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Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies

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ABSTRACT

We present a meta-analysis of experiments in which researchers used litter bags or similar enclosures to explore three questions: Do soil macrofauna increase the removal of litter from the soil surface? How is this mass loss of litter by macrofauna affected by climate and litter quality? To what extent does litter loss from litter layer by macrofauna correspond with litter mineralization? In total, we found 132 published field experiments in which authors compared litter bags with mesh sizes that did permit or not permit access by soil fauna. Meta-analysis of these experiments indicated that litter removal was significantly greater from bags that did permitted rather than did not permitted soil macrofauna access. When we divided these studies according to climate, a significant positive effect of soil fauna on litter removal was only evident from the warm humid, temperate regions with correspond to deciduous forest zone. When studies from this climate zone were sorted according to litter C:N ratio, the effect of fauna was significant in all cases except when the ratio was low (<20), and the effect of fauna was greatest when the ratio was intermediate (20–30). To assess how litter removal from litter bags corresponds with mineralization, we reviewed 11 published experiments that used litter boxes that were or were not accessible to soil macrofauna and 8 studies where fauna was experimentally removed and added. These boxes contained both litter and a mineral soil layer, which allowed researchers to estimate litter removal from the litter layer, the increase in C content (C sequestration) in the mineral soil, and overall C mineralization (difference of the former and the latter number). Analysis of these experiments indicated that fauna significantly increased litter removal from the litter layer, which agreed with the litter bag meta-analysis, but did not significantly affect overall C mineralization. This is consistent with meta-analysis of seven studies showing that rate of leaf litter decomposition is significantly faster than decomposition of macrofauna feces produced from the same litter.

1. Introduction

In terrestrial ecosystems, more than 50% of net primary production is returned to the soil via decomposition of plant litter [1,2]. Litter decomposition is driven by multiple factors including climate, litter and substrate quality, and soil fauna [2–5]. Climate directly affects litter decomposition because the biological processes contributing to decomposition are greatly affected by temperature and humidity [1]. Climate also influences decomposition in soil indirectly because it affects litter quality and the distribution of soil fauna [2,6]. Litter quality is an important determinant of the decomposition rate in terrestrial ecosystems. The chemical composition of leaf litter, especially the C:N ratio as well as the lignin–cellulose content, plays a significant role in determining the biomass and structure of the decomposers community [7–9]. Fast-growing plant species grow in fertile soils and produce easily decomposable litter, while slow-growing plants dominate in less fertile soils and produce litter that decomposes slowly [2,9–11]. Fast-growing plants promote bacterial-dominated food webs associated with rapid nutrient turnover, while slow-growing plants promote fungal-dominated food webs [2,9,12] associated with slow nutrient turnover [13].

Many studies [4,14,15] have recognized that soil fauna significantly affect decomposition rates by directly affecting microbial activity. In particular, soil macrofauna such as isopods, millipedes, earthworms, and gastropods are important drivers of leaf litter

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Table 1
List of studies used in individual meta-analysis. No. of exper. means number of experiments where both fauna and no fauna treatment were available for comparison.

