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**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.

Keywords: Detritivores, Assimilation efficiency, Faecal pellets, Microbiota-fauna interactions, Carbon mineralization, Nitrogen mineralization

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.

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 CO₂ 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.

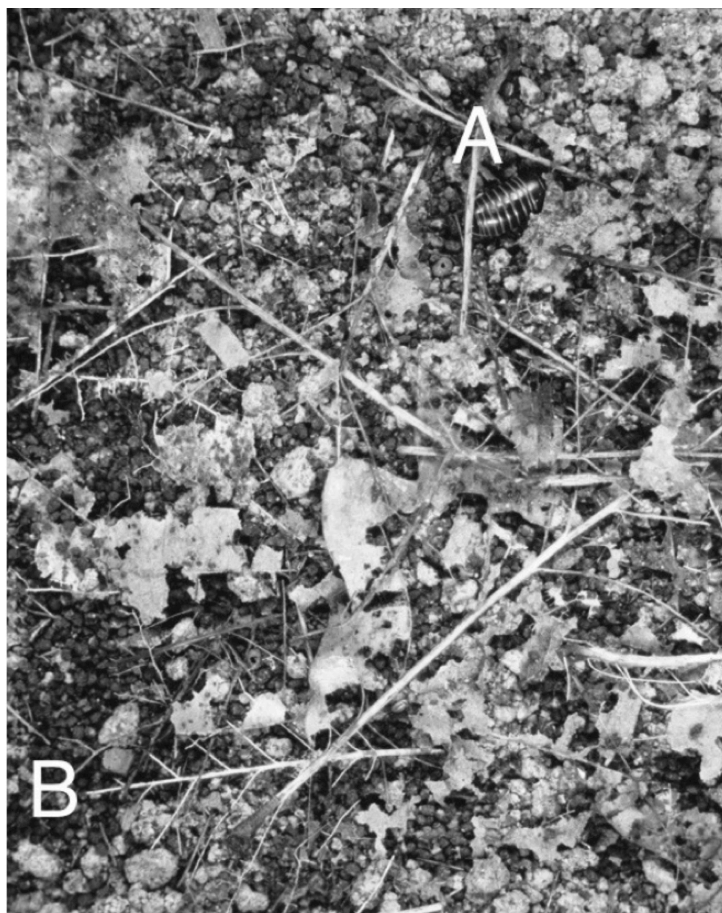


Fig. 1. Oak leaf litter that was consumed by the millipede *Glomeris marginata* (A) in a soil microcosm. This species transforms the lamina into faecal pellets (darker material, B) but the largest veins are not eaten.

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; Koprdoва 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 terms of animal nutrition, but also in terms of bacterial nutrition and growth in the gut and faeces (see below).

Finally, many macroarthropod species ingest soil, which is mixed with other food items in the gut (Shachak et al., 1976; Jambu et al., 1988; Kaneko, 1999). The desert millipede *Orthoporus ornatus* could not be induced to feed on plant litter in the absence of moist soil in the laboratory (Wooten and Crawford, 1975). Earthy faecal material is used during the life cycle of millipedes, e.g. to build moulting chambers and to protect eggs, but mineral soil may also have a direct bearing on nutrition if it acts as roughage or provides nutrients and digestive enzymes, as hypothesized by Dangerfield (1993) and Zimmer (2002).

