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FE SPOTLIGHT

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Pellets or particles? How can we predict the effect of soil macro-arthropods on litter decomposition?

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A pervasive belief in soil ecology is that consumption and gut passage of litter by soil macro-arthropods, such as earthworms, millipedes, myriapods, diplopods and various insect larvae (also referred to as litter transformers), hasten the rate at which litter decomposes (David, 2014). It has been repeated in the introductions of an uncountable number of papers and in most textbooks dealing with these animals. This belief can be traced to the faster disappearance of litter in forests with soil macro-arthropods, and the greater mass loss of litter from bags with coarser mesh, which allow soil macro-arthropods access. The difficulty with both of these observations is that they failed to track the fate and decay rate of the litter that had been decomposed and partially transformed into fragmenter faeces and thus "disappeared" from the litter bags. Instead, it was generally considered that faecal material, by virtue of its smaller size and lower C:N (relative to litter), would be quickly colonized and decomposed by soil microbes (van der Drift, 1951).

Another indication that soil macro-arthropods hasten litter decomposition is the commonly held view that decomposition is more rapid on sites with a mull humus form. This is a humus form in which organic residues are largely incorporated in the organic soil layer as an intimate clay-humus mixture (the abundance of litter-transforming fauna is a principle cause of variation in humus forms in forest soils, with mull humus forming on sites with abundant fauna and mor humus or "duff" forming on sites lacking such fauna). A mor humus form is where organic residues in varying stages of decomposition overlie the mineral soil with a sharp boundary but it also may show some weak mechanical admixture of mineral grains. In the original characterization by Müller (1879; 1884; 1887), these humus forms resulted from differences in the *type* of decomposition, primarily the presence of litter-transforming fauna. Later, Ramann (1911) espoused the opinion that the *rate* of decomposition was the essential difference between mull and mor formation, which came to be generally regarded as true. However, this universal belief in the rapid decay of mull and comparatively slow decomposition in mor is scarcely based on actual tests of any sort as Romell (1932) stated. Romell (1932) went on to present evidence of similar accumulations of organic matter under mull and mor humus forms (if measured to 1 m depth), which has been borne out by measurements of organic matter under different tree species on the same site (Frouz, Elhottová, Kuráž, & Šourková, 2006; Vesterdal, Schmidt, Callesen, Nilsson, & Gundersen, 2008).

Recent studies that have accounted for the litter removed from the bags and/or transformed via gut passage have found little difference in the rate of decay of intact and transformed litter (Frouz, Roubickova, Hedenec, & Tajovsky, 2015). Likewise, several laboratory studies measuring proxies of decomposition (mass, CO_2-evolution) have not reported faster decomposition of faunal faecal material relative to unconsumed litter (Coulis, Hättenschwiler, Fromin, & David, 2013; Frouz & Šimek, 2009; Nicholson, Bocock, & Heal, 1966; Rawlins, Bull, Poirier, Ineson, & Evershed, 2006; Suzuki, Grayston, & Prescott, 2013; Webb, 1977). In a consequent re-appraisal of the influence of litter-feeding macro-arthropods on decomposition processes, David (2014) concluded that soil macro-arthropods clearly play important roles in nutrient cycling, but their impact on carbon mineralization is much less clear.

With the dismantling of the simplistic generalization that litter-transforming macro-arthropods hasten litter decomposition comes the task of determining what their real effects are. Recent studies indicate that the effects are complex (Frouz, 2018) and differ depending on (a) the type of organism and species, (b) the nature of their faecal material with respect to surface area: volume, degree of conglomeration and cohesiveness of particles and (c) their food source. In the current issue of *Functional Ecology*, Joly, Coq, Coulis, Nahmani and Hättenschwiler (2018) suggest that the chemical transformations that occur during the hours of gut passage are analogous to those which occur over periods of months or years in forests without soil macro-arthropods. They collected faeces of millipedes (*Glomeris marginata*; Villers, 1789) that were fed with litter from one of seven tree species. They then measured rates of carbon and nitrogen losses from leaf litter of each tree species, and faeces produced by *G. marginata* feeding on each leaf litter, during a 3-month incubation. Gut passage had a homogenizing effect among species of litter on most of the measured characteristics; for example, there was substantially less variability in C:N, tannin content and water-holding capacity, among litter of the seven tree species, in faeces than in the original litters. C:N converged from an initial range of about 30–80 in litters to 22–35 in faeces. This convergence is strikingly similar to that previously noted in leaf litters decomposing in Canadian forests (at 80% C loss; Moore, Trofymow, Prescott, Fyles, & Titus, 2006) and suggests the chemical transformations on these forest floors are taking place in short time spans in the guts of macro-arthropods.

