

# Controls over leaf litter decomposition in a mixed evergreen and deciduous broad-leaved forest, Central China

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## Abstract

**Aims** Our understanding of the determinants of leaf litter decomposition is lacking for mixed evergreen and deciduous broad-leaved forests compared with tropical and temperate forests. This study aimed to assess the relative importance of litter properties, climate and soil on decomposition in a mixed above-mentioned forest in a transitional zone, central China.

**Methods** We utilized leaf litter from seven canopy tree species in conjunction with a transplant litterbag experiment along an elevational gradient over three years by measuring decomposition rate.

**Results** Initial leaf litter nitrogen (N), phosphorus (P) and magnesium (Mg) as well as C:P were robust predictors of leaf litter decomposition. Mg was the single best predictor of leaf litter decomposition across all species. Soil moisture and air temperature could predict leaf litter decomposition very well across the elevational gradient. The explanatory power of elevation-related variables (27.75 %) was much lower than that of species-related variables (38.97 %).

**Conclusions** More nutrients such as Mg than N and P commonly used in proposed indices should be taken into account when evaluating the decomposability of leaf litter. Tree species identity is the most important determinant of leaf litter decomposition in this target transitional mixed forest. Therefore, shifts in tree species composition may influence leaf litter decomposition rates more than changes in site conditions under the context of future climate change.

**Keywords** Leaf litter property · Decomposability · Species composition · Carbon and nutrient cycling · Climate change

## Introduction

Global climate change is likely to affect biodiversity through shifts in species composition (Hooper et al. 2012). These changes are anticipated to impact most regions of the northern hemisphere, and will be particularly pronounced in the Central China (IPCC, Intergovernmental Panel on Climate Change 2013). This region (*lato sensu*), located at the transitional zone between subtropical and temperate climates, is one of the 34 identified biodiversity hotspots in the world, based on its diversity and on the presence of a large number of endemic species (Myers et al. 2000). Besides, this region contains structuring species such as evergreen and deciduous broad-leaved tree species belonging Fagaceae family that are widespread and coexist in forest ecosystems. The mixed evergreen and deciduous

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broad-leaved forest is the zonal vegetation type of this region and is considered as extremely vulnerable to global climate change (Ge et al. 2013). Therefore, this forest is well suited to studying future global change effects on ecosystem processes.

Litter decomposition is a fundamental ecosystem process which drives carbon and nutrient cycling and has received growing attention in the last several decades (Berger et al. 2015; Prieto et al. 2016; Yue et al. 2015). Through the activity of decomposers and trophic transfer, nutrients like nitrogen (N), phosphorus (P) and some base cations in litter are made available to primary producers and higher trophic levels, and carbon (C) is released into the atmosphere or stored in the form of organic matter in soil (Anaya et al. 2012; Hobbie 2015; Santonja et al. 2015). Many studies have indicated that climate and litter chemical and physical properties exert strong controls over rates of litter decomposition (Aerts 1997; Portillo-Estrada et al. 2016; Zanne et al. 2015). Across a wide range of forest ecosystems, temperature and water-related parameters, as well as metrics of litter properties like nitrogen (N) and phosphorus (P) availability are good predictors of rates of litter mass loss at the different scales (Bradford et al. 2016; Currie et al. 2010; Cusack et al. 2009; Yue et al. 2016). Several recent lines of evidence have also shown global consistency in the predominant role of species traits in control litter decomposition, suggesting that decay of litter is a key ecological processes that has been well documented (Comwell et al. 2008; García-Palacios et al. 2013).

There is reason to believe that the relationships observed in many forest ecosystems may not hold true for mixed forests, which are located in the ecotone between evergreen and deciduous broad-leaved forests and are often sensitive to environmental fluctuations (Ge et al. 2013; Kent et al. 1997). The role of the environment (climate in particular) and litter chemical and physical properties in controlling litter decomposition remains poorly understood in the following aspects. First, studies in tropical and subtropical forests show that increasing precipitation and associated soil moisture are frequently correlated with accelerated rates of litter decomposition, while other studies in temperate forests such as Fagaceae species-dominated forests indicate that elevated temperature is positively related to litter decay (Wang et al. 2003). For less studied transitional mixed forests, the question of what and how precipitation and temperature influence litter decomposition remains unclear but are urgently needed to improve predictions of future

