Tansley insight

The impact of invertebrate decomposers on plants and soil

Authors: Hannah M. Griffiths†, Louise A. Ashton†, Catherine L. Parr, & Paul Eggleton

Affiliations

1 School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, United Kingdom
2 Division of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong, China
3 School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, United Kingdom
4 Department of Zoology & Entomology, University of Pretoria, Pretoria 0028, South Africa
5 School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, Wits, South Africa
6 Department of Life Sciences, Natural History Museum, London, SW7 5BD, United Kingdom

† These authors contributed equally

*Author correspondence:

Hannah Griffiths
Tel: +44 151 794 2000
Email: Hannah.griffiths@bristol.ac.uk

Louise Ashton
Tel: +851 2299 0313
Email: lashton@hku.hk

Received: 16 November 2021

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/NPH.17553

This article is protected by copyright. All rights reserved
Summary

Soil invertebrates make significant contributions to the recycling of dead plant material across the globe. However, studies focussed on the consequences of decomposition for plant communities largely ignore soil fauna across all ecosystems, because microbes are often considered the primary agents of decay. Here, we explore the role of invertebrates as not simply facilitators of microbial decomposition, but as true decomposers, able to break down dead organic matter with their own endogenic enzymes, with direct and indirect impacts on the soil environment and plants. We recommend a holistic view of decomposition, highlighting how invertebrates and microbes act in synergy to degrade organic matter, providing ecological services that underpin plant growth and survival.

Key words: Soil fauna, decomposition, invertebrates, microbes, nutrient cycling, plant growth and nutrition

I. Introduction
Along with fire, decomposition is the primary process by which the stores of nutrients and carbon captured by plants are recycled through the biosphere, converting dead organic material to simpler forms, which are available again for plants (Bishop et al., 2020; Pausas & Bond, 2020). While microbes are considered by many as the primary agents of plant decomposition in terrestrial ecosystems (e.g. Crowther et al., 2019; Lustenhouwer et al., 2020; Pausas & Bond, 2020), here, we synthesise recent advances in understanding of the roles that soil fauna play in biomass degradation and biogeochemical cycling, and the consequences of these processes for plants. In doing so, we build on previous studies highlighting the importance of invertebrates in terrestrial recycling pathways (Swift et al., 1979; Wall et al., 2008; García-Palacios et al., 2013; Briones, 2018) and emphasise the key role of invertebrates in decomposition and, crucially, that their contribution to plant growth, nutrition and survival should not be overlooked.

Decomposition has, traditionally, been thought to be hierarchically controlled by climate and litter quality with soil organisms exerting a comparatively weaker influence on decay rates globally (Hättenschwiler et al., 2005; Cornwell et al., 2008; Makkonen et al., 2012). However, this long-held view has recently been challenged by work showing that microbial communities and microclimate can exert an equally important influence on decay rates at local scales than those exerted by latitudinal gradients in climate (Bradford et al., 2016; Bradford et al., 2017). These findings have implications for plants, because sessile organisms are reliant on decomposition processes that drive the availability of soil nutrients in their immediate surroundings. Yet, the relative contribution of soil fauna to the factors controlling fine-scale heterogeneity in decay rates, and therefore the availability and accessibility of soil nutrients to plants, remains to be quantified despite invertebrate decomposers contributing significantly to the breakdown of dead organic matter across the globe. García-Palacios et al. (2013), for example, demonstrated that the exclusion of soil fauna from leaf litter decomposition bags reduced litter mass loss by an average of 35% across seven biomes. The factors mediating deadwood decay and other substrates (e.g. dung) are less well understood globally, with tropical deadwood decomposition studies, for example, representing just 14% of the published decomposition literature (Harmon et al., 2020). However, in tropical and subtropical systems, evidence is mounting that invertebrate decomposers (termites, in particular) are instrumental for the decomposition of coarse woody material, where they have been shown to be equally, if not more, important than free living microbes for deadwood mass loss (Griffiths et al., 2019; Griffiths et al., 2021; Guo et al., 2021).

