difference was not significant among forest types ($p>0.05$). Interactive effects of measurement seasons and forest types on LAI were significant

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($p$<0.01). Among three forests, LAI in the *P. massoniana - L. glaber* forest had relatively low variations, while LAI in the *L. glaber - C. glauca* forest had the highest variations. In the *P. massoniana - L. glaber* forest, LAI showed the largest variations (the highest CVs) in October and the lowest variations (the smallest CVs) in January. In the *C. axillaris* forest, the largest variation in LAI was found in April and the lowest was found in January. In the *L. glaber - C. glauca* forest, LAI showed the largest variations in April and had the lowest variations in July.

Mean LAI values in the three forests showed different seasonal variation patterns (Fig. 1). The *C. axillaris* forest exhibited a unimodal pattern of seasonal variations, with the maximum mean LAI value (3.11±1.18) occurring in July and the minimum mean LAI value (1.28±0.44) in January. In the *P. massoniana - L. glaber* forest and *L. glaber - C. glauca* forest, the maximum mean LAI value both occurred in October and the minimum mean LAI value appeared in January. During the growing season (April and July), the *C. axillaris* forest had the highest mean LAI value and the *L. glaber - C. glauca* forest had the lowest mean LAI value. During the non-growing season (October and January), the *L. glaber - C. glauca* forest had the highest mean LAI value in January, while the *P. massoniana - L. glaber* forest had the highest mean LAI value in October, the *C. axillaris* forest had the lowest mean LAI values.

Mean $\alpha$ values in the three forests showed different seasonal variation patterns (Table 2). The *C. axillaris* forest exhibited a unimodal pattern of seasonal variations in mean $\alpha$ value, with the maximum mean $\alpha$ value occurring in January and the minimum mean $\alpha$ value in July. No obvious seasonal

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247 variations were found for the mean $\alpha$ value in the *P. massoniana* - *L. glaber* forest and in the *L. glaber* -
248 *C. glauca* forest. Mean $\Omega_E$ values in the three forests were between 0.84-0.92, but they did not show
249 clear seasonal variations, and the standard deviations were small.

250

251 **3.2 Spatial heterogeneity of LAI values in three forests**

252 The semivariograms results for LAI in three forests during different measurement seasons were
253 summarised in Table 3. The spatially dependent variance [$C$] accounted for 88.9% - 98.4% of the total
254 variance [$C+C_0$] for LAI values measured in January in the three forests and also in April, July and
255 October in the *L. glaber* - *C. glauca* forest. This indicated the strong spatial autocorrelations of LAI
256 values at short distance. These LAI data were best fitted with gaussian model or exponential model ($r^2 >$
257 0.50).

258 Spatial autocorrelation range of LAI values differed among forests and measurement seasons (Table
259 3). In January, the largest spatial autocorrelation range was found in the *P. massoniana* - *L. glaber* forest,
260 and the lowest was found in the *C. axillaris* forest. In April, the largest spatial autocorrelation range of
261 LAI was found in the *C. axillaris* forest, and the lowest was found in the *P. massoniana* - *L. glaber*
262 forest. In July, the *P. massoniana* - *L. glaber* forest had the largest spatial autocorrelation range of LAI,
263 while the *C. axillaris* forest had the smallest spatial autocorrelation range. In October, the *L. glaber* - *C.*
264 *glauca* forest had the largest spatial autocorrelation range of LAI, while the *P. massoniana* - *L. glaber*
265 forest had the smallest spatial autocorrelation range. Seasonal changes of range showed one peak

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pattern for *C. axillaris* forest and *L. glaber* - *C. glauca* forest, where the large range appeared in the growing season (April and July) and the small range appeared in the non-growing season (October and January).

Spatial distribution pattern of LAI values also varied with forest types and measurement seasons (Fig. 2). For example, LAI values in January in three forests exhibited obvious patch and heterogeneous spatial distribution. In April and July, less spatial heterogeneity was found for LAI values in three forests especially in the *P. massoniana* - *L. glaber* forest. In October, heterogeneous and patch spatial distributions of LAI values appeared in the *L. glaber* - *C. glauca* forest, and banded spatial distributions of LAI values obviously appeared in the *C. axillaris* forest.

