

# Temperature sensitivity of plant litter decomposition rate in China's forests

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**Abstract.** The decomposition of litter from forest tree species is a fundamental process in the carbon (C) cycle of terrestrial ecosystems and is closely related to ongoing climate change. However, the spatial distribution of the forest litter decomposition rate ( $k$ ) and its potential response to changing air temperature (temperature sensitivity) remain poorly understood. Here, we estimated the spatial pattern of forest plant  $k$  values in China by performing a random forest model based on 433 standardized  $k$  values from 124 published studies. Nine potential predictors, including climate-related factors, vegetation characteristics, and soil physical and chemical factors, were considered in the model. The results of spatial extrapolation indicated that the average  $k$  value for China's forests was 0.53, and the mean annual temperature (MAT) was the most important factor. We also mapped the spatial pattern of the temperature sensitivity of the  $k$  value ( $Q_{10}$ ) by using a moving window method. We found that the  $Q_{10}$  values had considerable variation (from 0.05 to 11.68, 95% confidence interval, CI) across forest types and regions. The  $Q_{10}$  values were lower in the warmer regions (primarily in the sub-tropical evergreen forests) and higher in the semi-humid regions (primarily in the temperate deciduous forests and boreal *Larix* forests) than those in the other regions of China. However, the  $Q_{10}$  values of the broadleaved forests were higher than those of coniferous forests. These results suggest that the temperature sensitivity of the litter decomposition rate will decline under the ongoing global warming. Changing patterns of precipitation will also affect not only the forest litter decomposition rate but also its temperature sensitivity.

**Key words:** climate; litter decomposition rate;  $Q_{10}$  spatial pattern.

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## INTRODUCTION

The decomposition of plant litter is a fundamental process in energy flow and element cycling in terrestrial ecosystems (Berg et al. 1986, Paudel et al. 2015). The amount of carbon (C) in forest litter is relatively low (43 Pg, 1 Pg =  $10^{15}$  g), which accounts for no more than 5% of the C storage of global forests (Pan et al. 2011). In

China's forests, this storage represents only 2% of the national forest carbon storage (0.4 Pg C, Zhu et al. 2017). Compared to other components (e.g., vegetation and soil), litter may be negligible in regional C pools and budget estimates (Tang et al. 2018, Zhu et al. 2020). However, decomposition of this component is still a critical ecosystem process, representing a major pathway for C flux (Berg 2014).

Litter decomposition is regulated by several factors, including the quality of the litter, the physical and chemical environments, and the decomposer organisms (Swift et al. 1979). Climate has long been considered the dominant factor controlling the rates of litter decomposition (Berg et al. 1993, Gholz et al. 2000). When explaining the spatial variance in the litter decomposition rate, the mean annual temperature (MAT) and mean annual precipitation (MAP) have been used extensively (Meentemeyer 1978, Gholz et al. 2000, Zhang et al. 2008, Bonan et al. 2013). However, these variables are not necessarily the most important factors. During the last two decades, numerous studies have suggested that biotic factors might be more important than temperature or precipitation in explaining the variance in regional decomposition rate across various biomes worldwide (Cornwell et al. 2008, Wall et al. 2008, Currie et al. 2010, Bradford et al. 2014, 2016). For example, Cornwell et al. (2008) compared 1196 decomposition rate ( $k$ ) records and found that litter quality was the most important factor triggering the variance in the  $k$  value within biomes worldwide. Bradford et al. (2014) explored litter experiments along a latitudinal gradient (spanning  $\sim 12^\circ$  latitude) and found that fungal colonization was a better predictor of  $k$  than was air temperature. Nevertheless, the impacts of climate on the  $k$  of organic matter have been evaluated less often (Prescott 2010, Garciapalacios et al. 2013, Veen et al. 2015).

Climate has long been considered the primary factor related to the litter decomposition rate at the regional scale (Swift et al. 1979). Several studies have demonstrated that litter quality and soil decomposer traits might be more important than temperature or precipitation for controlling the decomposition rates in regional estimates (Cornwell et al. 2008, Currie et al. 2010, Bradford et al. 2014). Regardless, the effect of climatic factors on  $k$  values at the regional scale has received much attention. This attention is likely because climatic factors also affect the chemical composition of litter and the activity of soil decomposers at the regional scale (Stevens 1992, Liu et al. 2006, Bárcenas-Moreno et al. 2009, Bell et al. 2009). First, the quality of leaf litter is influenced by temperature and precipitation at the regional scale (Liu et al. 2006). Liu et al. (2006) found that

the nitrogen (N) concentration of forest litter increased with MAT in Eurasia. Lower ratio of C:N and lignin:N in the litter creates beneficial conditions for decomposition. In addition, climate determines the spatial distribution of vegetation composition and structure and thus shapes the distribution of different litter species (Stevens 1992, Fang et al. 2012) at the regional scale. Second, microbial communities and their activities are affected by climate (Bárcenas-Moreno et al. 2009, Bell et al. 2009). For example, Bell et al. (2009) demonstrated that fungal substrate activities displayed a positive correlation with soil temperature (15 cm) in grassland ecosystems. Therefore, climatic factors should not be considered as independent variables, as they will interact with soil decomposer organisms and litter quality and exert an indirect effect on the litter decomposition process (Aerts 1997). In addition, the spatial variations of climatic factors exert an influence on the litter species richness, and further control C and N cycling during the decomposition process through specific interactions in litter mixtures (Handa et al. 2014). Regardless of whether the climate is the dominant control affecting the rate of litter decomposition at the regional scale, it is a fact that the  $k$  value would be influenced directly and indirectly by the increasing global air temperature. The extent to which the  $k$  value responds to climate change (sensitivity of the  $k$  value to climatic factors) and whether this response will vary across biomes are still unknown.

Field experiments of litter decomposition are traditionally performed using the litterbag method (e.g., Bocock and Gilbert 1957). The  $k$  value could be quantified by the mass loss of litter with continuous sampling (Olson 1963). Unlike the calculation of the temperature sensitivity of the soil respiration rate, we could not obtain the temperature sensitivity of the  $k$  value at each study site. Environmental gradients could be used to explore and quantify the influence of temperature on the  $k$  values (Gholz et al. 2000, Salinas et al. 2011). Gholz et al. (2000) performed the Long-Term Intersite Decomposition Experiment (LIDET), involving 27 L species from 28 forest sites in North and Central America during the period of 1989–1994. They demonstrated that MAT significantly affected the decomposition process and quantified the temperature

sensitivity ( $Q_{10}$ , the change in the  $k$  value given a  $10^{\circ}\text{C}$  change in temperature) of leaf and fine root litter as 2.7 and 2.1, respectively. Salinas et al. (2011) quantified the  $Q_{10}$  value of the  $k$  values of 15 species by a large-scale leaf litter transplant experiment along an elevation gradient (210–3025 m above sea level) in Peru. They found that the  $Q_{10}$  value varied considerably from 1.3 to 5.4 across the different litter species. Limited by methodology, there are few studies on the sensitivity of the  $k$  value at the regional scale; thus, the spatial pattern of the temperature sensitivity of the  $k$  value is still unknown.

