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Insight into the indirect function of isopods in litter decomposition in mixed subtropical forests in China

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ABSTRACT

Aboveground consumers can shape belowground processes in brown-food webs of forests by converting litter into faeces. Woodlice are one of the important aboveground consumer groups driving the dynamics of belowground soil. Although considerable data on litter decomposition exists, the indirect effects of woodlice (different qualities of faeces) on litter decomposition need to be explored further. In this study, we assessed the influence of isopods (*Armadillidium vulgare*) and its by-products (three contrasting qualities of faeces) on the decomposition of broad-leaf and needle litter via soil incubation. Litter mass loss, soil microbial biomass and soil extracellular enzyme activities treated with different isopod by-products were determined in six-month laboratory incubations.

The results showed that after incubation, the indirect effect of fauna (faeces) did not significantly increase broad-leaf litter decomposition. However, faeces of isopods fed on high-quality legume litter significantly increased needle litter decomposition. The effects of isopod faeces on microbial activities were significant: most of the soil microbial biomass and extracellular enzyme activities increased significantly compared with non-faeces treatments in the soil of broad-leaved and coniferous forests; and high-quality faeces strengthened the correlation of litter mass loss with peroxidase and phenol oxidase in coniferous forest. The result suggests that faeces with higher concentrations of nitrogen and labile carbon can mediate the decomposition of refractory materials like lignin and phenolic compounds, which might be highly relevant for the litter decomposition process in ecosystems with high macrofauna abundance. This study infers that the indirect effect of isopods (faeces) on litter decomposition depends on the quality of the litter they consumed and the type of decomposing litter. Isopods indirectly accelerate the nutrient-poor litter decomposition process by converting high-quality litter into faeces. As such, the negative effects of litter recalcitrance on microbial decomposition in mixed forests are indirectly alleviated.

1. Introduction

Litter decomposition is a major process that drives the release of nutrients from its source (detritus) in terrestrial ecosystems. In the brown-food web, over 80% of the carbon fixed via photosynthesis in the forest falls as litter, which is then decomposed by microbes, detritivores, and their predators (Kaspari and Yanoviak, 2009; Wardle et al., 2011). Among these decomposers, microbes and soil fauna are of great importance in releasing carbon (C) into the atmosphere, recycling nutrients, and sustaining much of the forest's biodiversity (Lummer et al., 2012; Clay et al., 2013). Thus, studying their function in the litter decomposition process is necessary to elucidate the fluxes of nutrients in the brown-food web (Freschet et al., 2013).

Litter and consumers' faeces, which complexly interact through macro-detritivores, are two important intermediates that link above- and below-ground ecological processes (Wardle et al., 2004; Vos et al., 2013). In litter decomposition, biochemical fluxes and concentrated bioavailable nutrients are transmitted to detrital decomposers and microbes (Vauramo et al., 2006; Kagata and Ohgushi, 2013; Kaneda et al., 2013). Macro-detritivores convert large quantities of consumed litter into faeces, which could reach a critical level of energy and nutrient input for soil microorganisms (Hunter, 2001; Clark et al., 2010). Macro-detritivore faeces, with higher concentrations of nitrogen (N) and labile C compared with leaf litter (Madritch et al., 2007), were observed to increase

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bacterial counts (Suzuki et al., 2013), change the microbial community structure (Coulis et al., 2013), and accelerate decomposition (Coleman et al., 2004).

The quality of faeces (such as C:N ratio and tannin content) produced by macro-detritivores mostly depends on the litter they consume (Madritch et al., 2007; Kagata and Ohgushi, 2013). A mature forest is often composed of mixed arbor, in which detritivores preferentially feed on litter species with high quality, so with high N concentrations (Hättenschwiler and Jørgensen, 2010) and/or low concentrations of lignins, polyphenols, or tannin (Hättenschwiler and Gasser, 2005). Their different food selection makes them produce different qualities of faeces. These different-quality faeces provide different bioavailable nutrients for detrital microorganisms, which may enhance the average decomposition of litter mixtures. Thus, macro-detritivores can influence litter decomposition rates through indirectly providing nutrients for microorganisms. Although the indirect effects of macro-detritivores have been studied in much detail before (Lavelle and Spain, 2001; David and Gillon, 2002; Hunter et al., 2007; Bardgett and Wardle, 2010; Coulis et al., 2013; Suzuki et al., 2013), the effects of different qualities of faeces on litter decomposition need to be studied thoroughly.

Microorganisms are major decomposers in the litter decomposition process and provide nutrition for the entire soil food web (Enowashu et al., 2009; Allison et al., 2013). They produce extracellular enzymes that specifically degrade C, N, or phosphorus (P)-containing complex organic compounds into small utilizable molecules that are then assimilated by the microbes. Extracellular enzymes have been recommended as the most appropriate indicator of microbial decomposition, soil fertility, and ecological stability (Freeman et al., 2001; Lv et al., 2014). Thus, changes in soil extracellular enzymes and microbial biomass during treatments with different qualities of faeces can explain the ecological effects of macro-detritivore faeces on litter decomposition in forest ecosystems.