### 3.3 Factors affecting LAI variations in three forests

The multi-collinearity test indicated that the factors with significant effects on LAI in January and July selected by stepwise regression did not have multi-collinearity. Thus, BA, crown coverage, crown width, the proportion of deciduous species to total stand BA and forest types were included as explanatory variables in multi-factor analysis for LAI values measured in January in three forests (Table 4). The best fitted GAMs for LAI values in January was expressed as LAI ~ s(BA, 2) + s(crown coverage, 2) + s(crown width, 2) + s (the proportion of deciduous species to total stand BA, 2) +factor (forest types). For LAI values measured in July, species richness, crown coverage, stem number and forest types were included as explanatory variables in multi-factor analysis (Table 4). The best fitted

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285 GAMs for LAI values in July was expressed as LAI ~ s(species richness, 2) + s(crown coverage, 2) +
286 s(stem number, 2) + factor(forest types).

287 The explanatory variables included in GAMs reflected their effects on or relationship with LAI
288 variations. Given that other variables were fixed, LAI measured in January tended to increase as BA
289 increased and showed a negative nonlinear relationship with crown coverage and a positive nonlinear
290 relationship with crown width. The LAI values tended to decrease as the proportion of deciduous
291 species to total stand BA increased (Fig. 3). Given that other variables were fixed, LAI measured in July
292 tended to increase as species richness increased and showed a positive nonlinear relationship with
293 crown coverage and a negative nonlinear relationship with stem number (Fig. 4).

294

295 # 4 Discussion

296 ## 4.1 Seasonal variations in LAI values among three forests

297 LAI data in subtropical forests in southern China are less than that in other global regions (Asner et
298 al., 2003). This study provided seasonal LAI data in three subtropical forests that consist of contrasting
299 functional types of species. Mean LAI values in the three forests investigated in this study varied from
300 1.28 ±0.44 to 3.28 ±1.26 (Table 1). This result is close to LAI range (from 1.0 in winter to 4.0 in summer)
301 retrieved by remote sensing techniques from subtropical area of China during the period 2000 to 2010
302 (Liu et al., 2012). Compared with the LAI values estimated from allometric equations (Xiang et al.,
303 2016) and specific leaf area (SLA) at 40 m × 40 m quadrate plots of this study (5.29-9.19), the LAI

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304 values measured by hemipherical photography are low but significantly correlated ($r^2$=0.40 and
305 $p$=0.035). Previous studies (see Lopes et al., 2015) have proved the underestimation of LAI using
306 hemipherical photography. However, the hemipherical photography method is feasible to obtain LAI
307 data in forests and to investigate spatial and seasonal variations in LAI in forests (Coops et al., 2004;
308 Dovey & Toit, 2006).

309 The ratio of woody to total area ($\alpha$) and the clumping index ($\Omega_E$) have been recognised as the error
310 sources in LAI measurement by optical methods (Liu et al., 2015a; Bréda, 2003; Chen et al., 1997). So
311 far these two parameters have been measured in Northeastern China (Liu et al., 2015a; Liu et al., 2015b)
312 but they are not suitable for LAI correction in subtropical forests. Also the literature about them in
313 subtropical forests has been rarely reported. Our results showed that mean $\alpha$ values in the three forests
314 varied from 0.04±0.03 to 0.15±0.09 (Table 2). The variations of $\alpha$ value are probably due to the seasonal
315 variations and spatial heterogeneity of canopy structure in the three forests. In general, the $\alpha$ values are
316 consistent with the amount of leaf litter. Our results showed that the large mean $\alpha$ values occurred in
317 autumn for the *P. massoniana* - *L. glaber* forest and the *C. axillaris* forest, but in spring and autumn for
318 the *L. glaber* - *C. glauca* forest (Table 2). This seasonal change of mean $\alpha$ values in three forests was
319 generally consistent with the amount of leaf litter collected by litter tap installed in the three forests
320 (Guo et al., 2015). The average $\Omega_E$ value (0.87) in this study is smaller than the values of mixed
321 broadleaved - korean pine forest in Northeastern China (Liu et al. 2015b) and this could be attributed to
322 the different region and forests. The values of $\alpha$ and $\Omega_E$ obtained in this study fill the gap of calibration

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for optical measurement of LAI in subtropical forests.

Mean LAI values differed among the three forests and the differences were significant between the *C. axillaris* forest and other two forests at a given measurement season. The *C. axillaris* forest had the relatively high mean LAI value during the growing season but changed to the lowest mean LAI value during the non-growing season. The change in mean LAI values in the *C. axillaris* forest was consistent with the study of a deciduous species dominated forest reported by Naithani et al. (2013). It has been reported that the forests consisting of different plant functional types of species showed different LAI values (Asner et al., 2003; Iio et al., 2014). The differences and seasonal variations of LAI values in the three forests could be attributed to floristic composition and phenological defoliation pattern of tree species especially the deciduous species. The *C. axillaris* forest consisted of 74.15% deciduous species, 25.80% evergreen broadleaved species and 0.05% evergreen coniferous species while the proportions of deciduous species were 10.05% and 25.70% respectively in the *P. massoniana* - *L. glaber* forest and the *L. glaber* - *C. glauca* forest. Seasonal growth and defoliation of different functional types of species lead to the change in leaf lifespan and foliage area (Niinemets et al., 2010) during different seasons related to temperature and water availability, which are responsible for the unimodal pattern of seasonal variations in mean LAI values. This agrees with the results from Liu et al. (2012) that the highest LAI was found in summer (July), followed by autumn (October) and spring (April), and the lowest was found in winter (January).