Almost all major forest types in the Northern Hemisphere can be found in China, including boreal taiga forests, the cold temperate deciduous broadleaved forests, and the temperate mixed forests in the north and the evergreen broadleaved forests and tropical rainforests in the south (Fang et al. 2012). In this study, we re-calculated 433  $k$  values using the leaf litter in China's forests from 124 published studies (Olson 1963). We examined the climatic and biotic factors that determined the spatial distribution of the  $k$  values. To predict the spatial patterns of the  $Q_{10}$  values of the leaf decomposition rates of China's forests, we considered nine potential predictors of the leaf litter  $k$  value, including variables that define climatic and geographical factors (e.g., MAT, MAP, and elevation), vegetation characteristics (e.g., forest type and the normalized difference vegetation index; NDVI), and soil physical and chemical factors (e.g., soil pH, soil organic C [SOC] density, soil C:N ratio, and bulk density). Based on the distribution of the  $k$  value, the spatial distribution of the  $Q_{10}$  value was quantified by the moving window ( $21 \times 21$  pixels, 8-km resolution for each pixel) method (Cheng 1999, Neta et al. 2010, Zhang et al. 2020). Finally, in this study, we used the elevation gradient-based temperature sensitivity of the litter decomposition rate to evaluate the spatial distribution of the  $Q_{10}$  value.

## MATERIALS AND METHODS

### Data acquisition

We collected data from literature searches in China National Knowledge Infrastructure (CNKI), Web of Science (WOS), WANFANG Data (<http://www.wanfangdata.com.cn/>), and

Google Scholar (<https://scholar.google.com/>). The search rules were set to TS = ("litter decomposition") AND ("forest ecosystem") AND ("China"), and then, papers were selected based on the following criteria: (1) Litter decomposition rate was obtained from in-field experiments; (2) litter bags were used to measure the decomposition rate; and (3) only the  $k$  value calculated using Olson's single exponent model could be used directly (Eq. 1; Olson 1963).

$$\frac{M_t}{M_0} = e^{-kt} \quad (1)$$

where  $t$  (y) is the decomposition time.  $M_t$  is the residual weight of the litter at time  $t$ .  $M_0$  is the initial weight of the litter, and  $k$  is the decomposition rate (per year).

In the experimental studies, only the control group was considered. For raw data (including mass loss or mass remaining), we used the GetData Graph Digitizer (version 2.26) to obtain the mass loss or mass remaining at each sampling from each study and then re-calculated the decomposition rate of litter by using the exponent model (Eq. 1).

We finally obtained 433  $k$  values from 124 studies, which represented the geographical (Fig. 1) and climatic (Appendix S1: Fig. S1) space quite well. For each study, we also recorded the basic information, including location (latitude, longitude, and elevation), forest type, and litter species (Appendix S1: Table S1). Nine potential predictors for leaf litter  $k$  were obtained, including elevation, MAT, MAP, forest type, the NDVI, soil pH, soil bulk density, soil organic C density (C storage per unit area, SOC), and soil C:N ratio. We further divided these predictors into three groups: climate-related factors (elevation, MAT and MAP), vegetation characteristics (forest type and NDVI), and soil physical and chemical factors (pH, SOC, bulk density, and C:N ratio).

*Climate-related factors.*—The spatial distribution data of elevation in China (DEM) were from the Resources and Environmental Science Data Cloud Platform with a resolution of 1 km (<http://www.resdc.cn/>). The MAT and MAP were synthesized using monthly grid-cell data from 2006 to 2015. The monthly temperature and precipitation meteorological data were collected from 2480 conventional monitoring stations (<http://data.cma.cn/>), which were used to create gridded

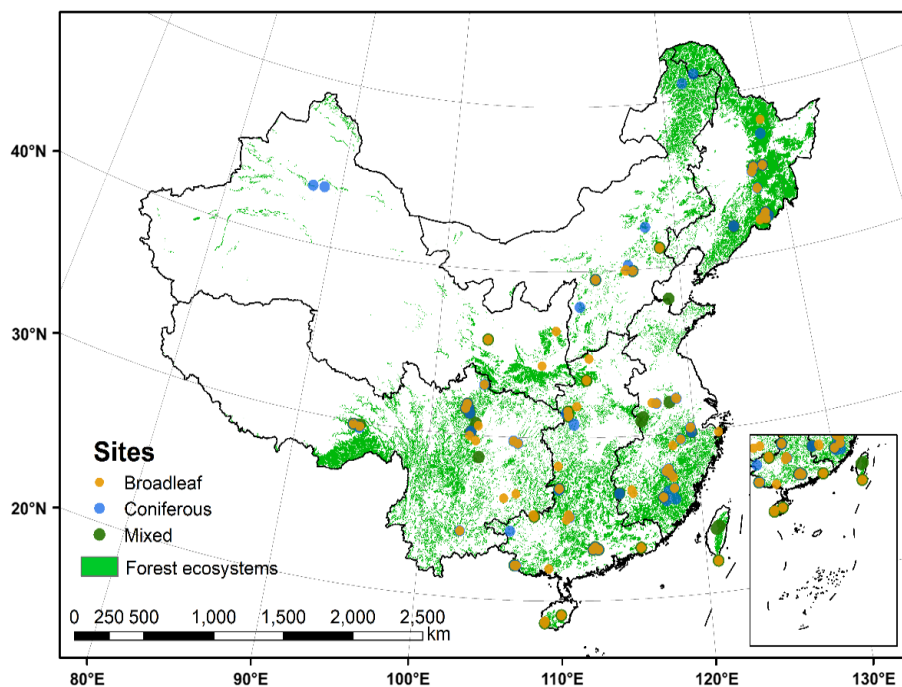


Fig. 1. Distribution of the forest sites based on the litter types. The green areas represent the pixels of the forests in China obtained from the digitalized 1:1,000,000 vegetation map (ECVMC 2007).

monthly products with a resolution of 8 km. An improved thin plate spline was used to create the products by using Anusplin 4.4 (Feng et al. 2019).

*Vegetation characteristics.*—The digitized 1:1,000,000 vegetation map was used to obtain the grid-cell forest types (ECVMC 2007). We further divided the forest types into three categories: coniferous forests, broadleaved forests, and the mixed forests. The maximum value synthesis method was used to denoise the GIMMS NDVI data and then obtain the monthly data, after which the annual data were synthesized with resampling to the same resolution (8 km) as that of the NDVI data (Tucker et al. 2005, Wang et al. 2010).

*Soil physical and chemical factors.*—These four factors were obtained from the Global Soil Database (GSB) provided by Zhao et al. (2019), which used a random forest model to estimate the indicators at the global scale.