Author(s)	Characteristic of the study	No. of exper.
Meta-analysis 1 – litter bags with different mesh sizes accessible for macrofauna or not		
Anderson [45]	England, temperate deciduous forest, *Castaneus* and *Fagus* litter	4
Anderson [46]	England, temperate deciduous forest, *Castaneus* and *Fagus* litter	2
Aubert et al. [14]	England, temperate deciduous forest, *Fagus* and *Carpinus* litter	6
Barajas-Guzmánd and Alvarez-Sánchez [47]	South America, tropical rainforest and tropical deciduous forest, *Ficus* and *Nectandra* litter	4
Bradford et al. [48]	England, temperate grassland, *Agrostis* litter	1
Brennan et al. [26]	Australia, temperate evergreen forest, *Eucalyptus* litter	3
Cárcamo et al. [49]	Canada, temperate coniferous forest, *Betula* litter	1
Carillo et al. [50]	South America, tropical grassland, *Amorpha*, *Trifolium*, *Pinus*, rye and wheat straw litter	5
Cortez and Bouche [51]	France, temperate deciduous forest, *Castanea*, *Quercus* and *Fagus* litter	4
Frouz et al. [52]	Netherlands, temperate heathland/grassland, filter paper litter	4
Frouz et al. [17]	Czech Republic, temperate deciduous forest, *Salix* and *Alnus* litter	4
Giesselmann et al. [27]	South America, secondary tropical rainforest, broadleaf tropical tree litter	1
Heath and Arnold [53]	England, temperate deciduous forest, *Quercus* and *Fagus* litter	4
Heath et al. [54]	England, temperate deciduous forest, *Quercus*, deciduous tree litter, bean, kale, maize, beet and lettuce litter	17
Hunter et al. [55]	USA, mixed deciduous temperate grassland, *Liriodendron*, *Quercus* and *Rhododendron* litter	3
Irmler [56]	Germany, temperate deciduous forest, wheat straw	6
Irmler [57]	Germany, temperate deciduous forest, *Fagus*, *Quercus*, *Corylus* and *Picea* litter	2
Meyer et al. [58]	Hawaii, tropical montane forest, *Metrosideros* litter	1
Milton and Kaspari [59]	South America, tropical rainforest, cellulose litter	2
Powers et al. [60]	Both Americas and Asia, tropical and subtropical forest, *Raphia* and *Laurus* litter	12
Riutta et al. [31]	England, temperate deciduous forest, *Quercus* and *Fraxinus* litter	2
Setälä et al. [61]	Canada, mixed temperate forest, *Pseudotsuga* litter	3
Schädler and Brandl [32]	Germany, temperate deciduous forest, deciduous broadleaf tree litter	3
Slade and Riutta [16]	England, temperate deciduous forest, *Acer*, *Fraxinus*, *Coryllus*, *Quercus* and *Fagus* litter	12
Smith and Bradford [62]	England, temperate grassland (old field), *Arrhenaterum*, *Holcus* and *Agrostis* litter	6
Smith et al. [36]	England, temperate grassland (old field), *Dactylis* litter	2
Staaf [63]	Netherlands, temperate deciduous forest, *Fagus* litter	3
Vitella and Proctor [64]	South America, tropical rainforest, *Ecclinusa* and *Peltogyne* litter	4
Xin et al. [65]	Kazakhstan, temperate grassland, *Stipa*, *Achnatherum*, *Lepedeza* and *Agropyron* litter	4
Yamashita and Takeda [28]	Indonesia, tropical rainforest, *Dipterocarp* litter	2
Yang and Chen [29]	Malaysia, tropical rainforest and broad-leaf tropical forest, various tropical tree litter	3
Meta-analysis 2 – litter boxes with litter and mineral layer accessible for soil macrofauna or not		
Frouz et al. [17]	Czech Republic, *Alnus glutinosa* or *Salix caprea* litter	4
Frouz et al. [42]	Czech Republic, *Alnus glutinosa* or *Salix caprea* litter	2
Frouz et al. [43]	Czech Republic, *Alnus glutinosa* or *Salix caprea* litter	4
Frouz et al. [44]	Florida, USA, hardwood litter	1
Meta-analysis 3 – litter boxes where fauna was experimentally removed and added		
Frouz et al. [20]	Czech Republic, *Alnus glutinosa* or *Salix caprea* litter, with litter feeding of geophagous community added or not	4
Frouz et al. [44]	Florida, USA, hardwood litter, *Armadilidium vulgare* added or not	1
Ayu et al. [66]	Japan, larch litter with *Parafontaria laminata* added or not	2
Frouz et al. [67],	Czech republic, *Alnus glutinosa* or *Salix caprea* litter with *Lumbricus rubellus* added or not	2
Meta-analysis 4 – litter bags un accessible for soil fauna (with dense mesh) filled either by litter or by macrofauna excrements from the same litter.		
Frouz and Šimek [19]	*Penthetria holosericea* feces from *Alnus glutinosa* litter	1
McInerney and Bolger [68]	Earthworm casts from *Quercus petraea* litter	2
Špaldoňová [69]	*Armadilidum vulgare* feces from *Alnus glutinosa*, *Salix caprea* and *Acer pseudoplatanus* litter	3
Tajovský et al. [70] and unpublished data about litter decomposition by Tajovský	*Glomeris hexasticha* feces from *Quercus robur* litter	1

decomposition in temperate deciduous forests [4,5,16]. In addition to fragmenting leaf litter and thereby increasing its surface area and contact with the soil substrate, soil fauna help distribute soil microorganisms [1,17,18]. At the same time, however, many studies have documented that macrofauna feces decompose slower than litter [19–21], suggesting that the faunal effect on litter mineralization could be negative or neutral.

Researchers have often used litter bags to study *in situ* decomposition in terms of litter mass loss and/or nutrient loss over time and under various climatic conditions [1,22]. By using litter bags with different mesh sizes, researchers can exclude or not exclude macrofauna from the bags and by comparison estimate the