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342 **4.2 Spatial heterogeneity and its controlling factors of LAI values within a forest**

343 Semivariograms of LAI values in the three forests were fitted with spherical models, gaussian models,
344 exponential models or linear models (Table 3). Based on the fitted models, the degree of spatial
345 autocorrelation could be evaluated. Spatial autocorrelation is weak when the determination coefficient
346 ($r^2$) of the best-fitted semivariogram model is less than 0.5 (Duffera et al., 2007). The ratio [$C/(C_0+C)$]
347 is also used to describe the degree of spatial autocorrelation. The ratio between 0 and 0.25 indicates a
348 weak spatial autocorrelation, between 0.26 to 0.75 means moderate and larger than 0.75 means strong
349 (Lopez-Granados et al., 2004). Spatial autocorrelation of LAI in this study varied with forests and
350 measurement seasons (Table 3). Strong spatial autocorrelation at short range for LAI values measured in
351 January in three forests indicated the sampling distance is reasonable for LAI variables within the
352 spatial range (Liu et al., 2008). On the contrary, weak autocorrelation within spatial autocorrelation
353 range indicated that more samples and smaller sampling intervals should be taken to determine spatial
354 dependency of LAI, such as LAI measured in April in the *P. massoniana* - *L. glaber* forest.

355 Spatial heterogeneity of LAI values was different in three forests and measurement seasons. Our
356 study respectively described spatial variations of LAI values by CV and analysis of geostatistics and the
357 results were basically consistent with each other. In general, the CVs of LAI values in three forests (in
358 particular *C. axillaris* forest) were higher for the period of leaf onset (April) and senescence (October)
359 than that for the period of leaf maturity (July) (Table 1). This reflects changes of leaves due to plant
360 phenology and is consistent with the study by Naithani (2013) that LAI became increasingly

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361 homogenous from leaf onset to maturity, but became more heterogeneous from maturity to senescence.
362 As a result, heterogeneity degree of LAI values in three forests tended to dwindle from leaf
363 non-growing season to growing season (Fig. 2).

364 The complex hydrothermal environment results in complex vertical and horizontal variations of
365 canopy layer and formed the unique spatial heterogeneity of LAI values. The results of stepwise
366 regression and GAMs showed that forest types, species diversity and stand characters affected the
367 spatial heterogeneity of LAI values significantly in three forests. This finding that floristic composition
368 and stand characters affected LAI values measured in July is consistent with the previous study that LAI
369 values increased with species richness (Yao et al., 2015). The positive relationship between LAI values
370 in July and crown coverage is also in agreement with the findings reported by Bequet (2012) that large
371 trees (high DBH, tree height, crown length and crown cover) had high LAI values measured in July. The
372 negative relationship between LAI values in July and stem number probably could be explained by the
373 strong competition among tree species in the three forests with diverse species composition.

374 Up to now, the relationship of LAI variations measured in non-growing season with forest types and
375 stand characters has seldom reported. In this study, forest types, BA, crown width, crown coverage and
376 the proportion of deciduous species to total stand BA were the factors significantly affecting LAI
377 variations in January. Because large trees (high crown width and BA) had high LAI values and January
378 is the leaf senescence period of deciduous species, LAI values in January increased with BA and crown
379 width but decreased with deciduous species ratio. The fact that LAI values in January decreased with

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380 increasing crown coverage could be explained that large crown coverage means more defoliation (in
381 particular deciduous species) in the forest in January.

382 Although the factors selected by regression could explain a small proportion (6%) of spatial
383 heterogeneity of LAI measured in July, the factors selected in January could explain 35% of the LAI
384 spatial heterogeneity (Table 4). The LAI heterogeneity also could be affected by that several other
385 factors, such as the topography (Naithani et al., 2012), soil features (Chloer et al., 2010), soil
386 temperature (Vitasse et al., 2009; Hardwick et al., 2015), microclimate, human activities and other
387 physicochemical properties. And yet, full leaf expansion of all tree species which covers up the effect of
388 other physicochemical properties on LAI leads to small difference in LAI in July. The effects of
389 environmental factors (such as temperate, rainfall, etc.) on LAI in the forests at fine scale should be
390 taken into account in the future studies.