global climate and C cycle interactions. Secondly, these forests exhibit extraordinary species diversity (Ge et al. 2013; Zhao et al. 2005), accompanying significant local- and regional-variation in species litter traits that is likely to affect leaf litter decomposition. The relative effects of litter traits appear to vary among forest types. Generally, in many tropical forests N is abundant but low P availability is common, so P-related litter variables play an important role in leaf litter decay (Cleveland et al. 2011; García-Palacios et al. 2013; Wieder et al. 2009). For example, high N:P ratio will lead to slower litter decomposition in tropical forests (Hättenschwiler et al. 2011). In temperate forests, the opposite situation is generally observed, indices of N availability are useful predictors of litter decomposition and high N:P ratio will lead to faster litter decay (Berg 2014; Wang et al. 2010). However, knowledge of the relative roles of different litter nutrients in leaf litter decomposition in mixed evergreen broadleaved forests is still lacking due to a paucity of data, while understanding the controls of leaf litter decomposition in this mixed forest could establish linkages between tropical and temperate forests.

Understanding how climate and litter properties interact to regulate litter decomposition in the mixed evergreen and deciduous broad-leaved forest is of paramount importance given that the potential for large climate shifts that may influence rates of C exchange and storage (Zhao and Running 2010). The mixed evergreen and deciduous broad-leaved forests have globally and regionally important effects on the terrestrial C cycle (Ni 2013; Zhou et al. 2000). Many analyses predict large changes in temperature and precipitation in these forests, but this direction and strength of these changes remains poorly understood (IPCC, Intergovernmental Panel on Climate Change 2013). The extent to which the carbon balance of these forests may be mediated by climate-driven changes in litter decomposition also remains unknown.

In this study, we used natural variations in leaf litter properties across multiple dominant species combined with a natural climatic gradient experiment to investigate the effects of leaf litter properties and climate on leaf litter decomposition in a mixed evergreen and deciduous broadleaved forest in central China. Specifically, we aimed to: (1) determine the relative importance of leaf litter properties and climate in leaf litter decomposition, and (2) detect the significance of climatic variables and tree species variables as predictors.

## Materials and methods

### Site description

The study area is located on the southern slope of the Shennongjia region (31°19'4" N, 110°29'44" E), northwest of Hubei Province, central China. This region is in the transitional zone between the subtropical and temperate climates and it is an important biodiversity hotspot in both China and globally (Myers et al. 2000). The annual precipitation of this area ranges from 1306 to 1722 mm and the mean annual temperature is 10.6 °C. The zonal vegetation is the mixed evergreen and deciduous broad-leaved forest (Ge et al. 2013). A detailed site description can be found in Ge et al. (2013).

### Experimental design

We established a three-year leaf litter transplant and decomposition experiment between 2011 and 2014 in five forest plots along an elevational gradient in Shennongjia, central China: 800, 1000, 1300, 1600 and 1800 m. We used five sets of HOBO Onset micro-climatic recorders (Onset Computer Corporation, USA) to measure soil temperature, soil moisture, and air temperature at one-minute intervals. We also determined soil organic carbon, total N and total P for five-centimeter topsoil (See Appendix 1).

We collected naturally senesced leaves of seven dominant tree species in the mixed forest. We choose the following species based on their dominance in this forest using species composition data from previous studies (Ge et al. 2012; Zhao et al. 2005): *Cyclobalanopsis multinervis* (the synonym of *Quercus hypargyrea*), *Cyclobalanopsis oxyodon* (the synonym of *Quercus oxyodon*), *Quercus engleriana*, *Fagus engleriana*, *Fagus pashanica*, *Quercus serrata* var. *brevipetiolata* and *Quercus aliena* var. *acuteserrata*. The nomenclature of tree species followed Flora of China (The Editorial Board of Flora of China 2004) and all selected tree species belonged to Fagaceae family. Individual species and bulk leaf litter samples were collected in 2011, oven dried at 65 °C for two days to a constant mass and homogenized. Ten grams of leaf litter samples for each species were sealed in 15 × 10 cm litterbags constructed from nylon (1.5-mm mesh). We also calculated the initial mean specific leaf area (SLA) of the leaf litter from the area estimated using a leaf area meter (LI-3000, Li-Cor, USA) (Pérez-Harguindeguy et al. 2013; Salinas et al.

