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Review paper

The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views

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ABSTRACT

Saprophagous macroarthropods are usually described as litter transformers that have low assimilation efficiencies and little direct effect on carbon mineralization. They are considered to enhance decomposition indirectly, by fragmenting leaf litter and increasing the surface area available for microbial colonization, thus stimulating microbial activity in their faeces. A review of experimental studies on the direct and indirect effects of macroarthropods on leaf litter decomposition does not confirm these views. (1) Laboratory estimates of assimilation efficiency are highly variable across studies, ranging from less than 5% to over 50%; this suggests that under field conditions that offer a variety of food choices, direct impacts of macroarthropods on carbon mineralization may be stronger than generally assumed. (2) Macroarthropod faeces are poor in easily assimilable organic compounds and rich in lignin; microbial respiration is only transiently stimulated in this material and, in the long term, there is no evidence of increased mass loss in faeces compared with intact leaf litter; faecal pellets are more akin to partially stabilized organic matter than to hotspots of microbial activity. (3) The overall impact of macroarthropods on microbial respiration in litter or soil-litter microcosms can be positive or negative; the results vary depending on animal abundance and litter type, but macroarthropod–microorganism interactions in unconsumed leaf litter may also be involved; recent studies have shown that macroarthropods grazing on fungi have complex, species-specific effects on fungal-mediated decomposition, which may partly explain the variability of microbial responses in microcosm experiments. (4) The most consistent effect of macroarthropods in decomposing leaf litter is an increased rate of nitrogen mineralization, which results predominantly from interactions with microorganisms and not from excretion; fresh macroarthropod faeces probably stimulate microfaunal activity, thereby increasing nitrogen release, although the actual mechanism remains unclear. It is concluded that soil macroarthropods play important roles in nutrient cycling, while their impact on carbon mineralization is much less clear. Significant alterations of carbon and nutrient dynamics may result from their interactions with fungi and more research is required in this area.

1. Introduction

Saprophagous macroarthropods are large-sized arthropods, typically ranging in length from 5 to 50 mm, which feed on decomposing plant material. This review focuses on the role of non-social macroarthropods that have been classified as "litter transformers" in terrestrial ecosystems (Lavelle and Spain, 2001; Wardle, 2002), such as millipedes (Diplopoda), woodlice (Crustacea, Isopoda), landhoppers (Crustacea, Amphipoda) and many insects at some phase of their life cycle. "Ecosystem engineers" such as termites and ants will not be discussed here, because most social insects that build elaborate nests have specific impacts on litter decomposition and soil formation, quite different from those of litter transformers (Bignell and Eggleton, 2000; Jouquet et al., 2006).

Macroarthropods consume large amounts of dead plant remains in ecosystems in which they are abundant (Fig. 1). The annual consumption rate of millipedes and woodlice under seasonal temperate conditions is in the order of 10–14 g (dry mass) of leaf material per g (live mass) per year (Van der Drift, 1975; David, 1987; Mocquard et al., 1987; David and Gillon, 2002). The most visible consequence of those feeding activities is the production of faeces, often in large amounts, which has attracted much interest to determine whether, and how, this processing by macroarthropods enhances decomposition.

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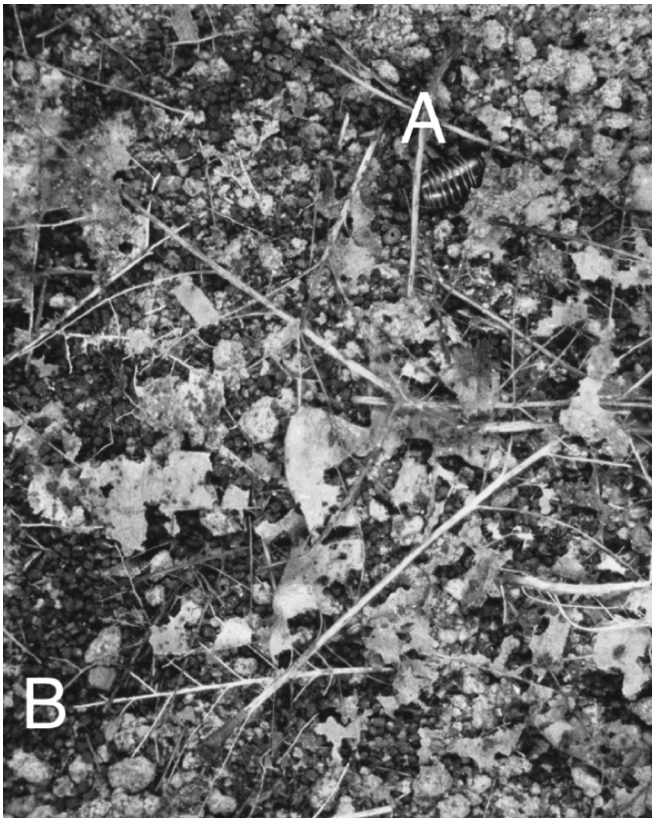

Fig. 1. Oak leaf litter that was consumed by the millipede *Glomeris marginata* (A) in a soil microcosm. This species transforms the lamina into faecal pellets (darker material, B) but the largest veins are not eaten.