391 Spatial heterogeneity of LAI in three forests can yield some useful information for sampling strategy
392 to accurate estimation of LAI by using indirect measurement. An optimal sampling strategy should
393 consider appropriate sampling plot size and the lowest sampling number as far as possible to obtain a
394 high sampling accuracy and a low sampling error (Bequet et al., 2012). Our study found that strong
395 spatial autocorrelations range were about 30m (Table 3), indicating that 30m range might serve as a
396 reference for sampling plot size to estimate LAI in subtropical forests. In addition, LAI heterogeneity
397 was closely related to floristic composition and stand characters, thus stand structural variables (BA or
398 DBH) are important for sampling strategy to measure LAI in forests (Bequet et al., 2012).

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399

## 400 5 Conclusions

401 This study measured LAI in three subtropical forests using hemispherical photography method in
402 four seasons and offered reliable data to analyse spatial and seasonal variations of LAI in the three
403 forests. Our results indicated that LAI differed greatly with forests and measurement seasons. Seasonal
404 variations of LAI occurred in the three forests reflect defoliation phenomenon due to plant phenology.
405 LAI values in the three forests exhibited different spatial autocorrelation in four seasons. Obvious patch
406 distribution pattern of LAI values was found in the three forests during the non-growing seasons and
407 this pattern gradually dwindled in the growing seasons. While BA, crown coverage, crown width, the
408 proportion of deciduous species to total stand BA and forest types significantly affected the spatial
409 variations in LAI values in January, species richness, crown coverage, stem number and forest types
410 significantly affected the spatial variations in LAI values in July. These findings supplement LAI data
411 for global synthesis and provide useful information for sampling strategies to accurate LAI estimates
412 and simulating the models of forest production and hydrological cycle in subtropical forests.

413

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609 **Table 1** Descriptive statistical characteristics of LAI values measured during period from April 2014 to

610 January 2015 in *P. massoniana* - *L. glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests (n=100).

611

| Month | Forest type | Minimum value | Maximum value | Variance coefficient (%) | *P* value of K-S test | Data transformation |
|---|---|---|---|---|---|---|
| January | *P. massoniana* - *L. glaber* | 1.29 | 4.03 | 27.5 | 0.021 | 0.275 |
| | *C. axillaris* | 0.53 | 2.38 | 34.0 | 0.260 | |
| | *L. glaber* - *C. glauca* | 0.43 | 6.98 | 40.2 | 0.018 | 0.243 |
| April | *P. massoniana* - *L. glaber* | 1.57 | 7.83 | 36.4 | 0.076 | |
| | *C. axillaris* | 1.34 | 8.33 | 47.0 | 0.047 | 0.535 |
| | *L. glaber* - *C. glauca* | 1.34 | 10.22 | 59.6 | 0.000 | 0.158 |
| July | *P. massoniana* - *L. glaber* | 1.56 | 8.16 | 38.0 | 0.003 | 0.075 |
| | *C. axillaris* | 1.73 | 8.17 | 37.8 | 0.166 | |
| | *L. glaber* - *C. glauca* | 1.68 | 7.58 | 33.1 | 0.010 | 0.170 |
| October | *P. massoniana* - *L. glaber* | 1.55 | 6.79 | 38.3 | 0.321 | |
| | *C. axillaris* | 0.37 | 6.51 | 44.1 | 0.102 | |
| | *L. glaber* - *C. glauca* | 1.49 | 7.88 | 49.3 | 0.000 | 0.212 |

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615 **Table 2** Average woody to total leaf ration ($\alpha$) and clumping index ($\Omega_E$) values in *P. massoniana* - *L.*
616 *glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests. Values in parenthesis are the standard deviation of
617 $\alpha$ and $\Omega_E$ values (n=100).

618

| Forest type | Month | $\alpha$ | $\Omega_E$ |
|---|---|---|---|
| *P. massoniana* - *L. glaber* | January | 0.06 (0.04) | 0.88 (0.09) |
| | April | 0.08 (0.05) | 0.87 (0.09) |
| | July | 0.07 (0.04) | 0.87 (0.09) |
| | October | 0.09 (0.10) | 0.85 (0.08) |
| *C. axillaris* | January | 0.15 (0.09) | 0.92 (0.08) |
| | April | 0.07 (0.06) | 0.85 (0.10) |
| | July | 0.04 (0.03) | 0.90 (0.07) |
| | October | 0.14 (0.14) | 0.87 (0.10) |
| *L. glaber* - *C. glauca* | January | 0.07 (0.09) | 0.87 (0.09) |
| | April | 0.15 (0.07) | 0.86 (0.09) |
| | July | 0.05 (0.03) | 0.87 (0.08) |
| | October | 0.09 (0.08) | 0.84 (0.09) |

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627 **Table 3** Semivariogram theoretical models and fitted parameters for LAI values in *P. massoniana* - *L.*

628 *glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests.