#### Data analysis

We analyzed the relationships between the decomposition rate of litter and all the nine potential predictors. First, we employed adj.  $R^2$

and  $P$  values to compare the fitness of several simple regression models, including linear, exponential, and logarithmic regressions. Second, we used a random forest model to simulate the spatial distribution of the  $k$  values. The random forest model is an integrated learning algorithm based on decision trees and can improve the prediction accuracy of a single decision tree (Liaw and Wiener 2002, Chen et al. 2015). Then, we conducted a tenfold cross-validation (Statnikov et al. 2008, Barnard et al. 2019) before modeling to determine the specific values of these two parameters (Table 1). To further analyze the uncertainty of the model, we used the resampling method to perform 500 random splits on the dataset, and 70% of the data were extracted as the training dataset for each segment to predict the spatial distribution of the  $k$  value; the other 30% of the data were used for verification. As a result, 500 random forest models were used to calculate the standard deviation. The IncNodePurity index was used for the predictor importance analysis to define the importance of the potential predictors in the model. A higher IncNodePurity index indicates a variable has



Table 1. Tenfold cross-validation of the random forest model.

mtry	ntree									
	100	200	300	400	500	600	700	800	900	1000
2	0.679	0.686	0.684	0.690	0.686	0.685	0.688	0.685	0.687	0.688
4	0.667	0.670	0.669	0.669	0.669	0.670	0.673	0.669	0.669	0.670
6	0.656	0.657	0.661	0.656	0.661	0.660	0.660	0.658	0.658	0.658
8	0.650	0.649	0.652	0.652	0.650	0.653	0.653	0.653	0.649	0.653

more importance in the model (Kuhn et al. 2008, Álvarez-Cabria et al. 2017). Final, the partial dependency analysis was used to help understand the effects of predictors in the model (Álvarez-Cabria et al. 2016, Cafri and Bailey 2016, Greenwell 2017). We obtained the partial dependence relationship between variable ( $X$ ) and the dependent variable by replacing the whole variable with its own element ( $X_i$ ); then, we input the new data into the random forest model. We finally described the relationship between each factor and the  $k$  value by a partial dependency plot.  $X_i$  was plotted on the  $X$ -axis, and the mean estimate was on the  $Y$ -axis (Cafri and Bailey 2016).

#### Predicted spatial distribution of the $Q_{10}$ value

To calculate the  $Q_{10}$  value, we calculated the temperature sensitivity coefficient ( $\beta$ ; Eq. 2):

$$k = \alpha \times e^{\beta \times T} \quad (2)$$

where  $T$  ( $^{\circ}\text{C}$ ) is the mean annual temperature of each forest site.  $\alpha$  is a fitting coefficient. The  $Q_{10}$  value was calculated by Eq. 3:

$$Q_{10} = e^{10\beta} \quad (3)$$

Average nearest neighbor analysis was used to determine the minimum distance for calculating  $Q_{10}$  (Eq. 4; Mitchell 2005):

$$D_0 = 0.5 / \sqrt{n/A} \quad (4)$$

where  $D_0$  is the observed average nearest neighbor distance,  $n$  is the number of data points, and  $A$  is the smallest rectangle containing all data points.

We estimated the spatial distribution of the  $Q_{10}$  values by using the moving window method. Specifically, we took the  $2D_0$  scale ( $21 \times 21$  pixels) as the size of the window (Feng et al. 2018, Ding et al. 2019). Within each

window, the calculation of the  $Q_{10}$  value was performed when at least 20  $k$  values were available within the  $21 \times 21$  pixels.

#### $Q_{10}$ verification

Salinas et al. (2011) provided a different method that used the natural elevation gradient to calculate the  $Q_{10}$  value. We sifted through the established database to filter out the data that could satisfy the elevation gradient-based calculation of the  $Q_{10}$  value. Fang et al. (2012) conducted a national investigation of mountainous forests in China. Based on the mountains, a 20-km buffer was set as the range of each mountain, and the range of variation in the predicted the  $Q_{10}$  value in this range was calculated. The method used to evaluate the accuracy of the  $Q_{10}$  value spatial distribution was affected by whether the result calculated by the elevation gradient fell within the range of the  $Q_{10}$  value of the mountain.

## RESULTS

#### Relationships between the $k$ value and the potential predictors

Across the 433 study sites, the  $k$  values ranged from 0.15 to 1.68 (95% confidence interval, CI), with average  $k$  values ( $\pm\text{SD}$ ,  $n$ ) of coniferous, broadleaved and mixed litter of 0.39 ( $\pm 0.21$ ,  $n = 121$ ), 0.70 ( $\pm 0.47$ ,  $n = 240$ ), and 0.60 ( $\pm 0.37$ ,  $n = 73$ ), respectively (Fig. 2a).

To separate the relative importance of different factors for decomposition, we examined the correlations between the  $k$  value and three primary categories of potential factors, including climate-related factors (MAT, MAP, and elevation), vegetation characteristics (forest types and the NDVI), and soil physical and chemical factors (soil pH, bulk density, soil C, and soil C:N ratio). Climate-related factors exerted significant

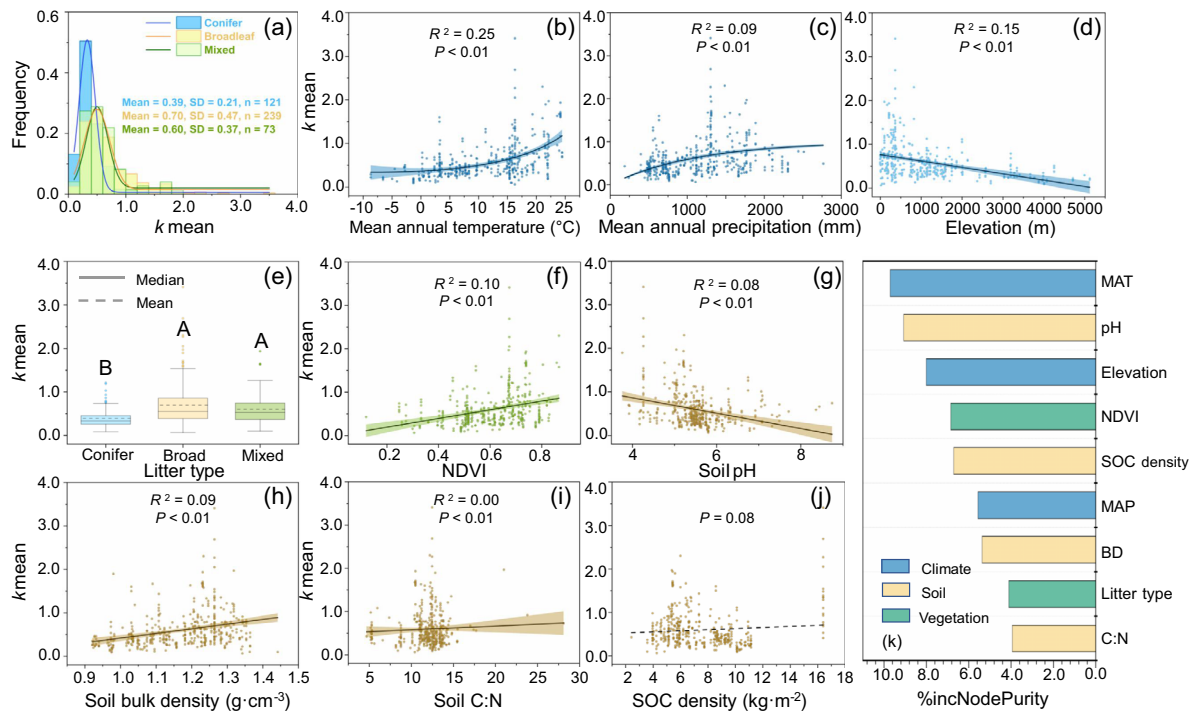


Fig. 2. Frequency distribution of the  $k$  values (a), relationships between the  $k$  values and climate-related factors (b–d), vegetation characteristics (e, f) and soil physical and chemical factors (g–j), and the relative importance of these predictors (k). We used the impurity reduction values calculated from the split variables of all tree nodes to compare the importance of the different factors. Different letters (A and B) denote significant differences at  $P < 0.05$  across different litter types via one-way analysis of variance. Abbreviations are MAT, mean annual temperature; MAP, mean annual precipitation; NDVI, normalized difference vegetation index; SOC, soil organic carbon.

