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Microbiota, fauna, and mesh size interactions in litter decomposition

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Plant litter decomposition is a key process in carbon and nutrient cycling. The critical role of soil-faunal community composition in decomposition has been demonstrated using different mesh size litterbags to control exposure of litter to different faunal size classes. However, the faunal community surrounding the litterbags has not been manipulated despite potentially large indirect effects of their activity on biotic and abiotic processes that control litter decomposition at the habitat-scale.

We combined microcosm and litterbag techniques to facilitate a more comprehensive understanding of the role of direct and indirect effects of soil-faunal community composition on litter decomposition. We placed litterbags of three mesh sizes across model grassland miniecosystems manipulated to enable communities containing 1) microfauna; 2) micro- and meso-fauna; 3) micro-, meso- and macro-fauna. All communities contained bacteria and fungi. The approach permitted correction of mesh size artefacts inherent to field studies. Indirect effects have been divided into two separate terms, direct-indirect effects and indirect effects.

Decomposition in micromesh litterbags was significantly decreased by the indirect effects of meso- and macro-fauna. In macrofauna communities, increased mesh size significantly increased decomposition through mesh size per se and faunal effects. Relative effects of manipulated faunal community composition on litter mass loss and C:N ratio were equivalent for green and senesced litter. The presence of meso- and macro-fauna increased litter decomposition rate overall despite inhibiting decomposition by microfauna, bacteria and fungi through indirect effects.

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The exclusion of specified faunal size classes from litter has demonstrated the importance of soil-faunal community composition as a controller of decomposition rate (Anderson 1973, Coûteaux et al. 1991, Setälä et al. 1996, González and Seastedt 2001). Changes in this community composition, through global environmental change (Jones et al. 1998), can reduce decomposition (Verhoef and Brussaard 1990) and nutrient mobilisation (Setälä et al. 1996) and consequently alter the way an ecosystem functions (Wolters 1997). To determine quantitatively the effects of such changes demands a detailed understanding of the role of micro-, meso- and macro-fauna in decomposition.

Typically, faunal exclusion studies have used either naphthalene or litterbags of different mesh sizes to exclude specific faunal groups from litter. Naphthalene, a biocide that repels microarthropods, can affect microbial activity (Blair et al. 1989) and these non-target effects must be borne in mind when assessing the role of fauna in decomposition (Heneghan et al. 1999). Similarly, experimental caveats exist with litterbags, for example, the effects of artificial enclosure on litter decomposition rate through changes in microclimate is often highlighted (Vossbrinck et al. 1979) but not assessed. Despite recognition of these limitations, one key caveat applicable to both approaches has been over-

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looked – the composition of the fauna in the soil surrounding the experimental patches may modify the activity of the biota colonising the litter. Thus, litterbag (and naphthalene) exclusion experiments not only quantify the contribution of a particular faunal group to decomposition but also the contribution of the presence of other faunal groups surrounding the exclusion patches. To predict reliably the effects of changed faunal community composition on litter decomposition requires experiments that exclude faunal groups from both the experimental litter and the habitat where the litter is placed.

Soil organisms have direct and indirect effects on litter decomposition (Petersen and Luxton 1982). In the case of litterbags, direct effects involve either consumption of litter or removal of litter from the bag (e.g. earthworm "ploughing-in"), while indirect effects involve modification of the direct effects of one organism group through the action of another. Examples of such indirect effects include mesofauna litter comminution increasing surface area for microbial colonisation or Collembola overgrazing of fungi reducing fungal biomass (Petersen and Luxton 1982). In studies of litter decomposition that have solely involved the exclusion of particular faunal groups from the experimental litter, this definition of indirect effects is adequate. However, if fauna are also excluded from the surrounding habitat, indirect effects must be more comprehensively defined to include indirect effects that are mediated both directly on the decomposing material and indirectly on the decomposing material through the surrounding habitat (see below). The suggestion that indirect effects can operate via both these pathways is not new (Beare et al. 1995, Lavelle 1997) but few, if any, studies have been attempted to elucidate the individual contribution of each pathway to litter decomposition. Investigating the two pathways separately will improve our mechanistic understanding of the role of indirect effects in decomposition.