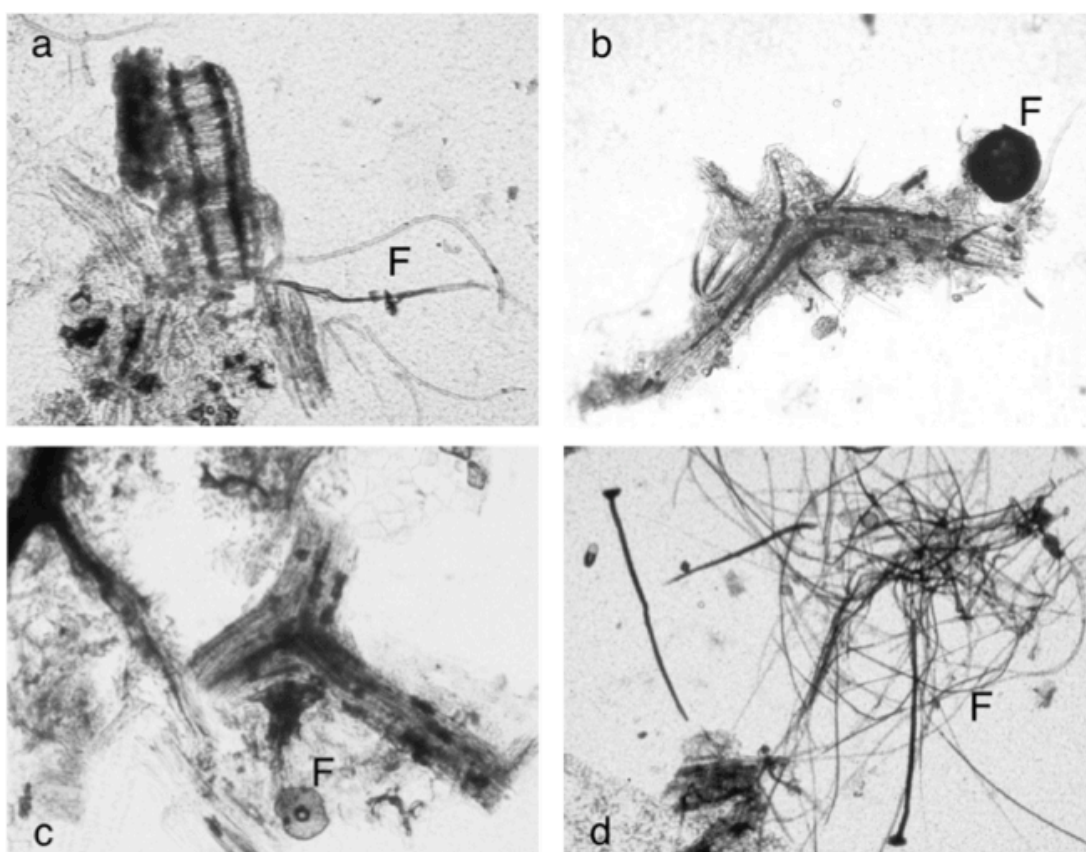


Fig. 2. Gut contents (magnified 125x) of millipedes caught in the field. Fragments of leaf litter, with easily identifiable structures such as the palisade layer in (2a) and trichomes in (2b), are often accompanied by a variety of fungal materials (F). Clusters of hyphae in the gut (2d) probably reflect selective grazing on fungi.

2.2. Digestion and assimilation

The effects of digestion can be assessed by comparing the biochemical composition of freshly egested faeces with that of the ingested food. Leaf litter is mainly composed of structural polysaccharides (cellulose, hemicellulose), lignin and tannins, plus many non-structural organic compounds (simple sugars, starch, proteins, fatty acids, secondary compounds), variable proportions of which are of microbial origin (Kögel-Knabner, 2002). Ash content is generally \leq 15%.

The concentration of non-structural compounds substantially decreases in macroarthropod faeces, which indicates that they are readily digested and assimilated (Jambu et al., 1988; Jocteur-Monrozier and Robin, 1988; Gillon and David, 2001; Rawlins et al., 2006). By contrast, lignin is a very recalcitrant compound, which is generally not digested and occurs at high concentrations in faeces (Reyes and Tiedje, 1976a; Neuhauser et al., 1978; Jocteur-Monrozier and Robin, 1988; Scheu, 1993; Gillon and David, 2001). Tannins are hydrolyzed and/or oxidized, sometimes extensively (Zimmer et al., 2002; Coulis et al., 2009), which contributes to the detoxification of the ingested food. A proportion of cellulose and hemicellulose is digested in the gut, but estimates vary substantially, even for a given macroarthropod species. Kondeva (1980) reported that 34 to 48% of the cellulose ingested in oak (*Quercus pubescens*) leaves was digested by the millipede *Pachyiulus flavipes*. Anderson and Bignell (1982), using ^{14}C -labelled leaf fibre, confirmed that *ca.* 36% of this substrate was utilized by the millipede *Glomeris marginata*. In another study, however, only 11% of the cellulose and hemicellulose was digested by the same species fed on holm oak (*Quercus ilex*) leaves (Gillon and David, 2001).

Although this variation may reflect different levels of cellulose accessibility in lignocellulosic fibres, it may also result from different enzymatic capabilities in macroarthropods. For example, Beck and Friebe (1981) found that gut extracts of the millipede *Polydesmus angustus* were more active against polysaccharides than those of the woodlouse *Oniscus asellus*. Deleporte and Charrier (1996) compared carbohydrase activities in two sciarid

fly larvae and found much higher enzymatic activities in *Plastosciara falcifera* than in *Bradysia confinis*. These differences may be constitutive or result from the presence of microbial exoenzymes released in the gut during digestion (Hopkin and Read, 1992; Zimmer, 2002). Kukor and Martin (1986) demonstrated that the efficiency of utilization of plant structural polysaccharides was significantly increased following the ingestion of fungal (*Penicillium*) cellulase by the woodlouse *Trachelipus rathkei*. Acquired microbial enzymes can thus lead to variable digestive capabilities depending on the bacterial and fungal species ingested, but these processes have been little studied in saprophagous macroarthropods.

Leaf litter-colonizing microorganisms (bacteria, yeasts, fungi) are ingested along with the food and many are digested in the gut (Reyes and Tiedje, 1976b; Zimmer and Topp, 1998; Frouz et al., 2003; Byzov, 2006). Digestibility varies greatly depending on the microbial species (Byzov et al., 1998; Byzov, 2006; Ihnen and Zimmer, 2008). For example, among fungi ingested by the millipede *Pachyiulus flavipes*, dark pigmented Dematiaceae were strongly affected by passage through the gut while others (*Penicillium* spp.) were much more resistant (Byzov et al., 1998). Microorganisms are presumably major sources of nitrogen, vitamins and minerals such as calcium (Cromack et al., 1977; Martin and Kukor, 1984), but studies using labelled food have shown that macroarthropods utilize both structural compounds and microorganisms as carbon and energy sources (Reyes and Tiedje, 1976b; Anderson and Bignell, 1982; Bignell, 1989; Frouz et al., 2003).