influences on the  $k$  value across various forest types (Fig. 2b–d). Briefly, the  $k$  value increased exponentially with MAT ( $R^2 = 0.25$ ,  $P < 0.01$ ), and the  $Q_{10}$  value for these  $k$  values was 1.3. The  $k$  value was also positively and logarithmically correlated with MAP but negatively correlated with elevation. In addition, the  $k$  values of broad-leaved and mixed litter were significantly higher than that of coniferous litter across these forests (Fig. 2e) and positively correlated with the NDVI (Fig. 2f). Soil physical and chemical factors exerted a significant influence on the  $k$  value. The  $k$  value decreased significantly with soil pH but increased with soil bulk density (Fig. 2g–h). The litter decomposition rate increased slightly with the soil C:N ratio (Fig. 2i). No significant increasing trend was detected between the  $k$  value and SOC density (Fig. 2j).

### The performance of the potential predictors

According to the tenfold cross-validation, the candidate features and the decision trees were 2 and 400, respectively, when the adj.  $R^2$  obtained the highest value. We established a random forest model to estimate the spatial distribution of the  $k$  value in China, and the model explained 74% of the variance in the  $k$  value. The predictor importance analysis suggested that MAT was the optimal factor for predicting the spatial variance of the  $k$  value in the random forest model (Fig. 2k).

We used partial dependence analysis to further evaluate the performance of a specific predictor on litter decomposition when the effects of the other predictors were under controlled for (Fig. 3). The relationships between the  $k$  value and the nine potential predictors under the

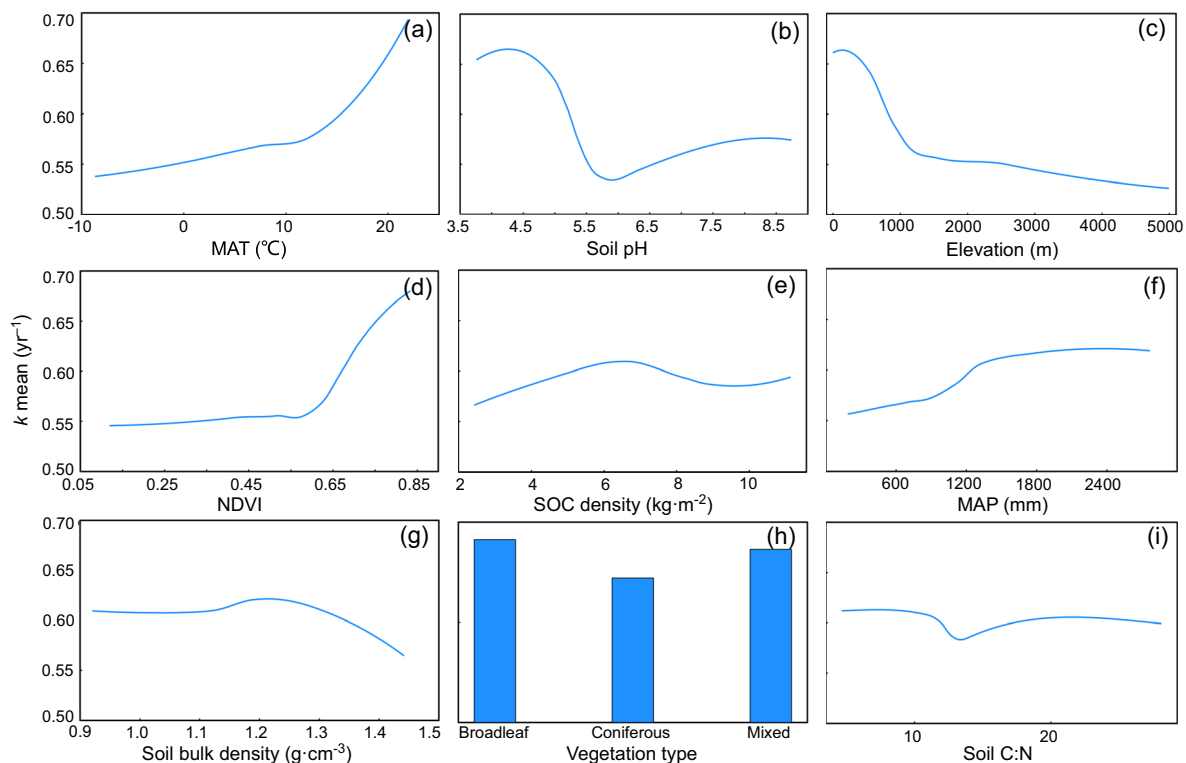


Fig. 3. Partial dependency analysis of the random forest model. Values show the influences between the  $k$  value and the (a) MAT, (b) soil pH, (c) elevation, (d) NDVI, (e) SOC density, (f) MAP, (g) soil bulk density, (h) vegetation type, and (i) soil C:N ratio when the other factors were controlled in the random forest model. MAT, mean annual temperature; NDVI, normalized difference vegetation index; SOC, soil organic carbon; MAP, mean annual precipitation.

partial dependence analysis were similar to those of the observed simple models (Fig. 2). The trend between the  $k$  value and the MAT was also similar, with an exponential and positive relationship (Fig. 3a). The  $k$  value reached its maximum and minimum when the pH was 4.5 and 5.5, respectively (Fig. 3b). The  $k$  value decreased with elevation (Fig. 3c) but increased with the NDVI (Fig. 3d), SOC density (Fig. 3e), and MAP (Fig. 3f). The  $k$  value decreased suddenly when the soil bulk density reached  $1.2 \text{ g/cm}^3$  (Fig. 3g). For the different forest types, the highest  $k$  value was detected for the broadleaved forests and the lowest for the coniferous forests (Fig. 3h). However, it should be noted that the positive relationship between the  $k$  value and soil C:N ratio detected by a linear regression model (Fig. 2i) changed to a slight negative relationship after the partial dependence analysis (Fig. 3i).