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| Month | Forest type | Model | Nugget ($C_0$) | Sill ($C_0$+$C$) | $C/(C_0+C)$ | Range ($A_0$/m) | $r^2$ | RSS |
|---|---|---|---|---|---|---|---|---|
| January | *P. massoniana* - *L. glaber* | Exponential | 0.0068 | 0.0614 | 0.889 | 27.00 | 0.607 | $9.762\times10^{-5}$ |
| | *C. axillaris* | Exponential | 0.0030 | 0.1820 | 0.984 | 13.80 | 0.504 | $1.219\times10^{-4}$ |
| | *L. glaber* - *C. glauca* | Gaussian | 0.0029 | 0.1178 | 0.975 | 15.42 | 0.888 | $3.468\times10^{-5}$ |
| April | *P. massoniana* - *L. glaber* | Exponential | 0.1220 | 0.7670 | 0.841 | 17.70 | 0.229 | 0.017 |
| | *C. axillaris* | Linear | 0.1760 | 0.1760 | 0.000 | 52.96 | 0.189 | $1.762\times10^{-4}$ |
| | *L. glaber* - *C. glauca* | Exponential | 0.0008 | 0.0152 | 0.951 | 26.40 | 0.978 | $2.290\times10^{-7}$ |
| July | *P. massoniana* - *L. glaber* | Linear | 0.0843 | 0.0843 | 0.000 | 92.69 | 0.074 | $1.383\times10^{-4}$ |
| | *C. axillaris* | Exponential | 0.1460 | 0.9340 | 0.844 | 17.70 | 0.258 | 0.017 |
| | *L. glaber* - *C. glauca* | Exponential | 0.0065 | 0.0684 | 0.905 | 22.80 | 0.951 | $5.781\times10^{-6}$ |
| October | *P. massoniana* - *L. glaber* | Exponential | 0.1620 | 1.6310 | 0.901 | 11.70 | 0.173 | 0.017 |
| | *C. axillaris* | Spherical | 0.0050 | 0.5830 | 0.991 | 11.90 | 0.000 | $1.870\times10^{-3}$ |
| | *L. glaber* - *C. glauca* | Exponential | 0.0005 | 0.0125 | 0.960 | 21.90 | 0.894 | $4.444\times10^{-7}$ |

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636 **Table 4** Estimated coefficients of the generalised additive models (GAMs) for the factors with effects
637 on LAI values measured in *P. massoniana - L. glaber*, *C. axillaris* and *L. glaber - C. glauca* forests.

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| Month | Parameter | *F*-value | *p*-value | $r^2$ | AIC |
|---|---|---|---|---|---|
| January | s (BA,2) | 15.146 | $1.236\times10^{-4}$*** | 0.3496 | 654.30 |
| | s (Crown width,2) | 1.588 | 0.209 | | |
| | s (Crown coverage,2) | 0.556 | 0.456 | | |
| | s (PDSB,2) | 49.324 | $1.556\times10^{-11}$*** | | |
| | factor(Forest types) | 44.355 | $< 2.2\times10^{-16}$*** | | |
| July | s (Species richness,2) | 3.165 | 0.076. | 0.0551 | 677.85 |
| | s (Stem number,2) | 8.381 | $4.086\times10^{-3}$** | | |
| | s (Crown coverage,2) | 0.006 | 0.939 | | |
| | factor(Forest types) | 2.475 | 0.086. | | |

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640 The significance of the regressions (*p*) are ., *, **, *** for $p<0.1$, 0.05, 0.01, and 0.001, respectively

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## Figure captions

**Fig. 1** Seasonal variations of mean LAI values (with standard deviation) in *P. massoniana* - *L. glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests. The values carrying with different letters indicate significant differences ($p<0.05$) among measurement seasons in a given forest.

**Fig. 2** Spatial heterogeneity map of LAI values interpolated through ordinary Kriging method for *P. massoniana* - *L. glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests.

**Fig. 3** Partial effects of total stand basal area (BA, $cm^2$), average crown width (m), crown coverage ($m^2$), the proportion of deciduous species to total stand BA (PDSB), and forest types (calculated for overstory trees with height larger than average stand height) on the LAI values observed in January in *P. massoniana* - *L. glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests.