2.3. Assimilation efficiency

The net assimilation rate is the difference between ingestion rate and egestion rate, expressed in terms of dry mass or – more correctly but more rarely – energy. Assimilation efficiency is the ratio of assimilation rate to ingestion rate (in %).

In keeping with the traditional view, remarkably low assimilation efficiencies, often less than 10% on a dry mass basis, have been recorded in macroarthropods (Van der Drift and Witkamp, 1960; Bocoock, 1963; Carcamo et al., 2000; David and Gillon, 2002). On a dry ash-

free basis, the assimilation of organic matter is only slightly higher, e.g. 11% instead of 9% for holm oak leaves ingested by *Glomeris marginata* (Gillon and David, 2001). However, results vary greatly within and among species (Köhler et al., 1991; Zimmer, 2002). Many studies have reported high assimilation efficiencies, similar to those of gastropods, e.g. 55% in the millipede *Trigonoilulus lumbricinus* (Pobozsny et al., 1992); 46-76% in larvae of the bibionid fly *Bibio pomonae* (Frouz and Sustr, 1996); 42-78% in the woodlouse *Porcellio dilatatus* (Sousa et al., 1998); 41-87% in the woodlouse *Porcellionides pruinosus* (Loureiro et al., 2006).

Food quality probably explains most of the intraspecific variation. Foods rich in readily assimilable nutrients are more likely to result in high assimilation efficiencies, which can lead to large variations when a macroarthropod species feeds on different litter species (Dudgeon et al., 1990; Kautz et al., 2002). Microbial tissues are very easily assimilated, with efficiency values in the 70-90% range for a variety of microorganisms (Bignell, 1989; Byzov, 2006; Ihnen and Zimmer, 2008), which increases the overall efficiency when microbial biomass is high in leaf litter. Taking also into account intra- and interspecific differences in fibre digestion capabilities (§ 2.2), it is not surprising that laboratory estimates of assimilation efficiency differ by one order of magnitude, with figures below 5% and in excess of 50%.

A number of authors suggested that there could be an inverse relationship between assimilation efficiency and ingestion rate, resulting in a relatively constant assimilation rate (Rushton and Hassall, 1983b; Soma and Saito, 1983; Striganova and Prishutova, 1990). However, there are examples of leaf litter species that are both readily consumed and easily assimilated by macroarthropods, e.g. *Celtis sinensis* leaf litter, which is highly consumed by the woodlouse *Burmoniscus ocellatus* with an assimilation efficiency of 64% (Dudgeon et al., 1990). Therefore high assimilation rates are quite possible, which suggests that abundant populations of macroarthropods may have much greater direct effects on carbon mineralization than generally assumed.

3. Indirect effects on decomposition through faeces production

3.1. Changes in microbial communities

In general, the bacterial:fungal ratio is considerably higher in fresh faeces than in leaf litter (McBrayer, 1973; Hanlon, 1981b; Hassall et al., 1987; Maraun and Scheu, 1996; Byzov et al., 1998). Fungal hyphae are probably more susceptible to disruption by animal feeding activities than bacteria (Anderson and Ineson, 1984; Visser, 1985) and, moreover, the hindgut of macroarthropods is a favourable environment for bacterial growth (Zimmer and Topp, 1998; Frouz et al., 2003; Byzov, 2006). After digestion of microbes in the anterior parts of the gut, counts of bacteria – but not counts of fungi – increase in the posterior parts (Zimmer, 2002). Whether or not this turnover results in an increase in the absolute number of bacteria in faecal material depends on the balance between digestion and growth. Contrasting results have been reported, ranging from bacterial counts several hundred times higher in faeces than in leaf litter to a lower abundance in faeces (Reyes and Tiedje, 1976b; Hanlon, 1981b; Ineson and Anderson, 1985; Hassall et al., 1987; Byzov et al., 1998; Suzuki et al., 2013).

The species composition of bacterial and fungal communities differs between leaf litter and faeces (Ineson and Anderson, 1985; Ullrich et al., 1991; Byzov, 2006). These changes result from both the differential digestion of microorganisms by macroarthropods (§ 2.2) and the presence of symbiotic bacteria in the gut, e.g. numerous Enterobacteriaceae in millipedes (Szabo et al., 1983; Byzov, 2006; Knapp et al., 2009), which are partly egested in fresh faeces. Specific gut symbionts, however, cannot proliferate outside the body (Byzov, 2006) and are therefore unlikely to influence the subsequent decomposition of faeces.