We then mapped the spatial distribution of the  $k$  value in China's forests at a resolution of 1 km (Fig. 4). Based on these calculations, the average  $k$  value in China's forests was estimated as  $0.53 \pm 0.15$  per year and showed considerable variation across forest types and regions. The average  $k$  values of coniferous, broadleaved, and mixed forests were  $0.47 \pm 0.14$ ,  $0.59 \pm 0.14$ , and  $0.52 \pm 0.09$  per year, respectively (Fig. 4). Geographically, the  $k$  value in China's forests was estimated to be  $0.65 \pm 0.15$  in the eastern region,  $0.58 \pm 0.11$  in the south-central region,  $0.52 \pm 0.09$  in the northeastern region,  $0.51 \pm 0.18$  in the southwestern region,  $0.45 \pm 0.10$  in the northern region, and  $0.39 \pm 0.11$  in the northwestern region of China. In addition, we evaluated the uncertainty of the  $k$  value at the pixel level and calculated the standard deviation (SD) based on 500 Monte

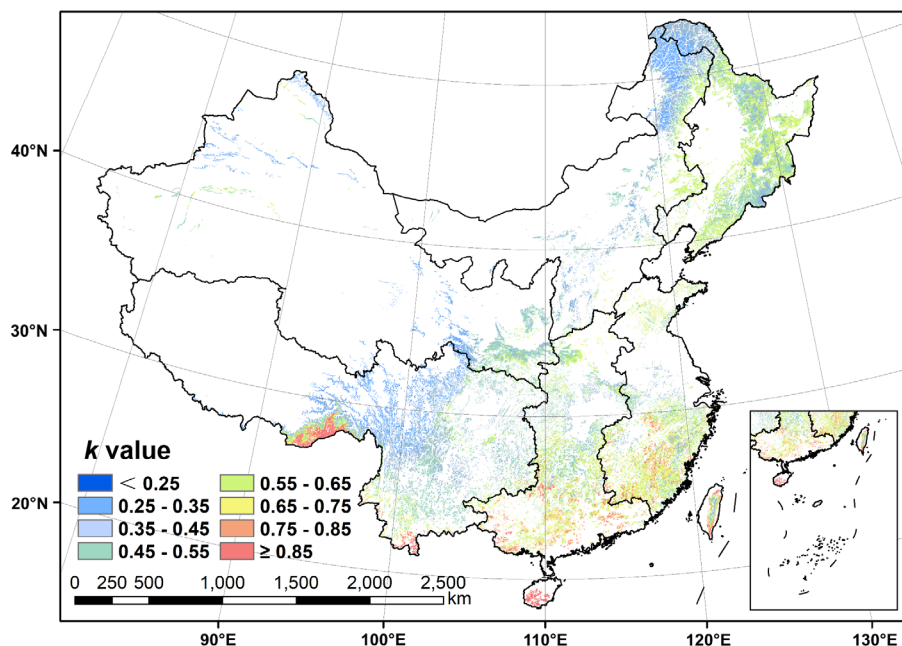


Fig. 4. Spatial distribution of the  $k$  value in China's forests.

Carlo simulations (Appendix S1: Fig. S2). The SD ranged from 0.02 to 0.11 (95% CI), with an average of 0.05 per year.

#### *Estimating the temperature sensitivity of the decomposition rate*

To quantify the spatial distribution of the temperature sensitivity of the  $k$  value, we calculated the exponential relationships between the  $k$  value and MAT by using the moving window method (Fig. 5). The  $Q_{10}$  value had a considerable spatial variance from 0.05 to 11.68 (95% CI), with an average value of 1.76 across China's forests. Nearly three-quarters of the grid-cell  $Q_{10}$  value was less than the experience value (2.0). The average  $Q_{10}$  value was lower in coniferous forests (1.56) and mixed forests (1.68) than in broadleaf forests (2.01). Geographically, the largest regional  $Q_{10}$  value (2.40) occurred in the forests of the northeastern region, followed by the northern (2.21), eastern (1.54), southwestern (1.47), and northeastern (1.46) forests. The smallest  $Q_{10}$  value occurred in the forests of south-central China (1.26). For each forest type, the regional  $Q_{10}$  values of broadleaved forests were 1.51, 2.33, 2.32, 1.66, 1.46, and 1.67 in the northwestern, northern, northeastern, southwestern, south-

central, and eastern regions, respectively. The regional  $Q_{10}$  value in coniferous forests of the northwestern (1.42), southwestern (1.38), south-central (1.18), and eastern (1.50) regions was smaller than the experience value (2.0), and the  $Q_{10}$  value in the northeastern region was the highest of all regions (2.61). According to the distribution of the  $Q_{10}$  value at the climatic space in relation to the MAT and MAP (Appendix S1: Fig. S3), the relatively lower  $Q_{10}$  values primarily occurred at the warmer regions where the MAT ranged from 15° to 20°C, while the higher  $Q_{10}$  values occurred at the semi-humid regions (where the MAP ranged from 400 to 800 mm).

## DISCUSSION

### *The $k$ value and potential predictors*

We summarized 433 leaf litter  $k$  values from 124 published studies in China's forests and estimated the average  $k$  value as 0.53 per year based on an exponential decay model (Olson 1963, Silver and Miya 2001). This average  $k$  value for China's forests was lower than that calculated for global forests (0.67; Zhang et al. 2008). For the different litter types, we found that the  $k$  value of the broadleaved leaf litter (0.59) was significantly



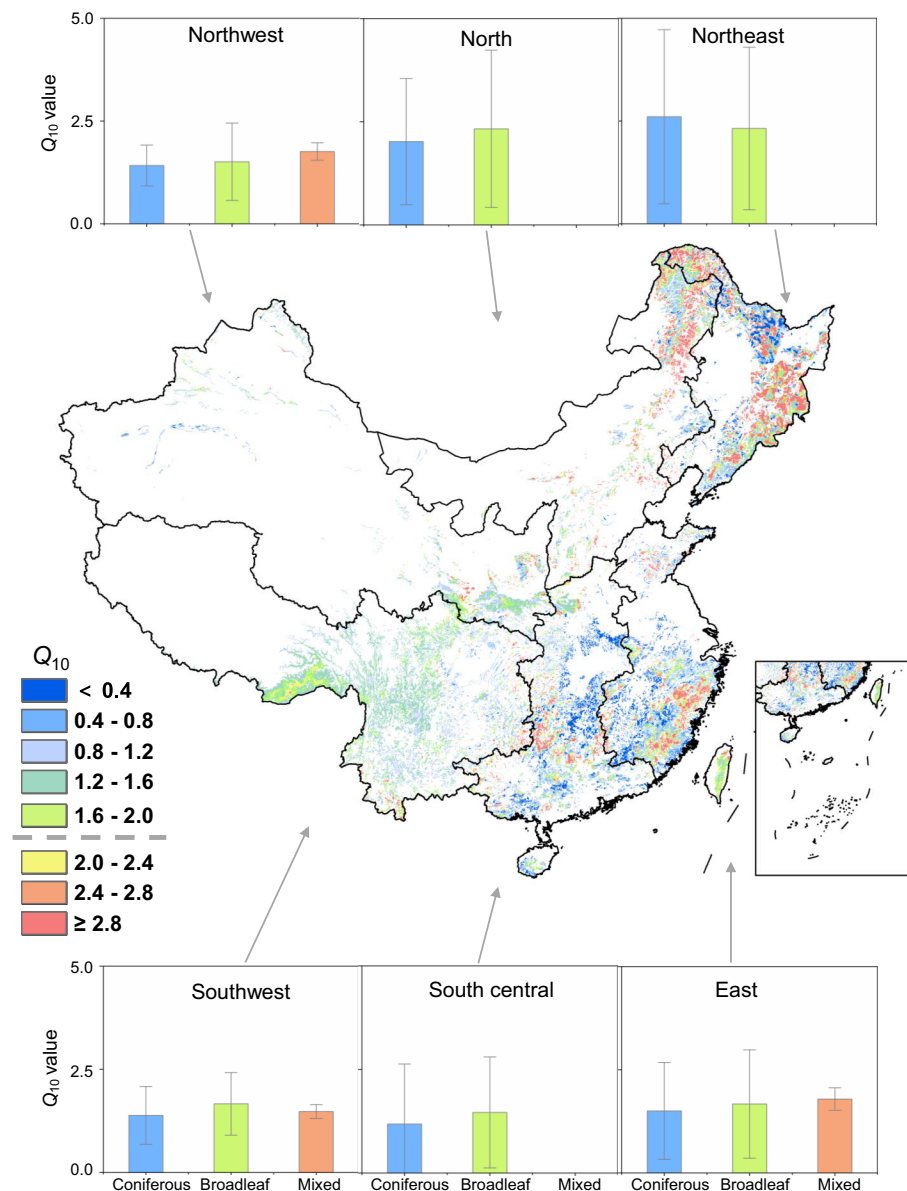


Fig. 5. The  $Q_{10}$  values of the litter decomposition rates in different regions of China.  $Q_{10}$  values are presented as the mean  $\pm$  1 SD, based on grid-cell differences. Forests in China are divided into six regions (Fang et al. 2001).

