

# Predicting soil fauna effect on plant litter decomposition by using boosted regression trees



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## ABSTRACT

Extensive studies have been conducted to evaluate the effect of soil fauna on plant litter decomposition in terrestrial ecosystems. However, scholars have reported inconsistent results on the direction and magnitude of the soil fauna effect. We present a global synthesis of 75 papers that cover 197 plant species with 543 cases of plant litter decomposition experiments and soil fauna effects on plant litter decomposition. By using a boosted regression tree model (BRT), we aim to provide a synthesis of existing data that comprehensively and quantitatively evaluates how climate, plant litter quality, and study methods interact with soil fauna in affecting plant litter decomposition. Global average effect size (ES) is  $-0.426$ , which indicates a 35% lower decomposition rate when soil fauna is excluded by physical or chemical exclusion techniques. The final model explains 32.3% of the variation in ES. The predictors that substantially account for the explained variation include mean annual temperature (MAT, 37.1%), mean annual precipitation (MAP, 9.7%), phosphorus (12.4%), nitrogen (5.6%), and lignin content (5.5%). By contrast, the heterogeneity of the study duration and soil fauna exclusion technique have negligible contributions (each <5%). Log effect size strongly decreases with both MAT and MAP. Plant litters with high quality have stronger soil fauna effect because the log effect size is negatively related to nitrogen and phosphorus content and positively related to lignin content. Our analysis demonstrates the critical role of climate and plant litter quality in determining the soil fauna effect on plant litter decomposition in terrestrial ecosystems. However, the large unexplained variation (67.7%) in ES in the BRT model indicates undiscovered mechanisms underlying the soil fauna effect in our analysis. We call for further studies on this topic in the future.

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## 1. Introduction

Plant litter decomposition is one of the main ecological processes in terrestrial ecosystems (Liski et al., 2003; Berg and McClaugherty, 2008). The decomposition process allows the recycling of carbon and nutrients from dead organic matter to fuel new primary production processes (Aerts, 2006). Simultaneously, plant litter decomposition releases CO<sub>2</sub> back to the atmosphere; thus, this process controls the carbon fluxes between the biosphere and atmosphere (Swift et al., 1979).

Soil fauna plays an important role in regulating litter decomposition, and this effect has been intensively studied over the past 40 years. However, the direction and extension of soil fauna effect reported by different authors are inconsistent. Several studies have shown that plant litter decomposition is significantly enhanced by including soil fauna (Heneghan et al., 1998; Hättenschwiler and Gasser, 2005; Castanho et al., 2012). However, other studies have reported either a suppression effect or insignificant changes (Silva et al., 1985; Barajas-Guzmán and Alvarez-Sánchez, 2003; Araujo et al., 2012). The possible mechanisms of soil fauna effect on plant litter decomposition have been suggested by previous studies (Read and Perez-Moreno, 2003; Kreuzer et al., 2004; Moore et al., 2004). Soil fauna alters litter decomposition in direct and indirect ways (Kampichler and Bruckner, 2009). The direct influence involves the passage of litter through the gut, as well as digestion. The

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indirect role of soil fauna involves factors such as litter inoculation with microbial organisms, microbial activity alteration by grazing, and litter fragmentation by feeding activity. However, the relationship between soil fauna and plant litter decomposition is still unclear. Consequently, the direction and extent of the soil fauna effect is still unpredictable.

The different responses of plant litter decomposition to soil fauna across various studies have been explained by a large set of environmental factors, such as climate and the chemical properties of plant litter (Smith and Bradford, 2003; Brennan et al., 2009). However, most studies on this topic were conducted in a single site or by using few plant litter types. Therefore, how environmental conditions influence the effect of soil fauna on litter decomposition is still unclear.