The bacterial:fungal ratio reverses again as faeces age. Van der Drift and Witkamp (1960) studied microbial succession on faecal pellets produced by two species: after 12 days of incubation, fungi covered the pellets of caddis-fly (*Enoicyla pusilla*) larvae; after 3 weeks of incubation, bacterial counts were much reduced while fungal abundance was increased in pellets of *Glomeris marginata*. Similarly, Nicholson et al. (1966) and Tajovsky et al. (1992) observed

rapid hyphal growth on the surface of faecal pellets of *Glomeris* spp., both in the laboratory and in the field. Fungal mycelium was sparser on pellets decomposing in the field, i.e. in the presence of potentially fungivorous mesofauna, but the general pattern of fungal species succession was the same as in the laboratory.

3.2. Microbial activity and mass loss rate in faeces

The respiration rates of intact leaf litter and macroarthropod faeces were compared at different times after egestion. In most studies, respiration increased in fresh faeces but only for a short time, ranging from a few hours to 2-3 weeks after egestion (Van der Drift and Witkamp, 1960; Nicholson et al., 1966; Hassall et al., 1987; Maraun and Scheu, 1996; Frouz and Simek, 2009). In the longer term, respiration was similar or even lower in faeces than in leaf litter. Different dynamics of microbial activity were observed in other studies (Scheu and Wolters, 1991; Suzuki et al., 2013), but the cumulative CO₂ production from faeces did not exceed that of intact leaf litter, even over 23 weeks.

The key point is that, despite the transitory stimulation of microbial respiration in faeces, no differences with leaf litter have been detected in terms of mass loss rate. The few studies that compared mass loss in the two substrates over long time periods, up to 1 year, have shown that macroarthropod faeces do not lose mass more rapidly than unconsumed leaf litter, or even less rapidly (Nicholson et al., 1966; Webb, 1977; Frouz and Simek, 2009). The near-infrared spectrum of fresh faecal pellets of *Glomeris marginata* confirmed their low decomposability compared with intact leaf litter (Gillon and David, 2001).

Therefore, litter fragmentation by macroarthropods does not automatically increase microbial decomposition. This may result, at least in part, from the structure of faecal pellets in many species. Hanlon (1981a) showed that the mechanical fragmentation of dead leaves in the laboratory increased the surface area available for microbial colonization, resulting in an increased respiration in the ground material, but also showed that the compaction of small particles reduced fungal respiration. By forming large and compact faecal pellets, many

millipedes may actually reduce the surface area available for fungal colonization (Webb, 1977), which was confirmed by the increased respiration recorded after grinding this material (Suzuki et al., 2013). Faeces of woodlice, which are generally less compact than those of millipedes (Fig. 3), might have different properties.

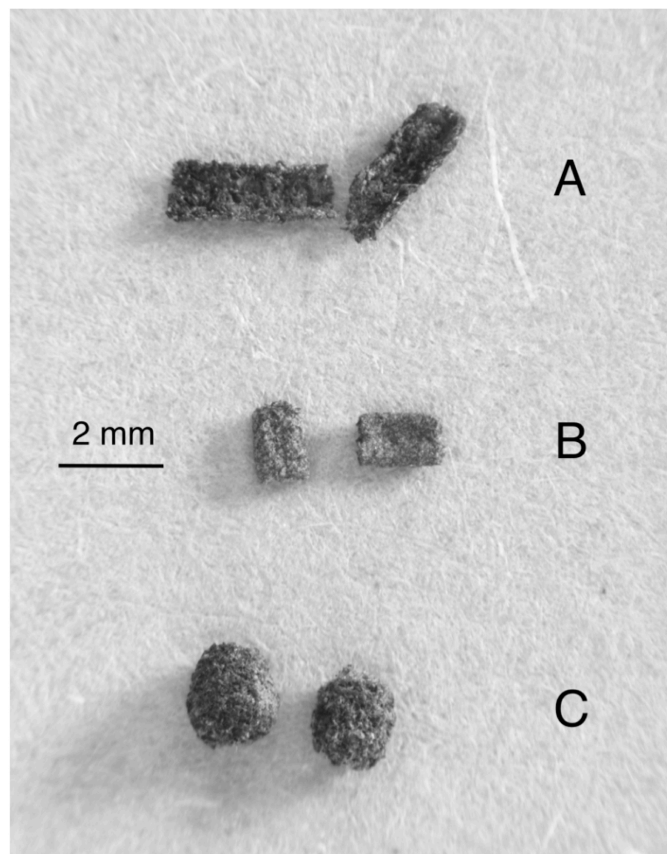


Fig. 3. Shape of faeces from three macroarthropod species of similar body size: thin and flat faeces of the woodlice *Armadillo officinalis* (A) and *Armadillidium vulgare* (B) compared with thicker, rounded pellets of the millipede *Glomeris marginata* (C).

The low quality of the resource (§ 2.2) is another likely explanation for the low mass loss rate in faeces. The extent to which microbial respiration is stimulated after egestion may reflect the amount of readily metabolizable organic constituents left over in fresh faeces (Reyes and Tiedje, 1976a; Maraun and Scheu, 1996; Wolters, 2000). This may vary with the type of food ingested since differences in microbial activity between litter species are retained after gut passage (Suzuki et al., 2013). However, once readily available resources are exhausted in the

faecal material, bacterial activity slows down and no significant increase in mass loss rate can occur (Reyes and Tiedje, 1976a; Rawlins et al., 2006, 2007).