In the litter and soil, it has long been established that decomposition, i.e. the gradual transformation of dead organic matter that is ultimately mineralized with release of CO_2 and nutrients, is primarily carried out by microorganisms (Petersen and Luxton, 1982). Bacteria and fungi are key actors in the decomposition process due to their large biomass, ubiquity, and broad range of enzymatic capabilities (Lavelle and Spain, 2001; Coleman et al., 2004; Bardgett, 2005). However, despite the relatively small contribution of invertebrates to soil respiration, their indirect effects on decomposition through interactions with microorganisms may be considerable (Visser, 1985; Wolters, 2000; Wardle, 2002; Crowther et al., 2012). This has led to many studies, especially laboratory experiments, on the impact of macroarthropods on microbial activity in leaf litter and soil.

A review on this topic is necessary because there is an obvious discrepancy between the accumulated experimental evidence and the general perception of the role of these animals in the soil biology literature. The statement that macroarthropods enhance decomposition primarily by fragmenting plant litter, thereby increasing the surface area available for microbial colonization and stimulating microbial activity in their faeces, has been repeated in the introductions of an uncountable number of papers and in most textbooks dealing with these animals (Lavelle and Spain, 2001; Wardle, 2002; Coleman et al., 2004). This view dates back to Van der Drift (1951) who stated that (1) macroarthropods have low assimilation efficiencies and egest a great proportion of the ingested food as faeces; (2) fresh faeces examined under a microscope contain almost unaltered litter fragments that show no evidence of chemical breakdown; (3) litter fragmentation promotes decomposition at a later stage by enhancing microbial activity in faeces. The "external rumen" hypothesis, which proposes that macroarthropods reingest their faeces to exploit the products of microbial activity, is simply an extension of this line of argument. However, an examination of the literature shows that the direct and indirect effects of macroarthropods on decomposition processes are much more variable and complex than in Van der Drift's interpretation. Direct effects refer to (1) the assimilation and subsequent mineralization of ingested food; and (2) the physical, biochemical and microbiological transformations of the unassimilated food that is egested in faeces. Indirect effects include all the interactions of macroarthropods with microbial decomposers, which occur not only in faeces after egestion but also in unconsumed litter. The available information shows that the stimulation of microbial activity in faeces is far from obvious, and further reveals that other effects of macroarthropods on litter decomposition may be potentially more important to ecosystem functioning.

2. Direct effects on decomposition

2.1. Food

Although saprophagous macroarthropods are capable to feed on a wide variety of leaf litter, laboratory tests have shown that some foods are clearly preferred to others. These preferences cannot be explained by a single litter quality parameter and the combination of litter nutritive value, toughness and levels of feeding-deterrents probably best explains the differences in palatability (Hassall and Rushton, 1984; Carcamo et al., 2000; Zimmer et al., 2002; David and Handa, 2010). In many plant species, freshly fallen leaves have high nutritive values in terms of simple sugars, starch, lower fatty acids and amino-acids (Berg and Laskowski, 2006) but are unpalatable due to their toughness and/or high concentrations of secondary compounds. Leaves subjected to leaching and microbial conditioning are then preferred (a wealth of references from Van der Drift, 1951 and Dunger, 1958 to Gerlach et al., 2012 and Wood et al., 2012). Preferred leaves often exhibit a high microbial activity (Köhler et al., 1991; Van Geffen et al., 2011; Collison et al., 2013; Coulis et al., 2013), which may reflect not only high concentrations of easily available nutrients in microorganisms, but also their ability to detoxify secondary compounds. However, in leaf litter without deterrent factors such as that from certain forbs, fresh material is palatable to macroarthropods and can result in better animal growth than well decomposed material (Rushton and Hassall, 1983a).

In addition to feeding on leaf litter and associated microorganisms, many macroarthropods graze directly on fungi (Fig. 2). This behaviour, which has been observed in several species in the laboratory (Tracz, 1984; Maraun et al., 2003; Crowther et al., 2011a) and sometimes in the field (Tracz, 1984; Bultman and Mathews, 1996), probably explains the large amounts of fungal material occasionally found in the gut of field specimens (Dunger, 1963; Soma and Saito, 1983). In choice experiments, clear preferences for certain fungal species have been demonstrated (Taylor, 1982; Tracz, 1984; Maraun et al., 2003; A'Bear et al., 2013). When fungi are embedded in leaf tissues, both are consumed together and it is likely that macroarthropods select leaves or even parts of leaves on the basis of their colonization by fungi or filamentous actinobacteria (Gunnarsson, 1987; Stöckli, 1990; Ihnen and Zimmer, 2008).

Most macroarthropods occasionally feed on additional foods that are rich in nutrients, such as fallen fruits, seeds, mammal faeces and dead invertebrates (Wooten and Crawford, 1975; Dangerfield and Telford, 1993; Saska, 2008; Koprdova et al., 2010). Even though these types of food remain marginal in the diet, as appears from the large amounts of leaf litter found in the guts of field-caught individuals, they may be important not only in