2011). Initial properties of leaf litter samples among different tree species were recorded in appendix 2.

We used the same experimental layout for all seven species. 90 samples from each species were placed in each plot in five clusters (replicates) of 18 samples litterbags (harvests) situated at distinct locations within the plot. One sample litterbag from each cluster was collected at every sample time. In total, 450 litterbags (5 replicates × 18 harvest litterbags × 5 plots) were installed for each species.

In November 2011, a total of 3150 sample litterbags from seven tree species were placed on the soil surface at the five different elevational plots and exposed to natural weather conditions. After deployment of these bags, one litterbag for the five replicated clusters was retrieved approximately every two months in each plot (each time interval being measured from the time of initial installation). Upon collection, litterbags were transported to the laboratory and the remaining litter was brushed carefully to remove adhered debris such roots, fauna and soil particles, dried at 65 °C until mass stabilized, and then weighed (Berg et al. 2015; Liu et al. 2016).

### Chemical analysis

We analyzed additional leaf litter samples for initial litter chemistry and soil chemistry. We determined leaf litter C and N concentration by an elemental analyzer (Model: vario macro cube, Germany), while leaf litter P, potassium (K), calcium (Ca) and magnesium (Mg) were analyzed by inductively coupled plasma spectrometry after digestion of samples in concentrated nitric acid (Thermo ICAP 6300) (Dale et al. 2015; Liu et al. 2016).

### Data processing

We calculated the proportion of initial mass by dividing the mass at harvest date by the initial mass. We also determined decomposition constants (k) by fitting the data for any one cluster of each species with a negative exponential decay model (Olson 1963; Manzoni et al. 2012).

We checked all leaf litter variables for normality and transformed data to normal distribution if necessary. We conducted two-way ANOVA to determine the effect of elevation, species, and their interactions on leaf litter decomposition rates. We also used Turkey's HSD test to compare decomposition rates among tree species and

elevations. We performed single and multiple regressions to examine the relationships between leaf litter properties and decomposition rates. We firstly performed simple linear regression to detect relationships between species and/or elevation-related variables and leaf litter decomposition rates. We also used stepwise multiple linear regressions with backwards elimination to determine how well variation in leaf litter properties and elevation related variables predicted observed decomposition constants (Wieder et al. 2009).

To assess the relative importance of species and elevation and to identify predictors of variation in the decomposition constant ( $k$ ), we performed a variation partitioning analysis, as conducted in previous studies (Kraha et al. 2012; Ray-Mukherjee et al. 2014). We evaluated significant differences for all statistical tests at the level of  $\alpha = 0.05$ . We performed all statistical analysis in R 3.0.0 (R Core Team 2013).

## Results

### Leaf litter decomposition among different species

Exponential decay curves for the three years of decomposition in the field described the data well (in all plots mean  $R^2 = 0.86$ , range  $R^2 = 0.58$ – $0.98$ ). The corresponding  $k$  value from the seven individual tree species varied by a factor of nearly five and were significantly different from one another ( $P < 0.05$ ), with *Quercus serrata* var. *brevipetiolata* having the most rapid decay rate and *Fagus engleriana* having the slowest decay rate. The overall mean of leaf litter decomposition  $k$  value was  $0.39 \text{ year}^{-1}$  (Fig. 1).

To eliminate the possible effects of climate and soil across the elevation gradient and to take into account the interaction of species and elevation (Table 1), we only explored the relationships between leaf litter decomposition  $k$  value and individual leaf litter properties at 1800 m. First, we conducted single regression to examine the relationship between individual leaf litter property and decomposition rate. We found that leaf litter Mg was the best single predictor of leaf litter decomposition (negative) ( $R^2 = 0.60$ ,  $P < 0.05$ ) (Fig. 2). Leaf litter C, Ca, and SLA were negatively related with  $k$  ( $R^2 = 0.31$ ,  $P < 0.05$ ;  $R^2 = 0.15$ ,  $P < 0.05$ ,  $R^2 = 0.51$ ,  $P < 0.05$ , respectively). There were no significant relationships between other leaf litter variables and  $k$  value ( $P > 0.05$ ).