For clarity, we divide what have previously been grouped as indirect effects into two categories, direct-indirect effects and indirect effects. Direct-indirect effects are indirect effects that are directly mediated on the material being decomposed. For example, litter comminution by mesofauna is directly manifested on the material being decomposed and indirectly affects the action of microorganisms. Conversely, indirect effects are indirectly mediated on the decomposing material and involve modification of the abiotic environment that regulates the biota acting on the decomposing material and/or the decomposer community in the bulk soil surrounding the decomposing material. We consider that a change in the activity or biomass of the decomposer community in the bulk soil would affect the initial colonisation rate of the decomposing material and thus its decomposition rate. These indirect effects could be produced through a multitude of mechanisms, e.g. alteration of the soil moisture regime through earthworm engineering (Jones et al. 1994). The earthworms do not directly modify the decomposing material but do affect the activity of the microorganisms decomposing the material through modification of the soil moisture regime. A second example could be mesofauna regulation of fungal activity in the bulk soil that could affect the initial litter colonisation rate by fungi. Note that if the mesofauna grazed fungi that had already colonised the material then this would be classed as a direct-indirect effect. In summary, it is the mode of action, either directly or indirectly manifesting on the material being decomposed, which determines the nature of the indirect effect.

In this study we combined microcosm and litterbag approaches to quantify the role of direct, direct-indirect and indirect effects of soil fauna on litter decomposition and also the influence of mesh size per se ("mesh effects"). Litterbags of three mesh sizes were placed across model grassland systems containing three different faunal communities established using body-size as a determinant of functional group (Peters 1983, Beare et al. 1995, Brussaard et al. 1997). The treatments formed a gradient of increasing soil-faunal functional complexity and were: 1) microfauna; 2) micro- and meso-fauna; and 3) micro-, meso- and macrofauna. All treatment communities contained bacteria and fungi. Body-size provides a good functional classification because it correlates with metabolic rate, generation time, population density and food-size (Peters 1983). The physical structure of the soil habitat also constrains access to resources for certain body-sizes and hence modulates interactions between organisms (Brussaard et al. 1997).

We asked three specific questions. First, does faunal community complexity influence decomposition in bags with the smallest mesh size? That is, does the presence of a functionally complex community indirectly affect the decomposition activity of a restricted (small mesh size) biotic functional complexity? This permitted us to investigate what we define as indirect effects on decomposition by microfauna, bacteria and fungi. Second, what effect does exclusion of different functional groups using litterbags of different mesh sizes have on litter decomposition in the most complex (macrofauna) communities? This part of the study is directly comparable to published field investigations, with the cumulative influence of direct interactions, indirect interactions (both types) and mesh effects being investigated. And, third, how does mesh size affect litter decomposition in the least complex (microfauna) communities? This investigated whether mesh size itself, irrespective of faunal community complexity, affected decomposition and permitted us to quantify separately mesh effects and fauna effects (both direct and indirect).

Methods

Microcosm community design and establishment

Fifteen 1 m^2 microcosms maintained in the Ecotron controlled environment facility (Lawton 1996) were used for this study. The model communities were analogues of an upland, temperate grassland system located on Rigg Foot Hill, Sourhope Experimental Farm, Scotland (NGR NT 855196). The soil was a freely draining, acidic brown forest earth.

Ecotron model communities were constructed using soil, fauna and flora collected from the Sourhope site. Soil was roughly homogenised by horizon or layer and was fumigated with methyl bromide (CH_3Br). The soil profile was reconstructed in 0.4 m^3 purpose-built containers, over a 10 cm gravel layer (for drainage), and included a litter layer. The soils were then inoculated with a microbial solution derived from Sourhope soil.

Seeds of the 10 most dominant plant species at the Sourhope site were collected and greenhouse-germinated. The plant species were, in order of decreasing dominance, *Agrostis capillaris* L., *Festuca rubra* L., *Nardus stricta* L., *Anthoxanthum odoratum* L., *Poa pratensis* L., *Trifolium repens* L., *Holcus mollis* L., *Potentilla erecta* L., *Galium saxatile* L., and *Luzula multiflora* (Ehrh.) Lej.