Climate is considered the key regulator of many ecosystem functions, including plant litter decomposition (Aerts, 1997; Moorhead et al., 1999). Therefore, climate can also modulate the soil fauna effect on plant litter decomposition (Swift et al., 1979). Wall et al. (2008) tested the hypothesis that the soil fauna effect on plant litter decomposition is climate dependent by using a global decomposition experiment. The results showed that soil fauna enhances plant litter decomposition in temperate and wet tropical climates but have neutral effects in cold and dry conditions. Gonzalez and Seastedt (2001) also reported the significant effects of soil fauna on litter decomposition rates in wet compared with dry tropical forests. However, other researchers showed the opposite results. For example, Powers et al. (2009) found no relationship between climate and soil fauna effects in a pan-tropical decomposition comparison. Riutta et al. (2012) reported that the soil fauna effect is unrelated to soil moisture treatment in both the edge and interior of a secondary forest. Hence, the relationship between climate and soil fauna effect is still unclear. Climate effects are often explained by using variables that include temperature and moisture, and these variables may differently determine the effect of soil fauna on plant litter decomposition. We still need to know the relative contribution of temperature and moisture on the soil fauna effect.

The quality of plant litter has been recognized as the most critical regulator of decomposition (Strickland et al., 2009). Some researchers suggested that the soil fauna effect is stronger in species with high recalcitrant litter compared with easily decomposing litters (Gonzalez and Seastedt, 2001; Yang and Chen, 2009; Riutta et al., 2012). However, other results showed that the soil fauna effect is unrelated to litter quality (Smith and Bradford, 2003; Carrillo et al., 2011). Considering that plant litter types in soil fauna effect studies are often few, drawing a general picture in a single study is difficult. The relationship between plant litter quality and soil fauna effect is still unknown.

The extrapolation of soil fauna effect on plant litter decomposition existing in the published papers and the understanding of the relationship between soil fauna effect and environmental predictors is difficult, since researchers can only focus on one or two environmental drivers in their study. However, this limitation can be overcome by re-analyzing the results from published papers. The objective of the current study is to provide a comprehensive and quantitative synthesis of the effect of soil fauna on plant litter decomposition at a global scale. This study evaluates how climatic factors, plant litter chemical properties, study length, and study methods interact with soil fauna to affect plant litter decomposition, as well as the relative contribution of environmental factors to soil fauna effect.

## 2. Material and methods

### 2.1. Data collection

We searched published journal articles in the databases of Web of Sciences, Elsevier ScienceDirect, SpringerLink, and Wiley

Blackwell for the period of 1950–2013 (last search data: 01/05/2013). The search terms were “litter decomposition,” “soil fauna,” “microarthropods,” “soil organisms,” and “soil animal.” This primary search yielded 85 papers. After carefully reading the abstract, methods, and results of the papers, we identified 75 studies where soil fauna exclusion was experimentally manipulated by using physical or chemical technique in the field (Appendix S1). The papers have to fulfill the following criteria to be included in our analysis. First, plant litter decomposition should be studied by the litterbag technique. Second, the effect of soil fauna activity should be suppressed by a physical method with different litterbag mesh sizes or by a chemical method with naphthalene. Third, experimental studies should include mean values with remaining mass of litter during decomposition. The authors of these studies were contacted to know if pertinent information was missing. If more than one paper reported the same experiment, the paper providing detailed information was considered. The location of each study was shown in Appendix S2. The digitizer in OriginPro 8.5.1 was used to extract data from figures in the original publication.

In addition to examining the overall effect of soil fauna on litter decomposition, an important goal of our study was to determine whether particular environmental or experimental conditions elicit different quantitative responses to soil fauna. We also collected information on the climate, the initial chemistry of plant litter, and the duration of each study. We noted that not all climatic information was provided in the studies; therefore, we obtained the mean annual temperature (MAT) and mean annual precipitation (MAP) from the National Aeronautics and Space Administration (<https://eosweb.larc.nasa.gov>), which modeled climatic information on the basis of a 22-year average. A good correlation between the modeled data and original data from the publications indicates that the modeled climatic data can provide a good estimate of the climatic information ( $r = 0.968$  for MAT;  $r = 0.706$  for MAP;  $N = 63$ ). The studies were mainly conducted in forest, grassland, agriculture, or desert ecosystems and were distributed across broad climatic regions from 46 °S to 71 °N. MAP ranged from 135 mm/yr to 3216 mm/yr, and MAT ranged from −10.8 °C to 32.5 °C. More than 170 different litter types were represented, and the initial nitrogen content, phosphorus content, and lignin content ranged from 0.125% to 3.6%, 0.016%–1.2%, and 4%–53.5%, respectively.