We further conducted stepwise multiple linear regressions with backward elimination to examine the relationship between leaf litter properties and decomposition rates and found that initial litter N ( $P < 0.05$ ), initial P ( $P < 0.05$ ) and Mg ( $P < 0.05$ ) as well as C:P ( $P < 0.05$ ) were the best predictors of observed decomposition rates (model  $R^2 = 0.75$ ,  $P < 0.05$ ).

### Leaf litter decomposition along the elevational gradient

Decomposition rates generally increased with decreasing elevation (Appendix 3). The mean of  $k$  value, averaged across all samples at each elevation, ranged from  $0.47 \text{ year}^{-1}$  at 1000 m to  $0.31 \text{ year}^{-1}$  at 1800 m (Fig. 3).

We related  $k$  to environmental variables associated with elevation using simple linear regression. We found that all measured elevation-related variables except for soil P, were significantly correlated with decomposition rate. Soil P did not correlate well with leaf litter decomposition  $k$  value ( $P > 0.05$ ). Soil temperature, air temperature, Soil N, N:P, and C were positively associated, while soil moisture were negatively associated with leaf litter decomposition  $k$  value ( $P < 0.05$ ). Air temperature was the single best predictor of leaf litter decomposition ( $R^2 = 0.25$ ) (Fig. 4).

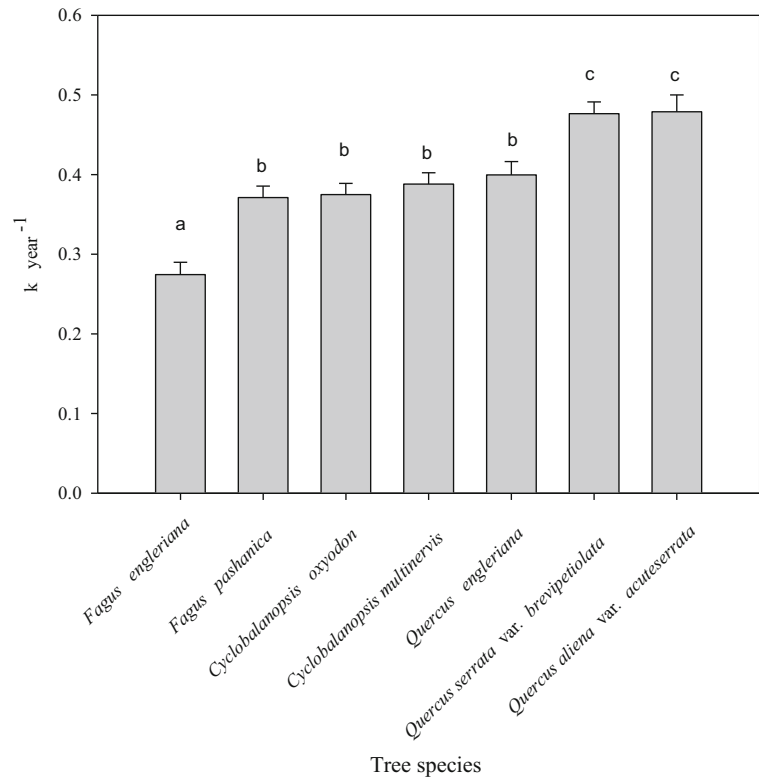
We further examined the relationship between elevation-related variables and decomposition  $k$  value by multiple linear regressions with backward elimination. We found that soil moisture ( $P < 0.05$ ) and air temperature ( $P < 0.05$ ) were the best predictors of leaf litter decomposition (model  $R^2 = 0.28$ ,  $P < 0.05$ ).

### The relative importance of different factors

No significant interactive effects of species identity and elevation on leaf litter decomposition were observed ( $P > 0.05$ ) (Table 1), indicating that the differences in leaf litter decomposition among species were robust against changes in elevation-related variables. Elevation and species explained 29.83 % and 40.33 % of variation in rate of leaf litter decomposition, respectively.