After plant establishment three experimental faunal treatments were imposed based on organism body-size. The size class that a species was assigned to was based on the size of the adult (e.g. earthworms) or largest larval stage (e.g. tipulids) and adhered to the general size class definition for terrestrial decomposer food webs (Swift et al. 1979). The treatments were: 1) microfauna only (< 100 μm dia.; primarily Protozoa, nematode worms); 2) micro- and meso-fauna (100 μm–2 mm dia., primarily Collembola, Acari, enchytraeid worms); and 3) micro-, meso- and macro-fauna (> 2 mm dia., primarily earthworms, slugs, insect larvae, staphylinid beetles). Hereafter, these treatments will be referred to as microfauna, mesofauna, and macrofauna, communities, respectively. Treatments were randomly assigned within five blocks defined by microcosm planting order.

Unless otherwise stated, fauna were extracted from Sourhope soil blocks. Nematodes and enchytraeids were extracted using a wet-funnel technique. Other mesofauna were dry-extracted using a Tullgren funnel designed to provide a standard faunal inoculum in terms of species diversity and abundance. For the macrofauna, standard numbers of staphylinids and chilopods, and standard biomass of tipulid larvae were collected using the same Tullgren funnel technique. Two earthworm species (*Allolobophora chlorotica* Sav. and *Lumbricus rubellus* Hoffm.) and a mollusc (*Arion ater* L.) were obtained from biological suppliers (Blades Biological, Edenbridge, UK).

Climate was based on mean June–July values for Sourhope from 1994–1998. Photoperiod was 18 hours, including a gradual dawn and dusk of 2 h. Temperature followed a sine curve between a maximum of 21.1°C during the day and a minimum of 9.5°C at night. Relative humidity also followed a sine curve between a maximum of 83% after a rainfall event (3.5 mm d^{-1}) and a minimum of 63%.

Litterbag experiment

All microcosm treatment inoculations were completed by 6 March 2000. The communities were allowed to stabilise for 14 weeks before the litterbag experiment began. Litterbags (9×8.5 cm) were constructed from nylon mesh (Northern Mesh and Technical Fabrics, Oldham, UK) and the edges heat-sealed. Bags were filled with 0.7–0.75 g of greenhouse-grown, homogenised, *Agrostis capillaris* blade material (dried at 36°C). Litterbag mesh sizes were based on the body-size classifications used for the microcosm treatments. The pore sizes were: 1) micromesh (100 μm), permitting entry of microfauna only; 2) mesomesh (2 mm), permitting entry of micro- and meso-fauna; and 3) macromesh (4.7 mm), permitting entry of micro-, meso- and macro-fauna. All mesh sizes permitted entry of bacteria and fungi. Eighteen litterbags (six bags per mesh size) were added to each microcosm community.

Bags were randomly placed beneath the vegetation canopy, in contact with the litter layer. Three bags of each mesh size (henceforth referred to as "repeat" bags) were removed per microcosm at 14 and 35 d. Dry (80°C) mass of the remaining litter, after separation from foreign material (soil, roots, fauna), was determined gravimetrically. Dried litter material from bags of equivalent mesh size, removed from the same microcosm community at the same time point, were bulked for total C and N determinations by coupled combustion chromatography analysis (Natural Resource Management Ltd, Bracknell, UK).

The experiment was repeated after a 12 week interval but using freshly-senesced (collected as standing dead) as opposed to green litter. Both green and senesced vegetation can be major sources of litter in agro-ecosystems (Harmon et al. 1999). "Traveller bags" (i.e. litterbags used to quantify litter loss during bag transportation, placement and retrieval; see Harmon et al. 1999) were used and confirmed that the faunal treatments and in situ mesh effects, not handling, were responsible for the observed differences in litter mass loss and C:N ratio.