### 2.2. Data analysis

Given that the decomposition dynamics of plant litter were reported as remaining mass loss in most of the studies, we re-analyzed each of the studies in the database by using the exponential decomposition model (Olson, 1963):  $M_t = M_0 e^{-kt}$ , where  $M_t$  and  $M_0$  are litter mass at time  $t$  and time zero, respectively;  $k$  is the decomposition constant ( $\text{year}^{-1}$ );  $t$  is time (year).

Effect size (ES) was calculated as a standardized measure of decomposition rate across studies (Hedges et al., 1999; Borenstein et al., 2009) by using a response ratio of  $ES = \ln(k_E/k_C)$ , where  $k_E$  is the decomposition rate in the soil fauna exclusion treatment and  $k_C$  is the decomposition rate in the soil fauna presence treatment. Thus, a positive ES indicates an enhancement, whereas a negative ES means a reduction of litter decomposition rate because of soil fauna exclusion.

We used boosted regression tree (BRT) to partition the independent influences of climate (e.g., MAT and MAP), initial chemistry of plant litter (nitrogen, phosphorus and lignin), and study duration and soil fauna exclusion technique on ES. BRT is a powerful modeling method that combines regression trees and boosting algorithm. The following advantages make BRT useful for ecologist to explore the relationship between ecological processes and predictors. Firstly, BRT can handle predictor variables with different

types and distributional characteristics. Second, BRT can handle missing values in predictors in an elegant fashion on the basis of “surrogate” splitting, which enables the inclusion of predictors with missing values in the analysis. Third, the independence of predictors is not required in BRT because the interactions of predictors are modeled automatically by the hierarchical structure of a tree.

BRT models were operated in R (version 2.15.2; R Development Core Team 2009) by using the *gbm* package (Elith et al., 2009). In the BRT analysis, we chose Gaussian as the error structure for the loss function because of the attribution of our response variable (Zhang et al., 2012). The fitting of a BRT model is also controlled by the following factors: 1) the learning rate determines the contribution of each tree to the growing model; 2) tree complexity controls the level of interactions in BRT; 3) bagging fraction sets the proportion of observations used in selecting variables; 4) cross-validation specifies the number of times to randomly divide the data for model fitting and validation (De'ath, 2007). To find the optimal settings based on the empirical rules recommended for ecological modeling, 27 BRT models were fitted with the combinations of the following settings: learning rate of 0.01, 0.005 and 0.001; bag fraction of 0.4, 0.5 and 0.6; 5-, 8- and 10-fold cross-validations; a tree complexity of 4 to account for potential high interactions. Among the fitted models, we found that the best model had a cross-validation deviance of 0.154 ( $\pm$ one stand error = 0.015) from a learning rate of 0.001, bag fraction of 0.4, and 5-fold cross-validation. The subsequent models were all fitted with these optimal settings. To reduce over-fitting and filter the data noise, we also applied monotonic constraints to study length, MAP, MAT, plant litter nitrogen, phosphorus and lignin content, the refitted model yielded a cross-validation deviance of 0.156 ( $\pm$ 0.010). Considering that the results are similar (Figs. 1 and 2), we interpreted the model with monotonic constraints.

The percentage of variation in ES explained by the BRT model was calculated as  $\{1 - [(\text{sum of squared residuals from a boosted regression trees model}) / (\text{sum of squared residuals from an intercept-only model})]\} \times 100$  percent, where “residuals” refer to test sample residuals (Robinson, 2008). We also examined the relative influence of predictor variables to quantify the importance

of predictors on ES. The influence of each predictor is based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. Then the relative importance is scaled such that the sum is 100, and higher numbers corresponds to a stronger influence on the soil fauna effect. The net effects of environmental predictors on ES average out the effects of the other predictors included in the BRT model, and are visualized in partial dependence plots.