**Fig. 4** Partial effects of species richness, individual stem number, crown coverage ($m^2$) and forest types (calculated for overstory trees with height larger than average stand height) on the LAI values observed in July in *P. massoniana* - *L. glaber*, *C. axillaris* and *L. glaber* - *C. glauca* forests.

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668 **Figure 1**

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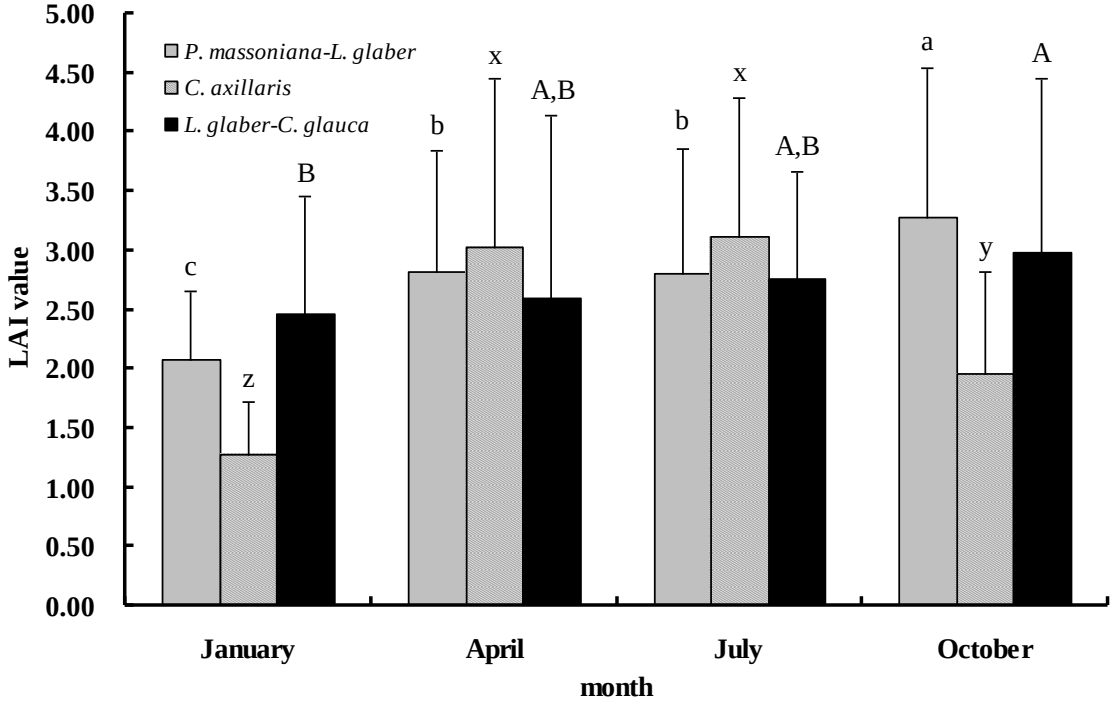