We further evaluated the effects of elevation- and species-related variables on variation in leaf litter decomposition rate using stepwise multiple regressions with backward elimination. We found that air temperature, soil moisture, litter P, Mg and C:P were the best indicators of leaf litter decomposition rate (model  $R^2 = 0.67$ ,  $P < 0.05$ ), and these variables explained

**Fig. 1** Leaf litter decomposition rates of the seven tree species. Data are means ( $n = 5$ ) and error bars represent standard error. Different letters denote significant differences resulting from Tukey's HSD test. Tree species was arranged in order of increased decomposition rate



approximately 24.97 %, 2.78 %, 10.10 %, 18.92 % and 9.94 %, respectively.

## Discussion

Data on leaf litter decomposition rates for the mixed evergreen and deciduous broad-leaved forests are mostly absent from both regional (Chinese) and global analyses (Cornwell et al. 2008; Zhang et al. 2008; Zhou et al. 2008). Here, we found that mean of leaf litter decomposition  $k$  value in our target mixed forest was  $0.39 \text{ year}^{-1}$ , indicating that the mean residence time of leaf litter ( $1/k$ ) was no more than three years. Not surprisingly, this rate fell within the range

reported for a wide variety of forests at the global scale (Zhang et al. 2008). The overall average  $k$  value for all tree species in this study was much lower than rates reported from tropical forest sites (Dale et al. 2015; Waring 2012; Wieder et al. 2009), but higher than temperate forests (Cusack et al. 2009). These differences may be due to interactive effects of climate and species composition between these forest ecosystems (Hättenschwiler et al. 2011).

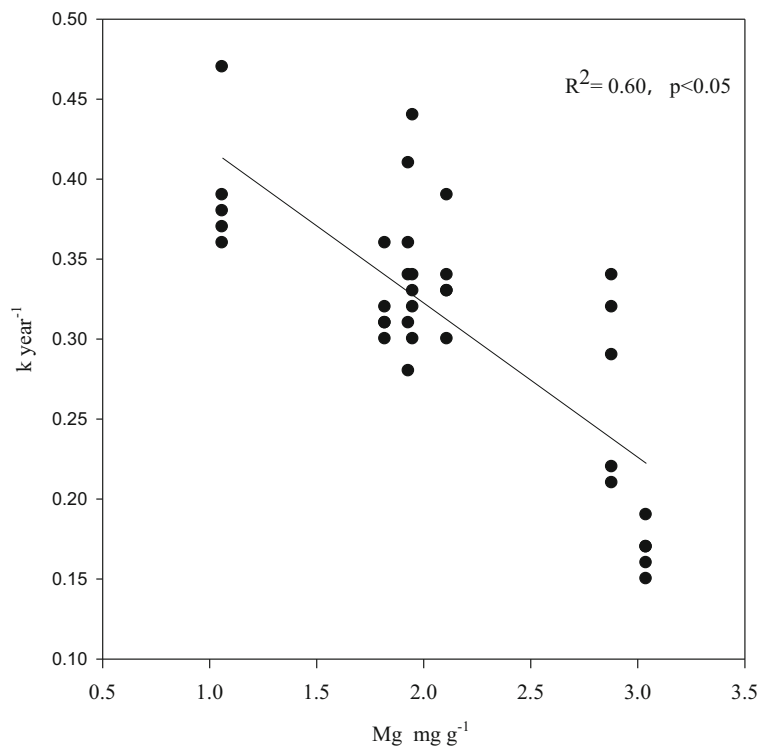
Leaf litter decomposition among these studied tree species

Results show that tree species was the predominant driver of leaf litter decomposition. We observed a nearly

**Table 1** Two-way ANOVA for elevation and species effects on leaf litter decomposition

Source of variation	Degrees of freedom	Sum of squares	Mean sum of squares	F-value	$p$ -value	% Sum of squares
Elevation	4	0.54	0.13	43.807	<2e-16 ***	29.83
Species	6	0.73	0.12	39.870	<2e-16 ***	40.33
Elevation $\times$ Species	24	0.11	0.00	1.493	0.079	6.08
Residuals	140	0.43	0.00			