### 3. Results

The global average of ES was  $-0.426$ , thus indicating that the plant litter decomposition rate decreases by 35% when soil fauna was excluded during decomposition. The BRT model explained 32.3% of the variation in the soil fauna effect. MAT and MAP contributed 37.1% and 9.7% of the explained variation, respectively (Fig. 1). In the range from  $0^\circ\text{C}$  to  $27^\circ\text{C}$ , the effect size decreased with mean annual temperature. When MAT was  $<0^\circ\text{C}$  or  $>27^\circ\text{C}$ , MAT had no effect on ES (Fig. 2a). ES decreased with MAP from  $150\text{ mm/yr}^{-1}$  to  $1600\text{ mm/yr}^{-1}$  then plateaued with MAP  $>1600\text{ mm/yr}^{-1}$  (Fig. 2b). Plant litter decomposition from different ecosystems showed different responses to soil fauna exclusion. Ecosystem type had a 24.5% relative influence on ES (Fig. 1). The predicted ES were  $-0.45$ ,  $-0.44$ ,  $-0.39$  and  $-0.30$  for agriculture, desert, forest, and grassland ecosystem, respectively (Fig. 2c). In addition, Fig. 3 showed that both MAT and MAP had similar effects on ES in different ecosystems.

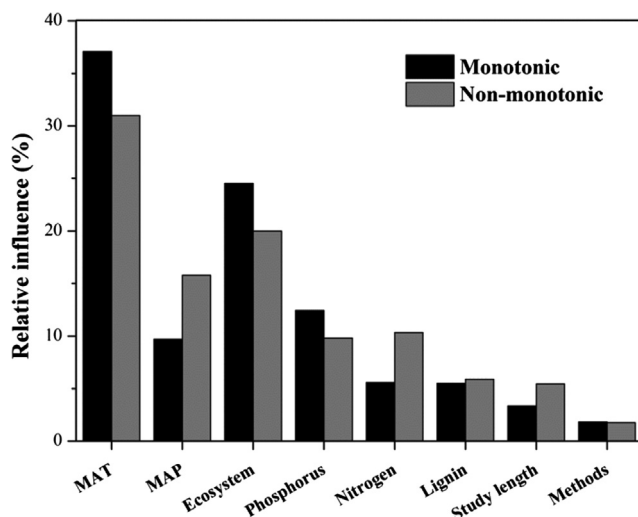
The initial chemical properties of plant litter had 23.5% relative influence on the soil fauna effect: 12.4% from phosphorus content, 5.6% from nitrogen content, and 5.5% from lignin content (Fig. 1). With increasing phosphorus content, the fauna effect decreased. Predicted ES showed a sharp decrease and then became constant when P content was  $>0.15\%$  (Fig. 2d). Similarly, ES indicated a modest decrease with increasing nitrogen content (Fig. 2e). On the contrary, a positive relationship between predicted ES and lignin content was observed in the current analysis (Fig. 2f).

The study duration and soil fauna exclusion technique had 3.4% and 1.8% relative influences on ES, respectively (Fig. 1), thus indicating that neither study duration nor exclusion methods is important for explaining the variation in observed soil fauna effect obtained by litterbag technique. The predicted ES only showed a slight decrease with increasing study length (Fig. 2g). The predicted ES of soil fauna exclusion were  $-0.35$  for the chemical method and  $-0.36$  for the physical method (Fig. 2h).