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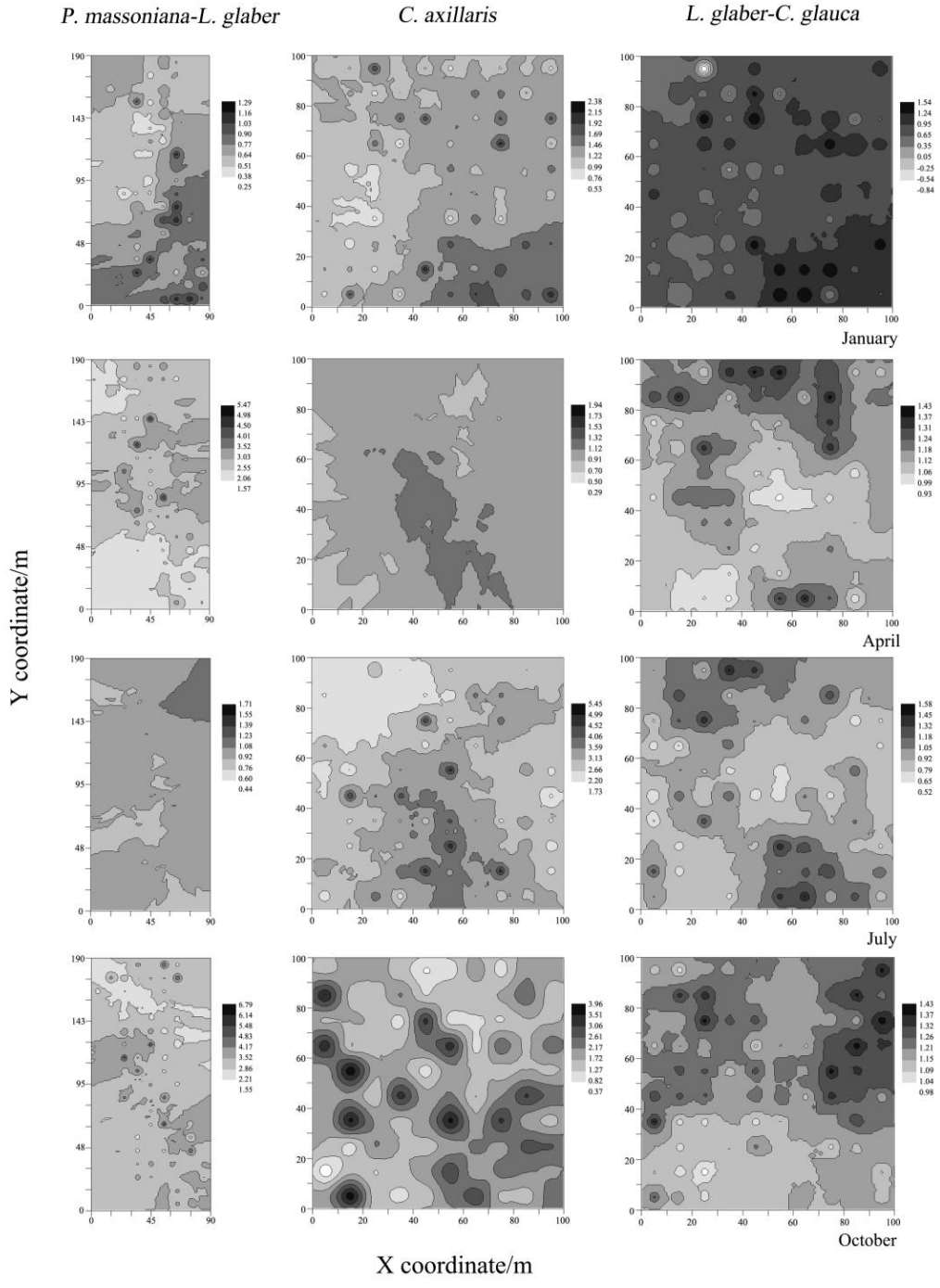
679 **Figure 2**

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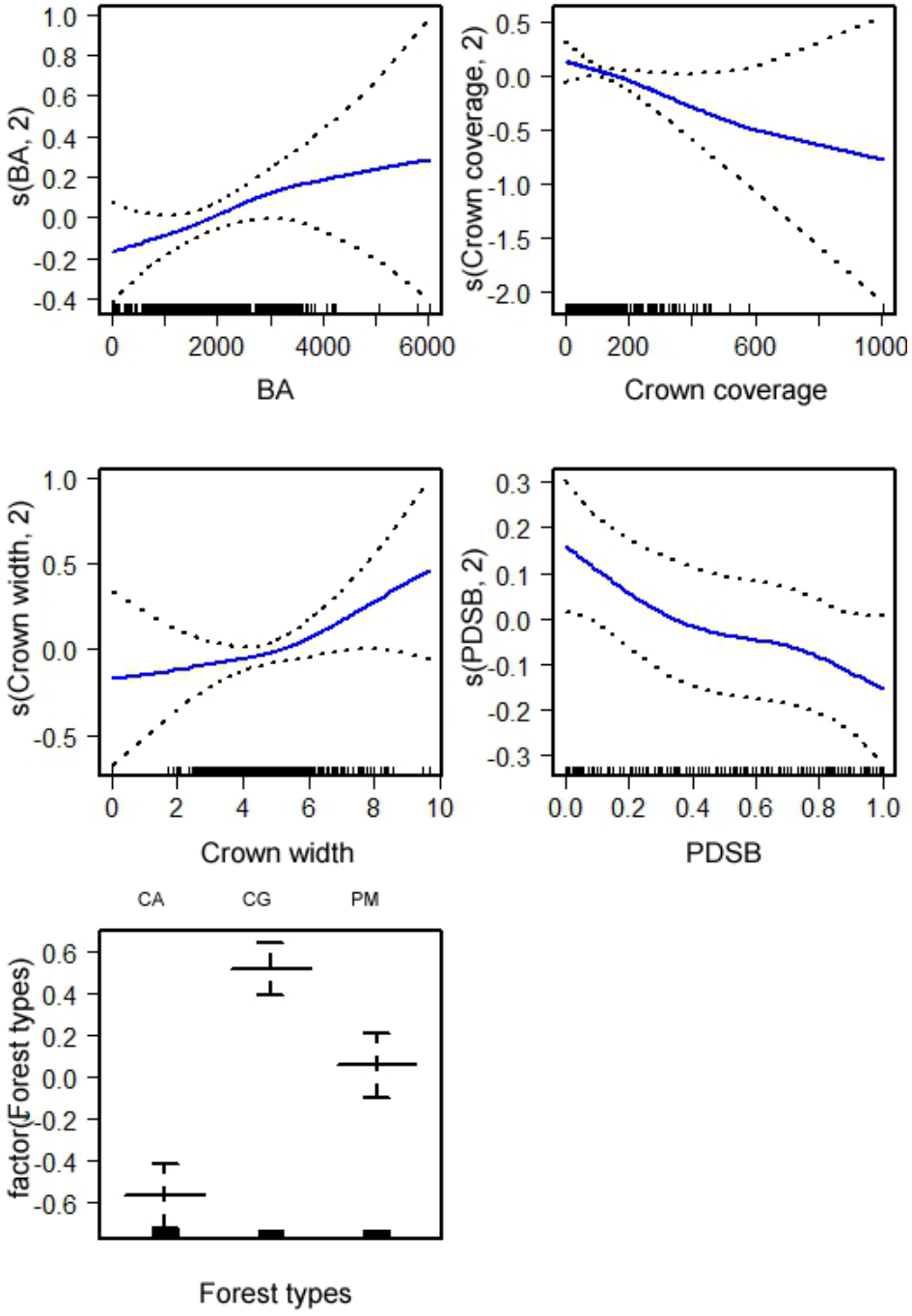
682 **Figure 3**