Isopods are saprophagous invertebrates that often are dominant members of soil fauna communities (David and Handa, 2010). They are voracious macro-detritivores that convert large amounts of dead and decaying organic matter (like litter) into faeces (Hunter, 2001; Clark et al., 2010). Thus, in this study, Isopoda (*Armadillidium vulgare*, Armadillidiidae) was chosen to assess its indirect role (faeces) in the decomposition of broadleaf (*Quercus acutissima*) and needle (*Pinus massoniana*) litter in a six-month laboratory experiment. Additionally, soil microbial biomass and enzymatic activities were measured to directly monitor the functional responses of microorganisms to isopods and/or their indirect faeces-derived effects in subtropical forest ecosystems. We hypothesize that by converting different-quality litter into faeces soil macro-detritivores might indirectly (1) have a positive effect on the decomposition of low-quality litter after ingesting high-quality litter and (2) have a negative effect on the high-quality litter decomposition after consuming low-quality litter.

2. Materials and methods

2.1. Collection of soil, leaf litter, and isopods

Soil and leaf litter for the experiments were collected from two forests of Zijin Mountain (32°5°′ N, 118°48′ E), Nanjing, China; a broad-leaved forest dominated by *Q. acutissima* and a coniferous forest dominated by *P. massoniana*. The mountain has an altitude of 447.1 m and a subtropical monsoon climate. The area has an annual mean temperature of 15.4 °C with a monthly mean temperature reaching a maximum of 28.2 °C in July and a minimum of 1.9 °C in January. The rainy season is from June to July, and the average annual precipitation is 1106.5 mm. The coverage degree of litter reaches as high as 90%. The soil is classified as slightly acidic Humic Cambisol with a pH of about 5.0 (FAO-UNESCO., 1987). The bedrock materials are sandstone and shale, and a considerable amount of nutrients and organic matter is accumulated in the humus layer.

Four discrete sites (2 m × 2 m), which are approximately 10 m apart, were chosen in both broad-leaved forest and coniferous forest. In October 2012, freshly fallen leaves of *P. massoniana* and *Q. acutissima* were collected at each of the four sites and then mixed, separately. Furthermore, freshly fallen leaves of legumes were also collected under *Robinia pseudoacacia* trees of the four forest sites. *R. pseudoacacia* is a tree with litter rich in N and low lignin and polyphenol levels in the Zijin Mountain and is sparsely distributed in the two forests. In our experiment, fallen leaves of *R. pseudoacacia* were considered as high-quality litter. Leaf litter of *P. massoniana*, with high levels of lignin and phenolic compounds, was defined as low-quality litter. All litter samples were taken back to the laboratory and oven-dried at 55 °C for 24 h to obtain a constant weight to be used in a subsequent study (the initial litter quality is shown in Table 1). Two soil samples from each forest were collected from the top layers (0–5 cm) of each site, sieved through a 2-mm mesh, and kept in a refrigerator at 4 °C until incubation.

A. vulgare is one of the most numerous species of arthropods in the forest (Chen, 2000), and the most extensively investigated terrestrial isopod species (Zimmer, 2002). It is reported to have prevailing densities as high as 10,000 individuals per m^2 in the USA (Frouz et al., 2004) and 100–500 individuals per m^2 in Nanjing (Tang and Gui, 1994). Adult samples (>1 cm) were hand-collected in broad-leaved forest and coniferous forest of Zijin Mountain in April 2013. The isopods were cultured in 1 L clear plastic containers with a medium of 95% plaster and 5% activated charcoal. All containers were then stored in the dark at 20 °C and moistened weekly using deionized water. All the isopods were starved for 24 h in pots before being introduced into the experimental microcosms. The isopods were fed weekly with three different moistened leaves. Faeces were collected every 3 days and added to the treatments representing the broad-leaved forest and coniferous forest.

2.2. Decomposition experiment in the laboratory

The decomposition of leaf litter was determined in a laboratory microcosm. Oven-dried litter (0.5 g ± 0.02 g) was mixed with 40 g of soil in 240 mL plastic boxes with a surface area of 95 cm^2 and covered with a lid. The soil samples derived from broad-leaved forest and coniferous forest were selected as the sources of

Table 1
Initial characteristics of three different qualities of leaf litter and isopod (*A. vulgare*) faeces used for the litter decomposition experiment. Different superscript letters in a transverse row denote significant differences ($p < 0.05$) among different types of litter and faeces.

Composition	Litter			Faeces		
	PL	QL	RL	PF	QF	RF
Total C (%)	51.1[a]	48.8[b]	46.3[c]	32.4[f]	40.3[e]	43.7[d]
Total N (%)	0.78[d]	0.66[d]	3.26[a]	1.46[c]	2.15[b]	3.02[a]
Lignin (%)	41.2[a]	30.9[b]	27.5[c]			
Total polyphenol (mg gallic acid equivalent g^{-1})	270[a]	193[b]	79.4[c]			
C:N	65.2[b]	73.6[a]	14.2[e]	22.2[c]	18.8[d]	14.5[e]
Lignin:N	52.6[a]	46.5[b]	8.46[c]			

Abbreviations: PL – *Pinus massoniana* litter; QL – *Quercus acutissima* litter; RL – *Robinia pseudoacacia* litter; PF – faeces of isopods fed on *Pinus massoniana* litter; QF – faeces of isopods fed on *Quercus acutissima* litter; RF – faeces of isopods fed on *Robinia pseudoacacia* litter.