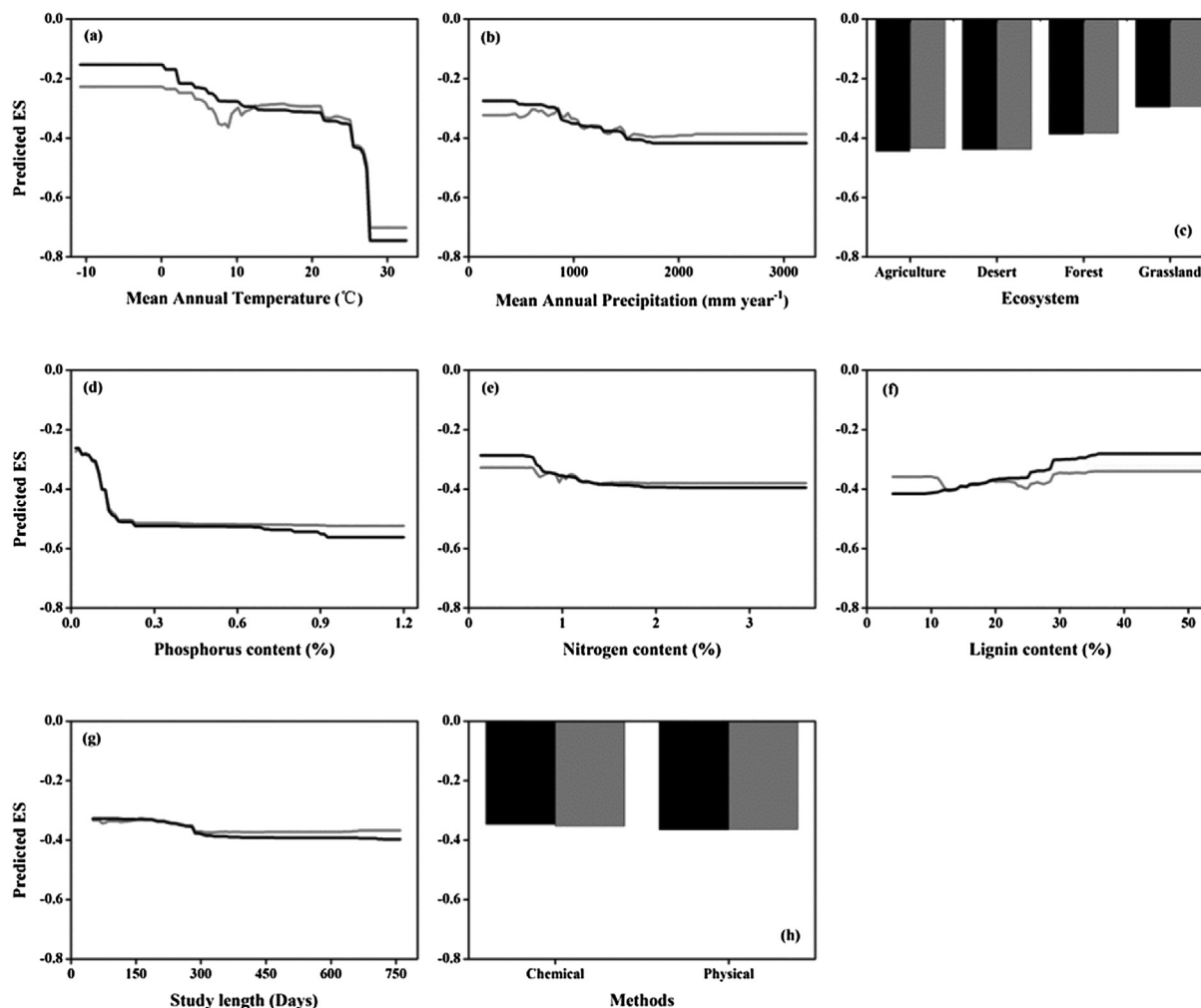
### 4. Discussion

Our results show that the plant litter decomposition rate decreases by 35% because of soil fauna exclusion and demonstrate that soil fauna plays an important role in plant litter decomposition. Although soil fauna has different effects on plant litter decomposition in different ecosystems (Fig. 2c), this exclusion effect is generally negative. This result suggests that the role of soil fauna in regulating litter decomposition is common across different ecosystems. The BRT model explains 32.3% of the variation in the soil fauna effect in our current analysis; this value is higher than the result (10%) from García-Palacios et al. (2013) from structural equation models based on similar dataset. This indicated that BRT is a powerful modeling method to explain the variation in ecological process for ecologists.