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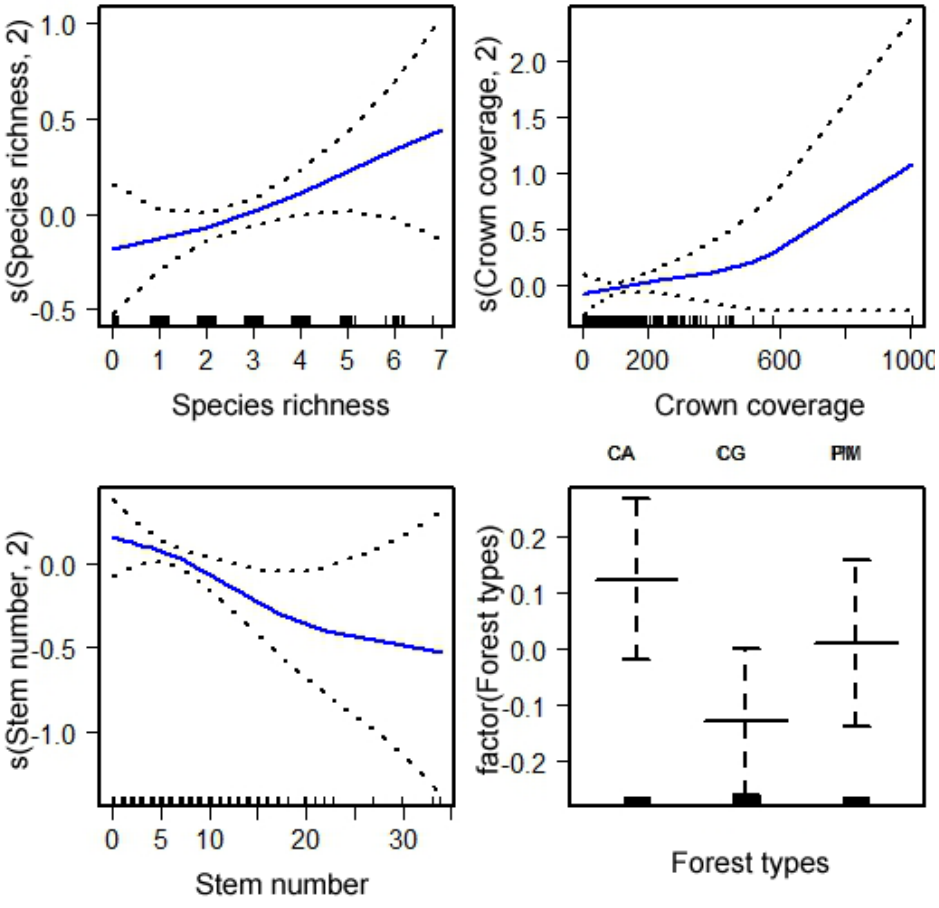
685 **Figure 4**

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