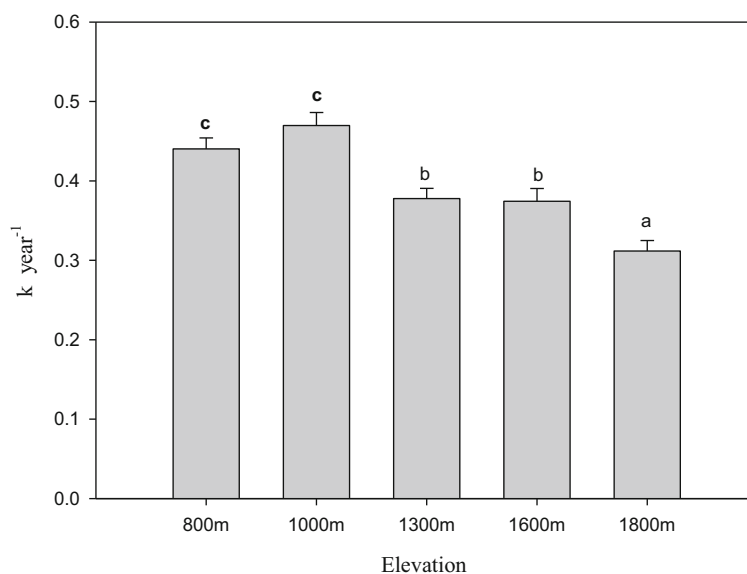
**Fig. 2** Regression analyses of leaf litter Mg and leaf litter decomposition among tree species in a mixed evergreen and deciduous broad-leaved forest



fivefold variation in decomposition  $k$  value among the seven tree species, which strongly supports the theory that species traits are the dominant determinant of ecosystem processes in forests at local scales (Bradford et al. 2016; Ward et al. 2015). It also suggests that vegetation acts as a pathway between global climate change drivers and ecosystem C and nutrient cycles.

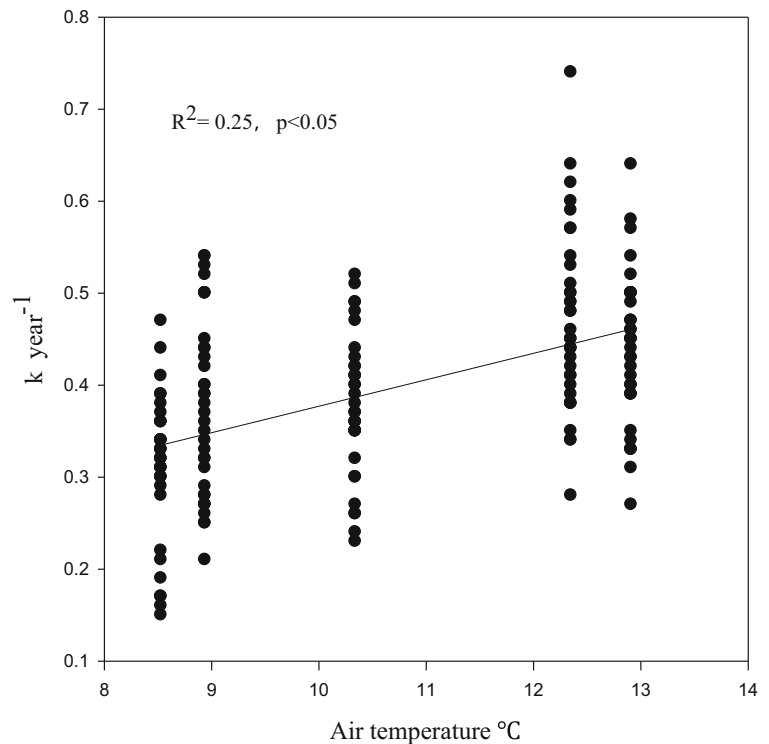
The relatively few studies that explicitly assessed the relative effects of species and site conditions on leaf litter decomposition supported our results (Dale et al. 2015; Osanai et al. 2012). For example, previous studies show that species identity had a greater influence on leaf litter decomposition than precipitation in lowland tropical forests in Costa Rica and Panama (Dale et al. 2015;

**Fig. 3** Leaf litter decomposition rates along the elevational gradient. Data are means ( $n = 5$ ) and error bars represent standard error. These different letters denote significant differences resulting from Tukey's HSD test among elevations





**Fig. 4** Regression analyses of air temperature and leaf litter decomposition rates ( $k$ ) in a mixed evergreen and deciduous broad-leaved forest