The above results provide little support for the external rumen hypothesis, in which macroarthropods are supposed to reingest their faeces to acquire nutrients resulting from increased microbial activity. Initially, this notion was based on the studies of Wieser (1966) in the woodlouse *Porcellio scaber* and McBrayer (1973) in the millipede *Apheloria montana*, who both reported feeding problems and mortality when access to faeces was denied in the laboratory. These observations were not confirmed in subsequent studies. Many millipedes do not, or rarely consume their faeces anyway (Wooten and Crawford, 1975; Bignell, 1989; Dangerfield and Milner, 1993; Lawrence and Samways, 2003; but see Szlavecz and Pobożny, 1995). Although coprophagy is more common in woodlice, at least in the laboratory, the importance of this behaviour for survival has not been confirmed (Hassall and Rushton, 1982) and its nutritional significance remains controversial (Ullrich et al., 1991; Zimmer, 2002). Coprophagy seems to be especially beneficial for woodlice when alternative foods are of poor nutritional quality (Hassall and Rushton, 1982; Kautz et al., 2002).

3.3. Incorporation of faeces into the soil

Faeces are mainly composed of particulate organic matter, i.e. partially decomposed plant material 50-2000 μm in size, which epigeic macrofauna contribute to incorporating into the topsoil (Anderson, 1988). Although earthworms are most efficient in this process of bioturbation (Wolters, 2000; Lavelle and Spain, 2001), macroarthropods also play a role – perhaps even species that are not adapted for burrowing such as the woodlouse *Armadillidium vulgare* (Frouz et al., 2008). Hassall et al. (1987) hypothesized that the incorporation of faeces into the soil could enhance their decomposition due to more favourable moisture conditions than on the soil surface, but this hypothesis has yet to be tested.

In mull soils with a wide range of macroinvertebrates, bioturbation is more complete because macroarthropod faeces have been shown to be an important food source for earthworm

species such as the epigeic *Lumbricus castaneus* and the endogeic *Aporrectodea caliginosa* and *Octolasion lacteum* (Scheu and Wolters, 1991; Scheu, 1993; Bonkowski et al., 1998). Macroarthropods and earthworms thus form a litter processing chain, which leads to an intimate mixture of faeces-derived organic matter and mineral soil. In general, this does not favour mineralization and contributes to the stabilization of organic matter, which is physically protected from microbial decomposition in soil aggregates created by earthworms (Wolters, 2000; Bossuyt et al., 2005). Scheu and Wolters (1991) showed that carbon mineralization in faecal pellets of *Glomeris marginata* was significantly reduced about two months after the pellets had been consumed and mixed into the soil by the endogeic earthworm *Octolasion lacteum*.

4. Indirect effects on decomposition through macroarthropod-microorganism interactions in uningested litter

4.1. Propagule transport

Passive transport on the cuticle and faeces deposition by macroarthropods (Fig. 4) facilitate the dissemination of microbial propagules in the litter and topsoil layers (Pherson and Beattie, 1979; Visser, 1985; Lilleskov and Bruns, 2005), with potentially important effects on microbial community composition in uningested material. Hanlon and Anderson (1980) found that the feeding activities of the woodlouse *Oniscus asellus* considerably increased the bacterial standing crop in oak leaf litter, presumably through faeces deposition. Coulis et al. (2013) showed that the addition of faecal pellets produced by the millipede *Ommatoiulus sabulosus* on moist *Cistus albidus* leaf litter significantly modified microbial communities, leading to a higher fungal:bacterial ratio in the leaf material.

The hypothesis that the mere deposition of faeces on leaf litter could not only favour microbial colonization but also significantly increase the rate of litter mass loss is attractive. Frouz and Simek (2009) suggested that such an indirect effect is more likely to occur when

uningested leaf fragments have been attacked by macroarthropods that strip leaf tissues, such as dipteran larvae. This type of interaction, however, has been little studied and the first experimental results are negative. Regular addition of faecal pellets of *Ommatoiulus sabulosus* on *Cistus albidus* leaf litter for 1 month did not significantly influence its mass loss rate in the short term (Coulis et al., 2013).



Fig. 4. A *Polydesmus angustus* millipede beside its own fresh faeces deposited on an intact dead leaf. Macroarthropod faeces deposition has the potential to alter microbial communities in uningested leaf litter.