Our model identified climate as the major control on the soil fauna effect on plant litter decomposition at a global scale. The negative relationship between ES and MAT or MAP confirms the result of previous studies (Swift et al., 1979; Wall et al., 2008)



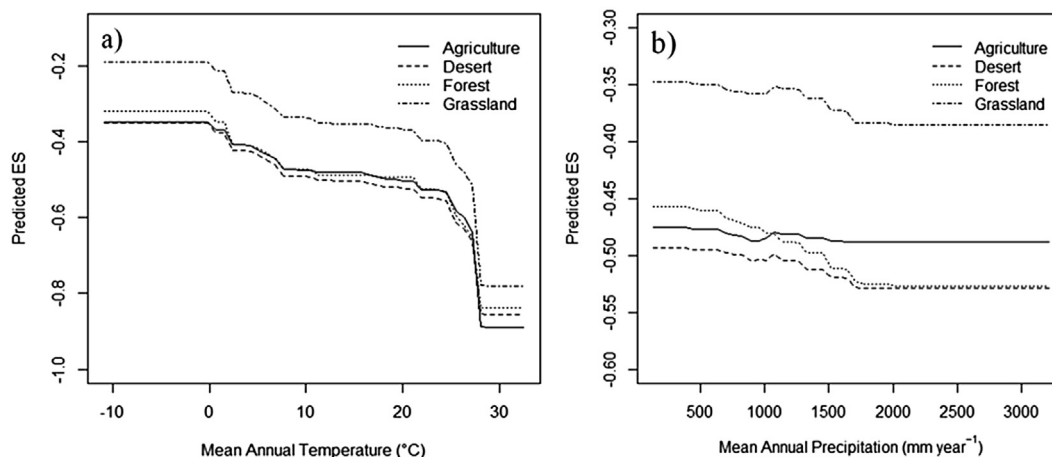
**Fig. 1.** Results from boosted regression tree (BRT) analysis showing the relative contributions of predictors in percentage on soil fauna effect size. Bars in black are values for the BRT model with monotonic constraints on, and those in grey for the model without the monotonic constraints.  $n = 466$  for MAT and MAP, 210 for phosphorus, 363 for nitrogen, 165 for lignin and 543 for remaining predictors.



**Fig. 2.** Partial dependence plots showing the variation in soil fauna effect size by each variable used in the BRT model: (a) mean annual temperature, (b) mean annual precipitation, (c) Ecosystem type, (d) phosphorus content, (e) nitrogen content, (f) lignin content of the initial litters, (g) duration of experiment, (h) methods of soil fauna exclusion (physical or chemical). The fitted function shows the relationship between ES and an explanatory variable while all other explanatory variables are kept constant at their mean level. The response of ES with monotonic constraints on MAT, MAP, Phosphorus, Nitrogen, Lignin content and study length are shown in black and without the constraints in grey.

wherein the soil fauna effect was found to be significantly higher in favorable conditions (warmer and moister) than in cold or dry climatic regions. As suggested by [Swift et al. \(1979\)](#), the possible mechanism underlying this phenomenon may be subjected to the

high density, diversity, and activity of soil fauna in such regions. For example, previous studies show that soil fauna is sensitive to temperature and moisture conditions ([David and Handa, 2010](#); [Hassall et al., 2010](#)). Therefore, soil fauna abundance and diversity



**Fig. 3.** Tree-dimensional partial dependence plots representing the interactions in the BRT model: a) between ecosystem type and MAT; b) between ecosystem type and MAP.



are likely to differ among regions with different climate conditions. Furthermore, the relations between ES and MAT or MAP are not linear. This finding may be the major reason that some previous studies show no relationship between soil fauna effect and climate (Powers et al., 2009).

Another important result in our analysis is that MAP contributes less to ES compared with MAT. This phenomenon is mainly caused by the following reasons. First, although a simple climatic index like MAP is a powerful tool to explain the moisture effect on ecological processes limited by water at global or regional scales (Craine et al., 2009; Yuan and Chen, 2009), the explanatory ability of MAP may be reduced by other ecological process in some cases. For example, the water retaining capacity of plant litter and surface runoff may reduce the difference in soil and plant litter moisture among different study sites, thus decoupling the relationship between soil fauna effect and MAP. We can explain more variations in soil fauna effect if the soil moisture during study is included in our analysis. However, this information is not provided in almost all studies. Hence, we call for more environmental information in ecology studies. Second, soil fauna has a large temporal and spatial variation; therefore, the relationship between the activity of soil fauna and MAP is complex. Third, the resistance and adaptation of soil fauna to desiccation may also reduce the response of soil fauna effect to MAP.