higher than that of the coniferous leaf litter (0.47) but not significantly different from the mixed (0.52) leaf litter, which is consistent with the findings from global estimates (Zhang et al. 2008). Weedon et al. (2009) stated that the decomposability of broadleaved litter was higher than that of coniferous litter due to the relatively lower lignin concentration and higher N and phosphorus

(P) concentrations in the former than those in the latter (Cornwell et al. 2008, Weedon et al. 2009). Numerous studies have demonstrated that litter quality, including concentrations of lignin and N, and the ratios of C:N and lignin:N influenced the decomposition rate of litter at the local scale (Berg et al. 1993, Hattenschwiler et al. 2005, Yue et al. 2017). At the regional scale, these litter traits

played key roles in controlling decomposition rates across various biomes (Cornwell et al. 2008, Currie et al. 2010, Hu et al. 2018).

Climatic predictors have long been considered the predominant factors that influence the  $k$  value at regional or global scales (Berg et al. 1993, Vitousek et al. 1994, Aerts 1997, Gholz et al. 2000, Zhang et al. 2008). Our results suggested that the spatial distribution of the  $k$  value changed significantly with MAT and elevation. The importance analysis indicated that MAT was the most important factor in the models among the nine potential predictors. According to the 500 model estimates, the  $k$  values ranged from 0.27 per year in the northeastern boreal forests to 0.90 per year in the southern tropical forests of China (95% CI), with an average value of 0.53 per year.

Previous studies suggested that biotic factors are also important driving predictors of the litter decomposition process (e.g., Coûteaux et al. 1995, Wardle et al. 1997, Trofymow et al. 2002, Hattenschwiler et al. 2005, Barlow et al. 2007, Makkonen et al. 2012). For different forest types, the  $k$  values in the broadleaved forests (including broadleaved, coniferous and their mixed leaf litters in the broadleaved forests) were higher than those in the coniferous forests. Geographically, broadleaved forests were mainly distributed in the south, while coniferous forests were mainly distributed in the north of China. The  $k$  values were also higher in the broadleaved forests than in the coniferous forests in the six regions of China (Appendix S1: Table. S2). Broadleaved forests and coniferous forests in the eastern region had the highest  $k$  values (0.80 and 0.60, respectively), and those in the northwestern region had the lowest  $k$  values (0.49 and 0.31, respectively) compared with other regions.

Soil pH can strongly influence the decomposition process by changing the composition and diversity of fungal and bacterial communities (Rousk et al. 2010), especially fungi, which assume dominant roles in the decomposition of lignin (Kuehn et al. 1999). The white-rot fungus was the best choice for lignin decomposition, and its abundance decreased with increasing soil pH (Rousk et al. 2010). The relationship between the  $k$  value and soil pH in the partial dependence plot also showed that the  $k$  value decreased with increasing soil pH (Fig. 3b). According to the linear regression, the soil C:N ratio showed a

slightly positive relationship with the  $k$  value. However, when controlling for other factors, the positive relationship between the decomposition rate and soil C:N ratio no longer existed or even showed a slight negative correlation (Fig. 3i).

#### *Spatial patterns of $Q_{10}$*

Previous studies have quantified the temperature sensitivity of forest soil respiration at local, regional, and global scales (Boone et al. 1998, Bond-Lamberty and Thomson 2010, Li et al. 2020), but few studies have focused on the temperature sensitivity of forest litter decomposition (Salinas et al. 2011, Bothwell et al. 2014). Limited by the litterbag method, the temperature sensitivity of the  $k$  value was difficult to quantify. Environmental gradient estimates or cultivation experiments in the laboratory could be used to quantify the  $Q_{10}$  value of the decomposition rate of litter (Salinas et al. 2011, Bothwell et al. 2014).

Several studies estimated the  $Q_{10}$  value of the decomposition rate along an elevation gradient (Salinas et al. 2011, Bothwell et al. 2014). In this study, the  $Q_{10}$  values of the broadleaved forests were higher than those of the coniferous forests. For the different regions, the average  $Q_{10}$  value (2.4) in the northeastern region was higher than that in the other regions (ranging from 1.3 to 2.4 across six regions; Fig. 5, Fang et al. 2001). Forests in the northeastern region sequestered the highest C storage among the vegetation biomass (Fang et al. 2018) and litter (Zhu et al. 2017). This result might suggest a higher C flux from the forest litter layer in the northeastern region than that in the other regions of China under the future climate warming scenario. Peng et al. (2009) and Li et al. (2020) demonstrated the spatial distribution of the sensitivity of soil respiration in China's forests and found that forest soil respiration sensitivity to temperature was greater in cold, high-latitude ecosystems than in warm, temperate areas, similar to the distribution of the  $Q_{10}$  value of litter decomposition in this study. The temperature sensitivity of litter decomposition and soil respiration had similar spatial patterns. At the climatic space, we also found that a higher MAT led to a lower  $Q_{10}$  value, and the relatively low  $Q_{10}$  values occurred primarily in the sub-tropical evergreen forests of China. The combination of a relatively lower temperature and precipitation promoted higher  $Q_{10}$  values for the

litter decomposition rate in semi-humid forests, where the MAP ranged from 400 to 800 mm.

We then evaluated the spatial patterns of temperature sensitivity by comparing our modeled estimate with the elevation gradient-based estimate (Table 2). We re-calculated  $Q_{10}$  from seven elevation gradients (17  $Q_{10}$  values) for the different litter types. More than half of the  $Q_{10}$  (4/7) gradients based on elevation gradient predictions could be comparable with our estimate. With changes in elevation, not only air temperature but also other environmental factors (e.g., soil moisture, soil microorganisms, litter types, and even forest types) experience considerable changes (Salinas et al. 2011). In this study, no obvious evidence showed that these factors could change suddenly within the  $21 \times 21$  pixels

windows compared with the large area of China's forests.

### Implications for the carbon cycle in China's forests

In the Northern Hemisphere, China contains almost all major forest types. Jia et al. (2018) established a dataset to estimate litterfall production in China's forests and found that annual litterfall production ranged from 0.3 to 17.0 ton/ha in different forest types, similar to Eurasian forests (0.3–15.1 ton/ha, Liu et al. 2004). Zhu et al. (2017) stated that the C storage of forest litter per unit area decreased during the past two decades. According to the different climate scenarios of the Intergovernmental Panel on Climate Change, temperature will increase by 1.5°–2°C by 2100 (IPCC 2014). Under these warming scenarios, the rates of litter decomposition and litter inputs will continue to increase (Liu et al. 2009, Richardson et al. 2013), but these increases might be lower than those predicted by the model. The  $Q_{10}$  value used by the Earth System Model (ESM) is 2.0, and we estimated a value of 1.76 in this study. With regard to future climate projections, the results indicate that the C dioxide release from the litter layer in China's forest ecosystems might be reduced.