How fast does this faecal material decompose relative to the leaf litter? On average, 50% more C was lost from faeces than from leaf litter during the 100-day decomposition. However, the difference varied among litter species—between 8.2% and 100.6%, indicating a significant effect of plant species on decay rate of faecal material produced from their litters. Faeces C loss correlated positively with litter C loss, indicating an enduring influence of litter quality on decay rate of faeces. While litter C loss was most closely related to litter C:N, faeces C loss was positively related to physical characteristic, particularly the specific area and perimeter of the *particles* within the faeces. Nitrogen was immobilized in leaf litter during the 100-day incubation, whereas net N release occurred in faeces derived from six of the seven litter species. Litter N loss negatively related to litter C:N ratio, whereas faeces N loss was most closely related to the specific area and perimeter of faeces *particles* (but not pellets).

To characterize the individual *particles* within faeces, Joly et al. agitated individual faeces in deionized water until completely dissolved, followed by filtering, photography under a stereo microscope and estimation of the surface area and dimensions of each particle with image analysis software. In contrast to faecal pellets, the specific area of the particles constituting the faeces was strongly *increased* by litter conversion into faeces for all litter species, and appeared to be largely responsible for the enhanced rate of C loss of faeces relative to litter in this experiment. Given that micro-organisms work at the scale of microns, analysis of the traits of faecal *particles* as well faecal pellets that influence microbial access to the individual particles may provide new insights into the characteristics of faeces that best predict their rate of decomposition. The influence of site (litter origin and background micro-organisms) and the identity of macro-arthropod species will improve our ability to predict the consequences of litter conversion to humus through the activities of soil macro-arthropods.

Overall, the study by Joly et al. (2018) shows that the negative relationship between biomass loss from the faeces and pellet specific area indicates that the repackaging of litter into faecal pellets participates in the accelerated decomposition of faeces. However, this seems to take place through the opposite mechanism than commonly assumed sensu "repackaging hypothesis" (Bardgett & Wardle, 2010). The "repackaging hypothesis" assumes an increase in surface area and thus an increase in decomposition rates at the scale of the whole pellet. Joly et al. found that contrary to litter, denser faecal pellets with low specific area decompose faster. They suggest that the mechanism of higher surface area available for microbial colonization plays out only at the scale of the particles composing the faeces, while the mechanism of litter compaction seems to play at the scale of the whole faecal pellet. So different mechanisms take place during gut travelling and decomposition of faecal pellets. Since the traits that determine decomposition of the litter are unrelated to the traits of the decomposition of the faecal pellets, it is difficult to predict decomposition rate of faeces from existing plant trait data on litter decomposition (also mentioned by Frouz, 2018). Even when homogenization of litter occurs, alterations of carbon and nutrient dynamics may result from their interactions with fungi and bacteria in the gut. But more research is required in this area (David, 2014; Frouz, 2018; Maraun & Scheu, 1996). As each decomposer has its own unique gut microbiome, biodiversity loss of decomposers could indeed have detrimental effects on decomposition rates and therefore on carbon and nitrogen dynamics in the future (Handa et al., 2014). Moving beyond generalization, it is important that we increase our knowledge on the specific effects of the gut microbiomes. Simultaneously, we need to increase our knowledge on the traits of faecal particles as well as the pellets. This will improve the accuracy of predicted decomposition rates which will then increase the accuracy of biogeochemical cycling and carbon budget models.

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CONFLICT OF INTEREST

We declare no conflict of interest.

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