Statistical analyses

Analysis of variance (ANOVA) was used to investigate the role of faunal community complexity in determining

both the rate of litter decomposition and the C:N ratio of decomposing litter. Full interaction linear models with four fixed, discrete factors (faunal treatment, mesh size, removal time, litter type – green/senesced) were constructed, with block included as a random factor. Sequential Bonferroni planned comparisons (Sokal and Rohlf 1995) were used to investigate the highest order significant interactions. Based on our specific study questions, we were interested in three comparisons: 1) effect of faunal community complexity on decomposition by microfauna, bacteria and fungi (the impact of indirect effects); 2) mesh size effects in macrofauna treatment microcosms (the combined impact of direct, direct-indirect, indirect and mesh effects); 3) mesh size effects in the microfauna treatment microcosms (the impacts of mesh effects per se).

Proportion of litter mass remaining and C:N data were arcsine square-root transformed to meet the assumptions of ANOVA. Litter mass remaining data were analysed as the mean litter remaining from repeat bags (these bags served to decrease the spatial variation in decomposition estimates within a microcosm replicate). ANOVA was used to investigate whether handling affected litter mass loss and C:N ratio differently for traveller bags of different mesh sizes.

Results

Litter mass loss

Faunal treatment, litterbag mesh size and timing of litterbag removal had a significant effect on litter mass loss (significant treatment × mesh size × removal time interaction, $F_{4,140} = 6.64$, $P = 0.00006$). The four-way interaction with litter type was not significant ($F_{4,140} = 1.83$, $P = 0.13$) indicating that relative effects of faunal community complexity on litter decomposition are approximately equivalent for both green and senesced litter.

Indirect effects of faunal community complexity: Mass loss from micromesh litterbags was significantly greater ($P < 0.05$) within the microfauna treatment than the macrofauna treatment at 35 d (Fig. 1). Intermediate levels of mass loss were observed for the mesofauna treatment but loss was not significantly different ($P > 0.05$) from the other two fauna treatments. At 14 d the same pattern was apparent (Fig. 1) but there was no significant difference between the micro- and macro-fauna treatments ($P > 0.05$).

Mesh size and litter loss: In the macrofauna treatment litter mass loss significantly increased ($P < 0.05$) as mesh size became coarser and the differences in mass loss between mesh sizes were more pronounced at the later removal time (Fig. 2a). Similarly, mass loss increased in the microfauna treatment when mesh size was increased from micromesh to either meso- or macro-mesh (Fig. 2b). However at 35 d, in contrast to the macrofauna treatment, there was no significant difference ($P > 0.05$) in loss between the meso- and macro-mesh bags and the difference in mass loss between mesh sizes was not more pronounced at 35 d than 14 d (Fig. 2b). Note also that the difference between loss from micro- and meso-mesh bags in the microfauna treatment at 14 d was approximately the same as in the macrofauna treatment at 14 d but by 35 d the difference in loss from these two mesh sizes was markedly greater in the macrofauna treatment (compare Fig. 2a and 2b). A similar but more marked pattern was observed for the difference in mass loss between the micro- and macro-mesh bags in the two treatments.

Litter C:N

Faunal treatment and litterbag mesh size had a significant effect on C:N ratio of remaining litter (significant treatment × mesh size interaction, $F_{4,140} = 4.7$, $P = 0.0013$). Changes in N concentration, not C concentration, were responsible for changing C:N ratio. The strongest higher order interaction was the three way interaction between faunal treatment, litterbag mesh size and timing of litterbag removal (treatment × mesh size × removal time interaction, $F_{4,140} = 2.0$, $P = 0.10$).

Indirect effects of faunal community complexity: There was no significant effect ($P > 0.05$) of faunal community complexity on C:N ratio of decomposing

