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

Weidong Zhang [a, b], Shufen Yuan [a, c], Ning Hu [d], Yilai Lou [d, *], Silong Wang [a, b]

[a] State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, PR China
[b] Huitong Experimental Station of Forest Ecology, Chinese Academy of Sciences, Huitong 418307, PR China
[c] University of Chinese Academy of Sciences, Beijing 100049, PR China
[d] Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing 100081, PR China

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A B S T R A C T

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.

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_2 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

* Corresponding author. 12 Zhongguancun Southern Street, Haidian District, Beijing, PR China. Tel.: +86 10 8210 5636; fax: +86 10 8210 6225.
E-mail address: louyilai@caas.cn (Y. Lou).

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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 reanalyzing 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 reanalyzed each of the studies in the database by using the exponential decomposition model (Olson, 1963): $M_t = M_0e^{-kt}$, where M_t and M_0 are litter mass at time t and time zero, respectively; k is the decomposition constant (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