4.2. Consequences of predation on fungi

Owing to the size of their mouthparts, saprophagous macroarthropods inevitably damage hyphae when ingesting leaf litter (Anderson and Ineson, 1984; Visser, 1985). As a result, fungal communities are likely to be seriously affected in partially consumed leaf remains. When the millipede *Blaniulus guttulatus* grazes directly on mycelium, mycelial extension is stopped

beyond the point of grazing (Crowther et al., 2011a). This predation on fungi, whether by fragmenting dead leaves or grazing directly on hyphae, has complex effects for several reasons. (1) Not all fungi are palatable and each macroarthropod species selects certain mycelia or leaves colonized by certain mycelia (Gunnarsson, 1987; Stöckli, 1990; Crowther et al., 2011a); this tends to reduce the growth of palatable fungi, but the impact on fungal community composition also depends on faunal community composition. (2) In some instances, the influence of grazers can translate into greater mycelial extension, due to overcompensatory growth of fungi when grazing intensity decreases (Crowther et al., 2012). (3) Most importantly, it has been established that grazing by macroarthropods stimulates the production of extracellular enzymes by some basidiomycete fungi (e.g. *Phanerochaete velutina*), whereas opposed effects are observed in other basidiomycetes (e.g. *Resinicium bicolor*) (Crowther et al., 2011b). Enzymes released by both saprotrophic and ectomycorrhizal fungi are the principal agents of lignocellulose degradation (Valaskova et al., 2007; Phillips et al., 2014) and changes in their production in response to invertebrate attacks are likely to have consequences for leaf litter decomposition. However, indirect effects of macroarthropods on fungal-mediated decomposition are very difficult to predict a priori, since they depend on the dominant faunal and fungal species present and are therefore expected to vary between soil communities.

5. Overall effects of macroarthropods in the soil-litter system

5.1. Overall effects on microbial respiration

The impact of macroarthropods on decomposition was also investigated in microcosms in which all the above-mentioned positive and negative interactions with microorganisms in faeces and leaf litter were combined. Some studies used only plant litter in very simple microcosm systems while others included a mineral layer or soil with its own microbial community. Results were highly variable, microbial respiration – after correction for animal respiration – being

either increased (e.g. Hättenschwiler and Bretscher, 2001) or reduced (e.g. Hedde et al., 2007; Snyder et al., 2009) in the presence of macroarthropods.

The population density of macroarthropods is a first cause of variability. In microcosms containing oak (*Quercus robur*) leaf litter fragments without soil, Hanlon and Anderson (1980) found that *Oniscus asellus* and *Glomeris marginata* increased cumulative microbial respiration over 40 days, except at high population density of woodlice. The negative effect of high numbers of macroarthropods was associated with a reduction of fungal standing crop, suggesting that microbial activity can be decreased by high grazing pressures on fungi.

Leaf litter quality may be another important cause of variability, but its influence is far from clear. Van Wensem et al. (1993) measured for four weeks the effects of *Porcellio scaber* on the cumulative microbial respiration of poplar (*Populus x canadensis*) leaf litter at different stages of decomposition. From their results and those of previous studies (Hassall et al., 1987; Couteaux et al., 1991), they generalized that macroarthropods have a positive effect on carbon mineralization in fresh litter with a high carbon:nitrogen (C:N) ratio, but a negative effect in older litter with a lower C:N ratio. However, the supposedly key role of the C:N ratio in those intraspecific differences was not confirmed by interspecific comparisons. Rouified et al. (2010) studied the impact of *Glomeris marginata* on the decomposition of four litter species in soil microcosms for five weeks and recorded no significant effect on carbon mineralization, whether with beech (*Fagus sylvatica*) and oak (*Quercus petraea*) leaf litter (C:N \geq 67) or hornbeam (*Carpinus betulus*) and lime (*Tilia platyphyllos*) leaf litter (C:N \leq 30).

In fact, those studies may have been done over too short periods of time to draw solid conclusions. In a longer study (198 days), Couteaux et al. (2002) found that the presence of *Glomeris marginata* at temperatures favourable for litter consumption (15 and 23°C) increased microbial respiration of pine (*Pinus halepensis*) needle litter, but this effect only became apparent beyond ten weeks. Although the data were not corrected for millipede respiration, the results of this study suggest that the influence of macroarthropods may be slow to appear and

that it may be better to assess their impact on microbial decomposition over relatively long periods of time (≥ 10 weeks).

Longer studies, however, have not eliminated the variability of results. In soil microcosms with beech (*Fagus sylvatica*) leaf litter, Scheu (1993) and Hättenschwiler and Bretscher (2001) observed increased microbial respiration in the presence of *Glomeris marginata* and *Oniscus asellus*, respectively. By contrast, Frouz et al. (2008) detected no effects of *Armadillidium vulgare* on carbon mineralization in soil microcosms with a mixture of deciduous leaf litter. Moreover, Frouz et al. (2007) found that a community of millipedes and Diptera larvae significantly increased carbon mineralization in soil microcosms with alder (*Alnus* spp.) leaf litter (C:N = 14.3), but not with a litter mixture composed mainly of *Salix caprea* (C:N = 28.7). These results do not support the generalization of Van Wensem et al. (1993) and indicate, on the contrary, that more positive effects of macroarthropods on carbon mineralization can be observed when leaf litter has a lower C:N ratio.

The overall impact of macroarthropods on microbially-driven carbon mineralization remains therefore poorly understood. It may vary depending on animal species, litter types and microbial species that colonize the leaf litter. Variations among studies may be linked, at least in part, to the highly species-specific interactions between macroarthropods and fungi mentioned above (§ 4.2).