The majority of terrestrial above-ground plant biomass is concentrated in tropical ecosystems (Crowther et al., 2019), which means that the decomposition of the majority of dead plant material
occurs in the tropics. Yet, the temperate bias in decomposition studies (Guerra et al., 2020) coupled with the dogma that invertebrates are not ‘true’ decomposers but are instead only facilitators of microbial decay (Crowther et al., 2019; Jones et al., 2020; Lustenhouwer et al., 2020) means that we lack an in-depth understanding of the biotic agents controlling the breakdown of the bulk of plant material on the planet. Furthermore, studies focussed on the consequences of decomposition for plant-soil interactions and associated outcomes for plant communities continue to overlook invertebrate contributions across all ecosystems (e.g. Baskaran et al., 2017). This inaccurate simplification hinders our ability to predict and mitigate the consequences of anthropogenic changes to the below-ground communities that underpin soil biogeochemical cycling and plant growth, nutrition and survival.

Here, we seek to redress this microbe-biased understanding of decomposition by: 1) summarising recent literature demonstrating that many invertebrates are true decomposers able to chemically break down dead plant material; 2) exploring the direct and indirect ways that invertebrate decomposers influence the soil environment and therefore plant growth, nutrition and survival; and 3) highlighting future research directions to deepen our understanding of invertebrate contributions to plant-soil interactions. (See Box 1 for glossary of terms used in this Tansley insight.)

II. Decomposition: chemical breakdown by microbes and invertebrates

Decomposition depends on enzymes that can degrade lignocellulose (i.e. cellulases, hemicellulases and lignases; Cragg et al., 2015). The idea that invertebrates are not directly involved in the catabolism of dead plant material was based on the notion that animal decomposers do not produce endogenous cellulases and appeared to have very low assimilation efficiencies (Van der Drift, 1951). Yet, in 1998, the first insect cellulase-encoding gene was found in a termite species – Reticulitermes speratus (Watanabe et al., 1998). Since then, cellulase-encoding genes have been isolated in various insects and other invertebrates (Chang & Lai, 2018). Crucially, although many invertebrates rely on a partnership with gut microbes for the breakdown of dead plant material (Cragg et al., 2015) and white-rot fungi are the main organisms capable of degrading lignin (Ayuso-Fernández et al., 2019), a growing number of animals have been shown to degrade organic material independently of microbial partners (Scrivener et al., 1989; Shelomi et al., 2020).

The idea that animal decomposers are capable of only poor assimilation efficiencies was most recently challenged by David (2014) who demonstrated that macroarthropods, such as
millipedes and woodlice, are able to digest more than 50% of the dry plant matter they consume. This study, by using $^{14}$C-labelled leaf substrate, confirmed that at least 38% of this material was assimilated or respired by the millipede *Glomeris marginata*. Furthermore, the digestion of leaf litter by macroarthropods (millipedes, woodlice and snails) has been shown to chemically degrade plant material (Joly *et al.*, 2020). This feeding activity converts huge quantities of leaf litter into faeces, which, when compared with unconsumed leaf litter, has lower C:N ratios and tannin concentrations; higher dissolved organic carbon and total dissolved nitrogen concentrations (Joly *et al.*, 2020); can have higher overall surface area (Joly *et al.*, 2018), and harbour higher microbial biomass and distinct microbial communities (David, 2014). Crucially, these physical and chemical changes accelerate C cycling by between 38 and 50% (Joly *et al.*, 2020) and have been shown to result in a switch from net N immobilisation in unprocessed leaf litter to net N release in the faeces of the millipede *Glomeris marginata* (Joly *et al.*, 2018). Therefore, growing evidence suggests that invertebrates do chemically break down dead plant material and may be more important in terrestrial degradation pathways than previously thought. Building on these advances, Scharf (2015) promoted the idea of the digestome, which describes the combined enzymes produced both by microbes and invertebrates, as a key factor in plant decomposition (Fig. 1).