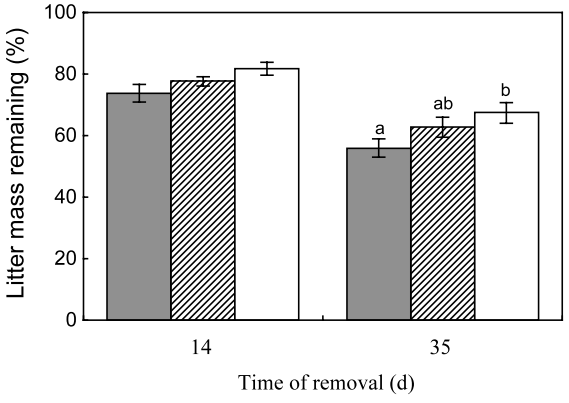

Fig. 1. Indirect effects of faunal community complexity on mass loss of *A. capillaris* litter. Mass remaining (mean ± 1 S.E.; percentage of original) in micromesh litterbags after 14 and 35 d exposure to the microfauna (shaded bars), mesofauna (striped bars) and macrofauna (white bars) treatments is shown. Means and standard errors were calculated from arcsine square-root transformed data at the plot level ($n = 10$; pooled litter type data) and then back-transformed. Means significantly different within one time point are marked by different letters ($P < 0.05$, based on Bonferroni comparisons).

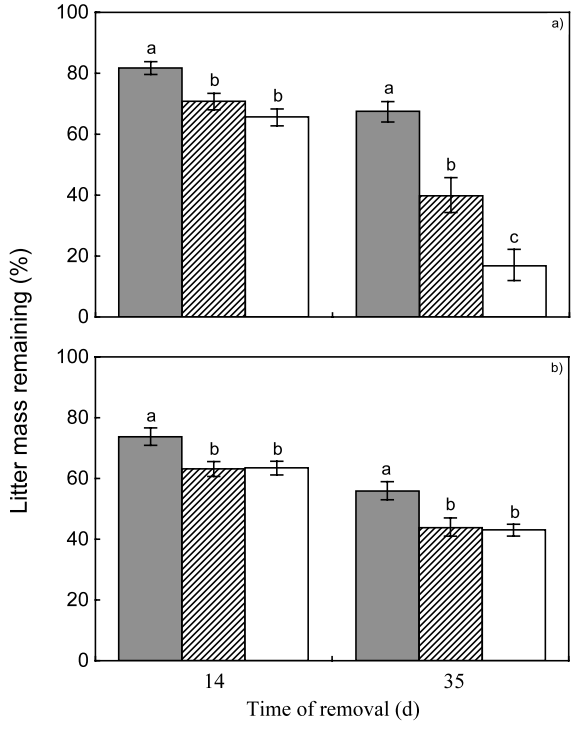

Fig. 2. Meso- and macro-fauna effects on mass loss of *A. capillaris* litter (Fig. 2a) and effects attributable to mesh size alone (Fig. 2b). Mass remaining (mean ± 1 S.E.; percentage of original) in micromesh (shaded bars), mesomesh (striped bars) and macromesh (white bars) litterbags after 14 and 35 d exposure to the macrofauna and microfauna treatment, respectively, is shown. Means and standard errors were calculated from arcsine square-root transformed data at the plot level ($n = 10$; pooled litter type data) and then back-transformed. Means significantly different within one time point are marked by different letters ($P < 0.05$, based on Bonferroni comparisons).

litter in micromesh litterbags (pooled removal time and litter type data; Table 1).

Mesh size and litter loss: The C:N ratio of litter was significantly higher ($P < 0.05$) in macromesh litterbags than either micro- or meso-mesh litterbags in the macrofauna treatment communities (pooled removal time and litter type data; Table 1); there was also a trend ($P < 0.1$) towards a higher C:N ratio in meso- than micro-mesh litterbags. To aid interpretation of these findings, the strongest higher order interaction (pooled litter type data only) was further investigated using planned comparisons. They revealed that at 14 d there was no significant difference in C:N ratio between the different mesh bags but at 35 d litter C:N ratio was significantly higher ($P < 0.001$) in macromesh than micro- or meso-mesh bags (19.75 vs 16.02 and 17.28, respectively). In contrast to the macrofauna communities, there was no significant effect of mesh size on litter C:N ratio in the microfauna treatment communities (Table 1).