5.2. Effects on nitrogen mineralization

Macroarthropod feeding activities in leaf litter considerably increase nitrogen mineralization, i.e. the conversion of organic nitrogen present in leaf material and microbes (proteins, nucleic acids, amino sugars) into ammonium-N and/or nitrate-N. In microcosms with oak (*Quercus robur*) leaf litter and a high biomass of *Glomeris marginata*, levels of nitrogen mineralization can be 10 to 15 times higher than in controls (Anderson and Ineson, 1984). This effect has been consistently observed in many microcosm experiments (Scheu, 1993; Kaneko, 1999; Carcamo et al., 2000; Hättenschwiler and Bretscher, 2001; Frouz et al., 2008; Pieper and

Weigmann, 2008). A number of studies conducted not only on macroarthropods but also on micro- and mesofauna have shown that such animal effects on nitrogen mobilization are largely independent from effects on carbon mineralization (Verhoef and Brussaard, 1990; Frouz et al., 2008).

Experiments using ^{15}N -labelled leaf litter and millipedes have shown that this process is not a direct contribution of macroarthropods through excretion, but results predominantly from interactions with microorganisms (Anderson and Ineson, 1984). The enhancement of nitrification by animal feeding activities is also indicative of indirect effects on nitrogen mineralization, since macroarthropods do not excrete nitrates (Hopkin and Read, 1992; Wright and Pena-Peralta, 2005). Furthermore, nitrogen release does not occur in a step-wise manner when animals are added or removed from microcosms, but can take several weeks to build up or decline (Anderson and Ineson, 1984). Although the detailed mechanism remains largely unexplained, this timing suggests that nitrogen release only starts after specific microbial communities have developed in leaf litter, in response to macroarthropod feeding activities. Considering the key role of microfauna (protozoa, nematodes) in nitrogen mineralization processes (Griffiths, 1994; Bonkowski et al., 2000), a possible explanation might be the activation of food chains based on large numbers of bacteria in fresh macroarthropod faeces, which stimulates the growth of bacterivorous microfaunal populations on this material (Tajovsky et al., 1992; Griffiths, 1994; Bastow, 2011). In turn, microfaunal activity is known to promote nitrogen mineralization. For example, Alpehi et al. (1996) showed that soil protozoa considerably stimulate nitrifying bacterial communities and thus increase the amount of nitrate-N released. Connections between the functioning of micro-food webs and the supply of fresh macroarthropod faeces to the soil-litter system certainly deserve more research.

6. Conclusions

Four key points emerge from this review:

(1) There is little evidence to support the paradigm that the primary role of saprophagous macroarthropods in soil processes is the fragmentation of plant litter, which enhances microbial decomposition in their faeces. Microbial respiration is, at best, transiently stimulated in faeces and, so far, there have been no reports of increased mass loss in this material in comparison with unconsumed leaf litter. Macroarthropod faeces are increasingly regarded not as microsites of intense microbial activity but as a stabilized form of organic matter (Rawlins et al., 2007). This largely invalidates the external rumen hypothesis, i.e. a strategy for resource acquisition based on faeces being progressively enriched in easily assimilable compounds.

(2) The high variability of published figures for assimilation efficiency also challenges the notion that the direct effects of macroarthropods on carbon mineralization are generally insignificant. Conflicting results may be due to the use of arbitrarily selected food in laboratory studies, whereas natural conditions offer more choices in terms of litter species, degree of decomposition, microbial colonization and additional food types that can be mixed with leaf litter in the gut. If macroarthropods are able to self-select the most profitable foods or food mixtures in the field, as many insects do (Waldbauer and Friedman, 1991), they may achieve as high assimilation efficiencies as those that are occasionally measured in laboratory studies, i.e. above 50%. This suggests that, in high-density populations, direct impacts of macroarthropods on carbon mineralization may be stronger than generally assumed.

(3) The strong predation by macroarthropods on fungi potentially influences decomposition in the whole litter layer, including unconsumed material. However, such effects are complex and depend on both the identity and abundance of plant litter, fungus and animal species that interact in each community (Crowther et al., 2012). This may partly explain why microbial respiration in litter and soil is either increased or reduced in the presence of macroarthropods, depending on whether they stimulate or inhibit the activity of the fungal

species present. For a better understanding of these processes, it seems necessary to conduct experiments with tight control not only over litter species, decomposition stage and macroarthropod species, but also over microbial populations that colonize leaf litter. Specific associations between soil macroarthropods and microorganisms, especially fungi, have not been sufficiently taken into account in this type of studies (Wolters, 2000).