Wieder et al. 2009). These findings also indicated that tree species traits played a significant role relative to climatic and other abiotic factors in driving leaf litter decomposition at the local scales (Bradford et al. 2016; Carbognani et al. 2014; Cornwell et al. 2008). This highlights the importance of local-scale species trait variability in governing leaf litter decomposition as indicated by recent studies (Bradford et al. 2016; Zanne et al. 2015). For example, Zanne et al. (2015) found that species identity and tissue construction could exert stronger controls on leaf litter decomposition in a temperate deciduous oak-hickory forest. Past work has shown that a diversity of ecological strategies of tree species are employed to balance trade-offs between leaf production, longevity, tree growth and nutrient acquisition which translates into biogeochemical diversity that influences leaf litter decomposability from local to global scales (Cornwell et al. 2008; Freschet et al. 2013; Wieder et al. 2009). Such strong species effects are also likely to be important in our target transitional mixed forest, where high species diversity cause large local and regional variation in leaf litter properties (Ge 2014).

Analysis of continuous leaf litter properties and decomposition rates provides correlative information and clues to underlying mechanisms and inter-specific

patterns in litter decomposition rates (Santiago 2010). Previous studies also indicate that large differences in decomposition rates among co-existing tree species occur globally and locally and are associated with leaf litter economics (Cornwell et al. 2008; Dale et al. 2015). Here, we found that the variation in leaf litter decomposition across the seven study species was significantly correlated with chemical and physical differences in leaf litter properties. Leaf litter decomposition involves the breakdown of C-rich but nutrient-poor organic substrates, necessitating a coordinated acquisition of resources to produce an assortment of enzymes by distinct microbes and provides a linkage between tree species function and ecosystem dynamics such as the positive feedback between tree species and soil nutrients (Bradford et al. 2014; Freschet et al. 2013; Hobbie 2015; Santiago 2010). Thus, in a variety of forest ecosystems across the globe, rates of leaf litter decomposition are significantly related to initial nutrient availability of litter. In this study, we found that similar metrics of leaf litter properties to previous studies were highly correlated to leaf litter decomposition rates (Barantal et al. 2012; Hättenschwiler et al. 2011).

We found that the initial N, initial P and Mg as well as C:P correlated well with leaf litter decomposition. We

found the strong autocorrelation between N:P and N (or P) ( $r = 0.86$ ), as also indicated by previous studies (Wieder et al. 2009). And we did not detect significant relationship between N:P and leaf litter decomposition rate with single regression. So we did not discuss the indicator N:P more here. Similar results have been observed in temperate and tropical forests (Berger et al. 2015; Cusack et al. 2009; Parton et al. 2007; Portillo-Estrada et al. 2016; Waring 2012). It appears that microbial activity in this mixed forest may be co-limited by N and P. Leaf litter Mg was the single best predictor of leaf litter decomposition at the local scale (excluding climatic effects), indicating a key role of Mg in the decomposition process. This result agrees well with earlier findings in tropical forests (Powers and Salute 2011). However, it is difficult to explain the role of Mg in leaf litter decomposition due to the fact that there are no field studies that have directly evaluated the role of Mg in litter decomposition at present. However, prior laboratory and field studies have demonstrated the inhibitory role of Ca, another divalent cation, in leaf litter decomposition processes through the formation of cation bridges (Lovett et al. 2016; Powers and Salute 2011). Here, we speculate a suppression effect of initial litter Mg on decomposition rates was linked to the composition of the decomposer community, analogous to the role of Ca (De Santo et al. 2009; Powers and Salute 2011; O'Brien et al. 2015). It is well known that magnesium oxalate is a common component of fungal cell walls in a variety of fungi. The compound provides a hydrophobic coating preventing hyphae from becoming hydrated and thus reducing microbial attachment. Magnesium-rich leaf litter may support a larger colonization by fungal populations with magnesium rich hyphae encrustations impeding decomposition explaining the inverse relationship found here between leaf litter Mg and decomposition rate across studied species belonging to Fagaceae family. Future studies such as controlled fertilization experiments should examine the role of this nutrient in leaf litter decomposition in greater detail (García-Palacios et al. 2016; Powers and Salute 2011). Our result also highlights that more nutrients such as Mg in addition to traditional nutrient indicators including N and P should be taken into account when evaluating the quality of the material and susceptibility for decomposition (García-Palacios et al. 2016; Powers and Salute 2011). Also, given the fact that tree species belonging to Fagaceae family are key components in many forests from subtropical to temperate regions, it

would be interesting to detect the roles of tree species lineages in leaf litter decomposition in future studies (Cornwell et al. 2008; Liu et al. 2014).