Discussion

Indirect effects of faunal community complexity

Indirect effects, as defined in this study, have not previously been quantified in decomposition studies. Yet, increased soil-faunal functional complexity inhibited litter decomposition by microfauna, bacteria and fungi by ca 11.5% (Fig. 1); indirect effects may, therefore, be an important determinant of decomposition rate and nutrient availability in terrestrial ecosystems. We hypothesise that indirect effects are mediated in two ways: 1) through a change in the abiotic environment regulating the biota acting on the decomposing material; e.g. changes in soil moisture caused by earthworms, 2) through changes in the activity or biomass of the decomposer community in the bulk soil that would affect the rate of initial colonisation of the decomposing material; e.g. mesofauna grazing effects on fungal activity and biomass. Any faunal mediated changes in the plant community that would, in turn, affect the abiotic environment or bulk soil decomposer community, would also be classed as indirect effects. While previous investigations (Irmler 2000) using variable mesh size bags have demonstrated that different biota size classes interact in litter decomposition, the extent of this interaction has not been rigorously assessed because litterbags have been surrounded by the full faunal diversity. This will not be the case in scenarios of altered faunal composition.

Mesh size and litter loss

Exposure of plant litter to increased soil-faunal functional complexity through manipulation of mesh size increased litter mass loss (Fig. 2a). This is as reported in numerous forest (Anderson 1973, Wise and Schaefer 1994), grassland (Curry 1969, Vossbrinck et al. 1979),

Table 1. Indirect effects (micromesh bags), meso- and macrofauna effects (macrofauna community), and mesh size effects (microfauna community) on *A. capillaris* litter carbon:nitrogen (C:N) ratios. Values are means calculated from arcsine square-root transformed data at the plot level ($n = 20$; pooled removal time and litter type data) and then back-transformed. Means significantly different within each group of three rows are marked by different letters ($P < 0.05$, based on Bonferroni comparisons).

Treatment community	Mesh size	Litter C:N ratio
macrofauna	micro	16.21 a
macrofauna	meso	17.72 a
macrofauna	macro	19.08 b
microfauna	micro	17.08
microfauna	meso	16.84
microfauna	macro	16.75
microfauna	micro	17.08
mesofauna	micro	17.05
macrofauna	micro	16.21

and microcosm studies (Setälä et al. 1996). However, in our study the higher loss associated with increased mesh size was not solely mediated by increasing faunal community complexity; artefacts caused by the different mesh sizes also played a role.

The use of different mesh sizes to investigate the role of faunal community complexity in litter decomposition has been criticised for three methodological reasons: 1) as mesh size increases litter loss will increase as material within the bags is fragmented by fauna or pulled from the bags (e.g. earthworm action); 2) mesh size will modify microclimate and thus the biological activity within the bags; and 3) increased mesh size will facilitate greater loss through handling effects and increased exposure to abiotic factors, e.g. rainfall, which may increase processes such as leaching. When dealing with the first criticism it is useful to consider the biological processes that will contribute to mass loss from a litterbag. As defined by Anderson (1973), loss will be the resultant of ''breakdown'', mediated by physical biotic processes such as fragmentation, and ''decomposition'', referring to catabolic degradation. Consequently, we consider that mass loss from litterbags includes breakdown as a functional role of meso- and macro-fauna, facilitating litter movement down the soil profile, and not as an artefact of the litterbag technique. The remaining two criticisms can be considered as artefacts of mesh size and will, if not considered appropriately, obscure the true role of faunal community complexity in litter breakdown and decomposition (henceforth referred to as ''decomposition'' only).

While traveller bags (Harmon et al. 1999, this study) can be used to correct for handling effects, loss due to increased exposure to abiotic factors and changes in microclimate are much harder to resolve. Both artefacts could significantly mislead the interpretation of the role of fauna in litter decomposition because loss due to leaching can be very marked (Anderson 1973) and, because microbiota are the dominant catabolic degraders (Petersen and Luxton 1982), changes in microclimate could significantly affect microbial activity and subsequent mass loss. In the current experiment, comparison of mass loss between mesh bags placed in the microfauna and macrofauna treatments permitted us to separate these artefacts from faunal community complexity effects.