(4) It is very likely that the strong stimulation of nitrogen mineralization resulting from macroarthropod feeding activities in leaf litter has important implications for soil and ecosystem functioning. There is substantial evidence that this process is mainly the result of multiple interactions with microorganisms in detrital micro-food webs, and is not directly due to animal excretion, contrary to a common assumption. Thus, litter-feeding macroarthropods help to transfer nitrogen and other nutrients to the soil through two distinct pathways, which function on two different time scales: a relatively rapid mobilization (over days or weeks) of organic nitrogen present in leaf litter, presumably due to the stimulation of micro-food webs, which may make nitrogen directly available to plants (Wardle, 2002); and a much slower enrichment (over months or years) due to the production of faeces, i.e. recalcitrant particulate organic matter that can be incorporated into the topsoil and very gradually decomposed by soil microorganisms (Seastedt, 2000). The conversion of litter into faeces by macroarthropods facilitates the feeding activities of earthworms, and this litter processing chain greatly promotes the formation of stable organo-mineral aggregates when both groups of macrofauna co-occur in mull-type humus (Schaefer et al., 2009) (Fig. 5).

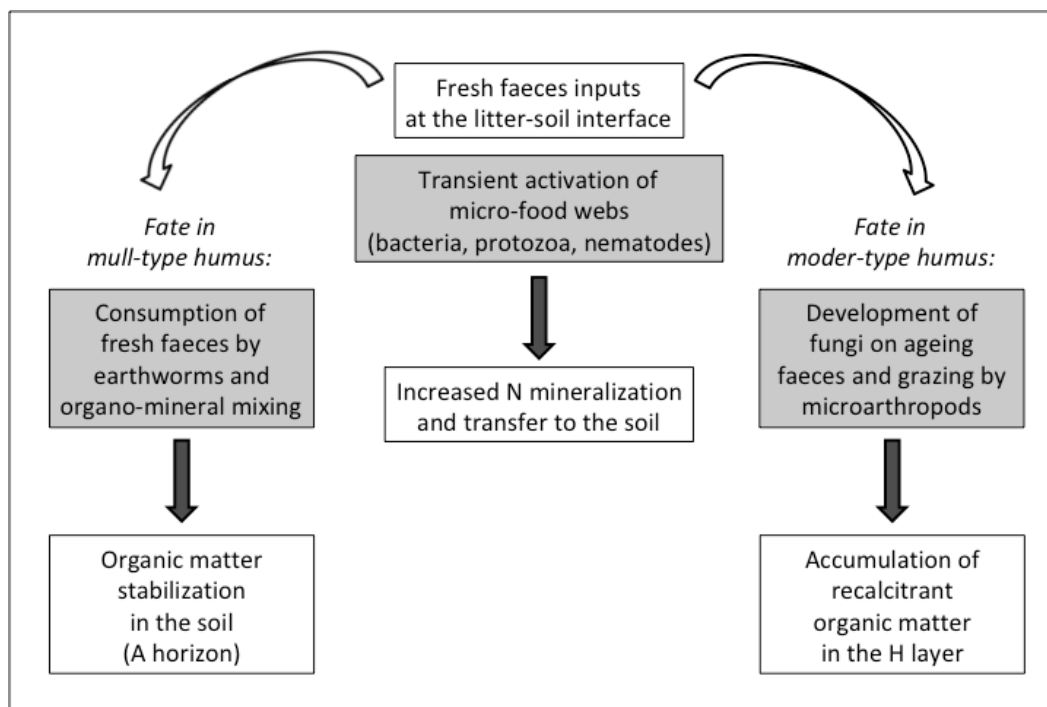


Fig. 5. Three major processes (shaded boxes) that may occur after macroarthropod faeces deposition at the litter-soil interface, and their consequences in terms of soil functioning (black arrows).

Although millipedes, woodlice and other saprophagous macroarthropods are undeniably "litter transformers", their role in decomposition processes is much more complex than originally proposed. These invertebrates probably exert significant control on nutrient cycling but their direct and indirect impacts on carbon mineralization are far less clear than initially thought. Macroarthropod faeces are not destined to decompose rapidly and, moreover, their fate largely depends on the presence and activity of other soil invertebrates. Depending on whether certain earthworm species are present or not, macroarthropod faeces can either be rapidly incorporated into organo-mineral aggregates (mull) or accumulate at the litter-soil interface (moder) (Fig. 5). In either case, most of the faeces-derived organic matter is mineralized slowly, even though its turnover rate differs between the two types of humus (Ponge, 2003). Furthermore, it is increasingly clear that macroarthropods may have important effects on carbon and nutrient dynamics not only as litter transformers but also through interactions with fungi, which rival those of microarthropods. A recent study showed that the inclusion of *Oniscus*

asellus in soil mesocosms considerably changed the fungal community structure, by decreasing the relative abundance of saprotrophic basidiomycetes fed upon by the woodlouse and increasing that of many other species, including mycorrhizal fungi (Crowther et al., 2013); significant changes in fungal exoenzyme production and collembola community composition were also identified when *O. asellus* was present (Ibid.). More research should focus on such processes and their consequences for soil functioning. The impact of macroarthropods on fungal-mediated decomposition may have potentially important implications in many terrestrial ecosystems – e.g. boreal and hemiboreal ecosystems, in which both saprotrophic and mycorrhizal fungi play key roles in litter decomposition (Lindahl et al., 2007; Phillips et al., 2014) and in which macro-detritivores are expected to spread as a result of climate change (David and Handa, 2010; Van Geffen et al., 2011).

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