#### Environmental drivers of leaf litter decomposition

Climate is the most important regulator of litter decomposition in forest ecosystems over large climatic gradients (Aerts 1997). However, we found that elevation explained less variation in leaf litter decomposition than species. Additionally, we detected no interactive effects between elevation and species indicating species effects on decomposition do not depend on the incubation site. This result aligns with previous large-scale litter decomposition studies that found different species had high, consistent effects on litter decomposition across latitudinal gradients (Dorrepaal et al. 2005; Makkonen et al. 2012). The inter-specific consistency we observed here indicates that decomposer organisms across the elevational gradient with distinct environmental conditions respond similarly to variations in leaf litter properties (Cornelissen et al. 1999; García-Palacios et al. 2013).

Air temperature and soil moisture were also identified as key elevation-related variables that influence leaf litter decomposition. The positive effect of air temperature on leaf litter decomposition found in our study supports data from other studies that have shown a direct positive effect of warming on leaf litter decomposition in temperate forests (Cusack et al. 2009; Gholz et al. 2000). However, this result contradicts several analyses from tropical ecosystems that showed a decrease in decomposition at very high temperatures. All of these results collectively support the theory of a temperature threshold, below which temperature is an important driver of leaf litter decomposition (Prescott 2010; Trofymow et al. 2002; Waring 2012). We also observed that soil moisture inhibited leaf litter decomposition, which agrees with earlier studies in some tropical forests, but disagrees with studies in other tropical forests and temperate forests (Powers et al. 2009; Wieder et al. 2009). This result indicates that leaf litter in this mixed forest was subject to soil anaerobic inhibition (Coûteaux et al. 2002), and precipitation-induced soil moisture continued to suppress litter decomposition, as evident by the negative relationship. These results also underscore the difficulties in generalizing climatic effects on leaf litter decomposition in diverse forests. However, the effect of soil water was less important than air



temperature in governing leaf litter decomposition in our study. Therefore, we assume that air temperature was the main climatic control over leaf litter decomposition across the elevational gradient.

#### Biochemical drivers of leaf litter decomposition

Climate and tree species traits may interact in complex ways to influence leaf litter decomposition (Pietsch et al. 2014; Ward et al. 2015). The results of the regression model based on elevation and species-related variables predicted leaf litter decomposition well ( $R^2 = 0.67$ ). The explanatory power of selected elevation-related variables (air temperature and soil moisture) was much lower than that of selected species-related variables (27.75 % vs. 38.97 %). This result once again emphasizes the aforementioned conclusion that species identity exerts strong controls over leaf litter decomposition. These findings have important implications for the effect of future climate change on this mixed forest ecosystem. Changes in temperature alone may have minimal direct effects on carbon and nutrient cycling but may influence litter decomposition indirectly via broad shifts in relative abundance of tree species and associated litter properties (García-Palacios et al. 2013; Santonja et al. 2015).

#### Concluding remarks

Overall, our results suggest widely used predictors of leaf litter decomposition in tropical and temperate forests, including Mg, are also robust in transitional mixed forests. Moreover, our study provides clear support for a dominant effect of tree species, relative to other factors, in mediating leaf litter decomposition. Air temperature was also a strong correlate of leaf litter decomposition. These results imply that any increases of temperature will likely accelerate leaf litter decomposition, unless litter quality concurrently decreases. Considering the importance of species-level litter traits in driving rates of litter decomposition, any predictions of climate effects will need to account for potential shifts in species composition and associated effects on litter properties. This study highlights the need for further research into interactions between climate, species composition, and litter traits to improve predictions of how litter decomposition and nutrient cycling may respond to future climate change and biodiversity scenarios in mixed

transitional forests. Given the excellent role of tree species belonging to Fagaceae family across many subtropical and temperate forests in the northern hemisphere, it will also be key to analyze these implications of species belonging to the Fagaceae family that coincide spatially form multi-species forests and how these taxonomic proximity of these species can affect leaf litter decomposition and associated ecological processes.

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