Mass loss was significantly less ($>10\%$) from the micromesh bags than from the meso- or macro-mesh bags in the microfauna communities (Fig. 2b), showing that mesh size had a significant effect on mass loss, independent of community complexity. Contrary to this finding, finer mesh size is considered to increase artificially decomposition through changed microclimate (Irmler 2000) but the realised direction and magnitude of the effect will depend on the litter's moisture status (Swift et al. 1979). In support of our findings, coarser mesh bags are more exposed to leaching of soluble compounds and this is associated with increased mass loss (Anderson 1973). However, if leaching had been the dominant mechanism then we would have expected larger mass loss differences at the earlier removal time (leaching effects decrease over time) and a concomitant increase in the C:N ratio of the coarser mesh bags (Curry 1969) but this was not observed. A third possible mechanism might be that a finer mesh presents a physical restriction, slowing initial microbial (and microfaunal) litter colonisation (Wise and Schaefer 1994), and hence decomposition rate. Regardless of the exact mechanism(s) responsible, what is obvious is that mesh effects could significantly influence estimates of decomposition rate made from litterbag studies using different mesh sizes to manipulate faunal community composition. In addition, we consider that the resultant magnitude of the mesh effects in situ will be determined by the relative contribution of microclimate, leaching and restriction to colonisation, and that this will vary between different environments.

The equivalence in mass loss differences in the microfauna communities between the micromesh bags and the two coarser mesh sizes at both removal times (Fig. 2b) suggests that mesh effects were consistent over the time of the study. Consequently, the increasing difference in mass loss between bags in the macrofauna communities (Fig. 2a) indicates that faunal community complexity became increasingly important with time. In addition, the similarity in the difference in mass loss between mesh sizes at 14 d in both the micro- and macro-fauna communities suggests that only mesh effects were apparent in the macrofauna communities at 14 d, with faunal community complexity effects only becoming apparent at 35 d. The C:N ratio data support this contention: there were no significant effects of mesh size on C:N ratio in the microfauna communities and in the macrofauna communities significant effects were only observed at 35 d. Therefore, the mesh size effect on C:N ratio in the macrofauna communities must have been due to actions of the meso- and macrofauna. Interestingly, C:N ratio increased for litter which had undergone the greatest mass loss (C:N normally declines as decomposition progresses (Swift et al. 1979)) which may suggest that the meso- and macro-fauna were preferentially feeding on higher quality litter fractions. The C:N and mass loss data suggest that the role of faunal community complexity in decomposition may become more important as litter age increases. This is consistent with the form of facultative succession whereby microbial colonisation of fresh litter facilitates the action of meso- and macro-fauna (Wall and Moore 1999).

In the current study we manipulated below-ground community composition by constraining the body-size of soil organisms introduced to a treatment community. Global environmental changes, such as elevated atmospheric CO_2 and land-use change, are unlikely to alter

soil community composition in such a clearly defined way. However, our study is useful to help predict the potential impacts of a major shift in soil-faunal community composition, in particular by facilitating an improved interpretation of the findings from field investigations where different mesh size litterbags have been used. Exclusion of macrofauna, and then both meso- and macro-fauna, from litter in the macrofauna communities using different mesh sizes, decreased decomposition by ca 20% and 50%, respectively, at 35 d (Fig. 2a). However, ca 12% of this difference was accounted for by mesh effects (Fig. 2b). The difference can be further decreased by 7% and 11% if indirect effects of mesofauna and, meso- and macro-fauna, respectively, on decomposition by microfauna, bacteria and fungi are accounted for (Fig. 1). If we extrapolate these results to field litterbag investigations, then almost half of the difference in mass loss between mesh bags permitting entry of microfauna only and the full community could be due to mesh- and indirect-effects. Furthermore, the impacts of macrofauna exclusion only on mass loss would be reduced to only a few percent. Clearly, estimates of meso- and macro-fauna impacts on litter decomposition, derived from litterbag mesh experiments, must be considered as maximum potential impacts; in reality the impacts are likely to be markedly lower.

We have defined the indirect effects of soil organisms on litter decomposition as two separate terms to facilitate an improved mechanistic understanding of the role of indirect effects in decomposition. Direct-indirect effects are directly manifested, and indirect effects indirectly manifested, on decomposing material. This terminology describes biologically relevant phenomena that must be considered when assessing the role of soil-faunal community composition in decomposition. We conclude that direct and direct-indirect effects of meso- and macro-fauna will increase litter decomposition despite inhibiting decomposition by microfauna, bacteria and fungi through indirect effects.

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