## CONCLUSIONS

The spatial distributions of the  $k$  value and its temperature sensitivity in China's forests were estimated in this study. The estimated  $Q_{10}$  value in this study had considerable variance across forest types and biomes; the variance ranged from 0.05 to 11.68, with an average of 1.76. Such variations in litter decomposition sensitivity to the MAT with the abiotic and biotic factors observed in China's forests should be considered in the projections of future regional C budgets.

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Table 2. Comparison between elevation gradient-based  $Q_{10}$  and spatial distribution of  $Q_{10}$  in different mountains.

Elevation gradient-based $Q_{10}$	Site name	Spatial distribution of $Q_{10}$	SD
1.8	Taiwan†	1.8	0.2
2.1	Jianfengling Mountain	1.3	0.5
4.0	Jianfengling Mountain	1.3	0.5
3.4	Wuyi Mountains	1.4	0.9
2.9	Wuyi Mountains	1.4	0.9
2.9	Wuyi Mountains	1.4	0.9
2.9	Wuyi Mountains	1.4	0.9
2.3	Wuyi Mountains†	1.4	0.9
2.1	Wuyi Mountains†	1.4	0.9
2.2	Changbai Mountain†	3.1	2.0
2.0	Changbai Mountain†	3.1	2.0
4.3	Changbai Mountain†	3.1	2.0
2.7	Changbai Mountain†	3.1	2.0
1.3	Mountain Shennongjia†	1.1	0.2
5.0	Jiuzhaigou valley	1.5	0.2
3.4	Jiuzhaigou valley	1.5	0.2
3.1	Yaoluoping Nature Reserve	0.9	0.8

† Indicates mountains for which  $Q_{10}$  could be comparable with our estimate.

organizations that could inappropriately influence our work, and there are no professional or other personal interests of any nature in any product, service, and/or company that could be construed as influencing the position presented in or the review of this manuscript.

## LITERATURE CITED

- Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–449.
- Álvarez-Cabria, M., J. Barquín, and F. J. Peñas. 2016. Modelling the spatial and seasonal variability of water quality for entire river networks: relationships with natural and anthropogenic factors. *Science of the Total Environment* 545: 152–162.
- Álvarez-Cabria, M., A. M. Gonzalez-Ferreras, F. J. Peñas, and J. Barquín. 2017. Modelling macroinvertebrate and fish biotic indices: from reaches to entire river networks. *Science of The Total Environment* 577:308–318.
- Bárcenas-Moreno, G., M. Gómez-Brandón, J. Rousk, and E. Bååth. 2009. Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. *Global Change Biology* 15:2950–2957.
- Barlow, J., T. A. Gardner, L. V. Ferreira, and C. A. Peres. 2007. Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *Forest Ecology and Management* 247:91–97.
- Barnard, D. M., M. J. Germino, D. S. Pilliod, R. S. Arkle, C. Applestein, B. E. Davidson, and M. R. Fisk. 2019. Cannot see the random forest for the decision trees: selecting predictive models for restoration ecology. *Restoration Ecology* 27: 1053–1063.
- Bell, C. W., V. Acosta-Martinez, N. E. McIntyre, S. Cox, D. T. Tissue, and J. C. Zak. 2009. Linking microbial community structure and function to seasonal differences in soil moisture and temperature in a Chihuahuan desert grassland. *Microbial Ecology* 58:827–842.
- Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils—a mini review. *Scandinavian Journal of Forest Research* 1:359–369.
- Berg, B., et al. 1993. Litter mass-loss rates in pine forests for Europe and Eastern United State: some relationships with climate and litter quality. *Biogeochemistry* 20:127–159.
- Berg, B. 2014. Decomposition patterns for foliar litter – A theory for influencing factors. *Soil Biology and Biochemistry* 78:222–232.
- Bocock, K. L., and O. J. W. Gilbert. 1957. The disappearance of leaf litter under different woodland conditions. *Plant and Soil* 9:179–185.
- Bonan, G. B., M. D. Hartman, W. J. Parton, and W. R. Wieder. 2013. Evaluating litter decomposition in earth system models with long-term litterbag experiments: an example using the Community Land Model version 4 (CLM4). *Global Change Biology* 19:957–974.
- Bond-Lamberty, B., and A. M. Thomson. 2010. Temperature-associated increases in the global soil respiration record. *Nature* 464:579–582.
- Boone, R. D., K. J. Nadelhoffer, J. D. Canary, and J. P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396:570–572.
- Bothwell, L. D., P. C. Selman, C. P. Giardina, and C. M. Litton. 2014. Leaf litter decomposition rates increase with rising mean annual temperature in Hawaiian tropical montane wet forests. *PeerJ* 2: e685.
- Bradford, M. A., B. Berg, D. S. Maynard, W. R. Wieder, and S. A. Wood. 2016. Understanding the dominant controls on litter decomposition. *Journal of Ecology* 104:229–238.
- Bradford, M. A., R. J. Warren II, P. Baldrian, T. W. Crowther, D. S. Maynard, E. E. Oldfield, W. R. Wieder, S. A. Wood, and J. R. King. 2014. Climate fails to predict wood decomposition at regional scales. *Nature Climate Change* 4:625–630.
- Cafri, G., and B. A. Bailey. 2016. Understanding variable effects from black box prediction: quantifying effects in tree ensembles using partial dependence. *Journal of Data Science* 14:67–95.
- Chen, L., S. Peng, and B. Yang. 2015. Predicting alien herb invasion with machine learning models: biogeographical and life-history traits both matter. *Biological Invasions* 17:2187–2198.
- Cheng, Q. 1999. Spatial and scaling modelling for geochemical anomaly separation. *Journal of Geochemical Exploration* 65:175–194.
- Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11:1065–1071.
- Coûteaux, M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10:63–66.
- Currie, W. S., M. E. Harmon, I. C. Burke, S. C. Hart, W. J. Parton, and W. L. Silver. 2010. Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. *Global Change Biology* 16:1744–1761.