On the basis of large dataset analysis at the global scale, our model shows that soil fauna effect on litter decomposition is litter-quality dependent to a certain extent. The underappreciated role of litter quality in previous empirical studies (Carrillo et al., 2011; Powers et al., 2009) can be attributed to the limited levels of plant litter type in those experiments. Furthermore, our results show that soil fauna effect is greater in the decomposition of readily decomposable litters than in recalcitrant litter because ES is positively related to nitrogen and phosphorus content and negatively related to lignin content. This differs from previous studies (Smith and Bradford, 2003; Yang and Chen, 2009) that show that the soil fauna effect is greater for recalcitrant plant litter (with lower N concentration and higher C: N ratio). They attributed this phenomenon to the enhancement of N concentration and decrease of C concentration of the recalcitrant plant litter because of the presence of soil fauna. This mechanism cannot explain the pattern of soil fauna effect-litter quality relationship in the present study because the implicit assumption that soil fauna can consume both low quality and high-quality litter equally is obviously unrealistic.

Soil fauna feeding preferences may be used to explain the variation of the soil fauna effect among plant litters with different qualities (Coq et al., 2010). High-quality litters with more nutrients and energy can be palatable to soil fauna, thus enhancing the soil fauna effect on litter decomposition. Low-quality litters with more defensive materials, such as tannin, can avoid the feeding of soil fauna, thus lowering the soil fauna effect (Coq et al., 2010). However, a good predictor for litter decomposition is not necessarily a good predictor for the soil fauna effect. For example, Mg and tannin contents in plant litters are supposed to play an important role in predicting soil fauna effect because they are needed or toxic in the development of soil fauna (Hagerman and Butler, 1991). However, such data are only available for a few studies (Coq et al., 2010) and are excluded in our analysis. As an alternative method, we used nitrogen, phosphorus, and lignin content to estimate the quality of plant litter and evaluate the role of litter quality in mediating the soil fauna effect. The low data availability of litter chemical properties in our analysis may also underestimate the importance of litter quality. Much research is still needed to study the relationship between litter quality and soil fauna effect, and explore the underlying mechanisms in the future.

Our results show that the study duration and exclusion method of soil fauna have negligible influences on the soil fauna effect. This result is consistent with previous reviews (Kampichler and Bruckner, 2009; García-Palacios et al., 2013) wherein the soil fauna effect was found to be unrelated to the study duration or exclusion technique. This result allows us to compare the soil fauna effect across studies by using different exclusion techniques and study length. However, both chemical and physical exclusion techniques are criticized for the following reasons: 1) the litterbag experiment with different mesh sizes show not only a pure-soil fauna effect but also the effect of the mesh size; 2) the chemical exclusion technique inhibits both soil fauna activity and microbe growth (Kampichler and Bruckner, 2009). Physical techniques are proven to be reliable methods for studying the soil fauna effect because the microclimatic differences between litterbags of different mesh sizes are minimal, and litter mass loss in the absence of soil animals are similar between mesh sizes (Bokhorst and Wardle, 2013). Naphthalene, which was used to exclude soil fauna, was also found to have negligible effects on soil bacterial and fungal growth (Blair et al., 1989) under field conditions. Therefore, we suggest that the soil fauna effect on plant litter be evaluated properly across all studies on this topic. However, the variability of mesh sizes used by different authors prevented us from determining which soil fauna group contributed mostly to the pattern of the ES.

In conclusion, our results show an average of 35% slower decomposition rate of plant litter when soil fauna is excluded. This effect is complicated by many factors. Soil fauna effect is closely related to MAT and MAP, thus suggesting that climatic factors are important drivers of soil fauna effect. Moreover, our results indicate that the strength of this effect is closely related to the initial quality of the plant litter. Only 32.3% of the variation in ES is explained by our BRT model, although this machine learning-based regression is suggested as one of the best modeling approaches to predict the response of dependent variables to multiple predictors (Schonlau, 2005). The large remaining unexplained variation indicates a highly complicated relationship between soil fauna and plant litter decomposition. Therefore, we call for further research with standard experimental procedures to reveal the soil fauna effect pattern and the underlying mechanisms.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2014.12.016>.

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