- Ding, J., et al. 2019. The paleoclimatic footprint in the soil carbon stock of the Tibetan permafrost region. *Nature Communications* 10:1–9.
- ECVMC, Editorial Committee of Vegetation Map of China, Chinese Academy Science. 2007. Vegetation Map of the People's Republic of China (1:1000000). Geological Publishing House, Beijing, China.
- Fang, J., A. Chen, C. Peng, S. Zhao, and L. Ci. 2001. Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292:2320–2322.
- Fang, J., Z. Shen, Z. Tang, X. Wang, Z. Wang, J. Feng, Y. Liu, X. Qiao, X. Wu, and C. Zheng. 2012. Forest community survey and the structural characteristics of forests in China. *Ecography* 35:1059–1071.
- Fang, J., G. Yu, L. Liu, S. Hu, and F. S. Chapin. 2018. Climate change, human impacts, and carbon sequestration in China. *Proceedings of the National Academy of Sciences of the United States of America* 115:4015–4020.
- Feng, Y., S. Wu, P. Wu, S. Su, M. Weng, and M. Bian. 2018. Spatiotemporal characterization of megaregional poly-centrality: evidence for new urban hypotheses and implications for polycentric policies. *Land Use Policy* 77:712–731.
- Feng, Y., J. Zhu, X. Zhao, Z. Tang, J. Zhu, and J. Fang. 2019. Changes in the trends of vegetation net primary productivity in China between 1982 and 2015. *Environmental Research Letters* 14:124009.
- Garcíapalacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters* 16:1045–1053.
- Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6:751–765.
- Greenwell, B. M. 2017. pdp: an R package for constructing partial dependence plots. *The R Journal* 9:421–436.
- Handa, I. T., et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509:218–221.
- Hattenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 36:191–218.
- Hu, Z., S. T. Michaletz, D. J. Johnson, N. G. McDowell, Z. Huang, X. Zhou, and C. Xu. 2018. Traits drive global wood decomposition rates more than climate. *Global Change Biology* 24:5259–5269.
- IPCC. 2014. Climate Change 2014: mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Pages 1–1435 in O. R. Edenhofer, et al. editors. *Climate Change 2014: mitigation of Climate Change*. Cambridge University Press, Cambridge, UK and New York, New York, USA.
- Jia, B., Z. Xu, G. Zhou, and X. Yin. 2018. Statistical characteristics of forest litterfall in China. *Science China Life Sciences* 61:358–360.
- Kuehn, K. A., M. O. Gessner, R. G. Wetzel, and K. Suberkropp. 1999. Decomposition and CO<sub>2</sub> evolution from standing litter of the emergent macrophyte *Erianthus giganteus*. *Microbial Ecology* 38:50–57.
- Kuhn, S., B. Egert, S. Neumann, and C. Steinbeck. 2008. Building blocks for automated elucidation of metabolites: machine learning methods for NMR prediction. *BMC Bioinformatics* 9:400.
- Li, J., M. Nie, E. Pendall, P. B. Reich, J. Pei, N. J. Noh, T. Zhu, B. O. Li, and C. Fang. 2020. Biogeographic variation in temperature sensitivity of decomposition in forest soils. *Global Change Biology* 26:1873–1885.
- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R News* 2:18–22.
- Liu, C., B. Berg, W. Kutsch, C. J. Westman, H. Ilvesniemi, X. Shen, G. Shen, and X. Chen. 2006. Leaf litter nitrogen concentration as related to climatic factors in Eurasian forests. *Global Ecology and Biogeography* 15:438–444.
- Liu, C., C. J. Westman, B. Berg, W. L. Kutsch, G. Z. Wang, R. Man, and H. Ilvesniemi. 2004. Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. *Global Ecology and Biogeography* 13:105–114.
- Liu, L., J. S. King, F. L. Booker, C. P. Giardina, H. L. Allen, and S. Hu. 2009. Enhanced litter input rather than changes in litter chemistry drive soil carbon and nitrogen cycles under elevated CO<sub>2</sub>: a microcosm study. *Global Change Biology* 15:441–453.
- Makkonen, M., M. P. Berg, I. T. Handa, S. Hattenschwiler, J. Van Ruijven, V. P. M. Bodegom, and M. A. Aerts. 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters* 15:1033–1041.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465–472.
- Mitchell, A. 2005. The ESRI guide to GIS analysis, volume 2: spatial measurements and statistics. Environmental Systems Research Institute Press, University of Redlands, Redlands, California, USA.
- Neta, T., Q. Cheng, R. L. Bello, and B. Hu. 2010. Upscaling reflectance information of lichens and mosses using a singularity index: a case study of



- the Hudson Bay Lowlands, Canada. *Biogeosciences* 7:2557–2565.
- Olson, J. S. 1963. Energy storage and balance of producers and decomposers in ecological systems. *Ecology* 44:322–331.
- Pan, Y., et al. 2011. A large and persistent carbon sink in the World's forests. *Science* 333:988–993.
- Paudel, E., G. G. Dossa, M. de Blecourt, P. Beckschafer, J. Xu, and R. D. Harrison. 2015. Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. *Ecosphere* 6:1–20.
- Peng, S., S. Piao, T. Wang, J. Sun, and Z. Shen. 2009. Temperature sensitivity of soil respiration in different ecosystems in China. *Soil Biology and Biochemistry* 41:1008–1014.
- Prescott, C. E. 2010. Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101: 133–149.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Rousk, J., E. Bååth, P. C. Brookes, C. L. Lauber, C. Lozupone, J. G. Caporaso, R. Knight, and N. Fierer. 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal* 4:1340–1351.
- Salinas, N., et al. 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist* 189:967–977.
- Silver, W. L., and R. K. Miya. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419.
- Statnikov, A., L. Wang, and C. F. Aliferis. 2008. A comprehensive comparison of random forests and support vector machines for microarray-based cancer classification. *BMC Bioinformatics* 9:319.
- Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist* 140: 893–911.
- Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, California, USA.
- Tang, X., et al. 2018. Carbon pools in China's terrestrial ecosystems: new estimates based on an intensive field survey. *Proceedings of the National Academy of Sciences of the United States of America* 115:4021–4026.
- Trofymow, J. A., et al. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Canadian Journal of Forest Research* 32:789–804.
- Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, and N. El Saleous. 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International Journal of Remote Sensing* 26:4485–4498.
- Veen, G. F., G. T. Freschet, A. Ordonez, and D. A. Wardle. 2015. Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos* 124:187–195.
- Vitousek, P. M., D. R. Turner, W. J. Parton, and R. L. Sanford. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. *Ecology* 75:418–429.
- Wall, D. H., et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14:2661–2677.
- Wang, X., S. Piao, P. Ciais, I. A. Janssens, M. Reichstein, S. Peng, and T. Wang. 2010. Are ecological gradients in seasonal  $Q_{10}$  of soil respiration explained by climate or by vegetation seasonality. *Soil Biology and Biochemistry* 42:1728–1734.
- Wardle, D. A., K. I. Bonner, and K. S. Nicholson. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79:247–258.
- Weedon, J. T., W. K. Cornwell, J. H. Cornelissen, A. E. Zanne, C. Wirth, and D. A. Coomes. 2009. Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters* 12:45–56.
- Yue, K., D. A. Fornara, W. Yang, Y. Peng, C. Peng, Z. Liu, and F. Wu. 2017. Influence of multiple global change drivers on terrestrial carbon storage: Additive effects are common. *Ecology Letters* 20:663–672.
- Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* 1:85–93.
- Zhang, D., X. Xu, S. Yao, J. Zhang, X. Hou, and R. Yin. 2020. A novel similar habitat potential model based on sliding-window technique for vegetation restoration potential mapping. *Land Degradation and Development* 31:760–772.
- Zhao, X., Y. Yang, H. Shen, X. Geng, and J. Fang. 2019. Global soil-climate-biome diagram: linking surface soil properties to climate and biota. *Biogeosciences* 16:2857–2871.

- Zhu, J., et al. 2017. Carbon stocks and changes of dead organic matter in China's forests. *Nature Communications* 8:151.
- Zhu, J., et al. 2020. Increasing soil carbon stocks in eight permanent forest plots in China. *Biogeo-sciences* 17:715–726.

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