III. Decomposition and soil processing by invertebrates and the consequences for plants

Ecologically important decomposer invertebrates include earthworms, termites, woodlice, snails, millipedes, beetles (especially their larvae) and mesofauna such as collembola. There is a wealth of experimental evidence demonstrating these invertebrate decomposers contribute significantly to the mass loss of dead plant matter across the globe (e.g. García-Palacios *et al.*, 2013; Fujii *et al.*, 2018; Griffiths *et al.*, 2019; Yang & Li, 2020; Griffiths *et al.*, 2021; Guo *et al.*, 2021). However, few studies look beyond the effects of soil fauna on decay rates to the consequences for plants, and the majority of those investigations have been carried out in temperate regions or laboratories (e.g. Setälä & Huhta, 1991; Bardgett & Chan, 1999; Eisenhauer *et al.*, 2018; Winck *et al.*, 2020). Invertebrate decomposers can affect plants via trophic effects, which influence soil nutrient mineralisation as a result of enzymatic degradation within the gut (digestive effects on the nutrient status of the decomposing substrate and/or soil e.g. Joly *et al.*, 2020; Joly *et al.* 2018; Winck *et al.*, 2020); and/or via non-trophic effects resulting from movement and nest building, which alters soil structure (soil particle distribution, aeration, soil moisture status: e.g. Ashton *et al.*, 2019; Tuma *et al.*, 2019) and can in turn can influence soil chemical status (Dangerfield *et al.*, 1998).
Trophic and non-trophic mechanisms affect the soil environment and plant fitness while also initiating cascading changes to microbial communities (Bray et al., 2019; Des Marteaux et al., 2020). For example, the presence of soil invertebrates in a temperate grassland was recently shown to enhance the biomass and diversity of microbial communities, increase extracellular enzyme activity by 37.5%, carbon mineralisation by 19% and nitrate mineralisation by 30% (Bray et al., 2019). Furthermore, while white-rot fungi are the main organisms capable of degrading lignin (Ayuso-Fernández et al., 2019), the mineralisation of lignin in soils was enhanced 24% by earthworms, likely through increased availability of phosphate in earthworm casts and labile carbon in earthworm mucus stimulating microbial communities (Marhan & Scheu, 2006).

However, studies focusing on the effect of invertebrate decomposers on plants tend to look at just one aspect of these multi-trophic and interdependent interactions (separate paths in Fig. 2) rather than exploring the consequences of invertebrate decomposition in full (i.e. the combined cascading effects of the enzymatic degradation of plant material and modification of soil structure by soil fauna on soil properties, microbial communities, and the resultant outcomes for plants). Consequently, our knowledge of the mechanisms by which invertebrate decomposers drive plant-soil interactions is patchy and incomplete.

**Trophic effects of invertebrate-mediated decomposition on soil nutrients and plants**

Experimental work has demonstrated that the direct positive effect of invertebrate decomposers on soil nutrient availability can translate into benefits for plant growth and nutrition (Pathway 2, Fig. 2). Setälä and Huhta (1991), for example, showed that in the presence of soil invertebrates, leaf and stem biomass of silver birch (*Betula pendula*) were 2.6 and 1.7 times greater, respectively, leaf N content was three times higher, and elevated concentrations of KCl-extractable nutrients were found in soil compared with treatments where soil fauna were absent. This suggests that soil fauna facilitate more efficient root nutrient uptake, possibly due to enhanced nutrient mobilization (which was shown to be the case in macroinvertebrate faeces; Joly et al., 2018) and/or because of increases in soil moisture where invertebrates were present. Similarly, the number and N content of leaves of the grass, *Lolium perenne*, increased in the presence of collembola, along with soil ammonia concentrations (Winck et al., 2020). Eisenhauer et al. (2018) demonstrated that adding earthworms and collembola to microcosms resulted in higher root and shoot biomass of wheat and concurrent increases in soil water nitrate concentrations. Indeed, much work has focused on the benefits of enhanced soil fertility by earthworms, showing that their presence can promote plant growth by up to 20% (Xiao et al., 2018) and increase the aboveground biomass of crops by up to 25% (Van Groenigen et al., 2014). The magnitude of these effects, in agroecosystems, was found to be dependent on the

This article is protected by copyright. All rights reserved
presence of crop residue, earthworm density and the type and rate of fertilization, indicating that earthworms may stimulate plant growth predominantly through releasing nitrogen locked away in residues and soil organic matter (Li et al., 2020). Uncertainties remain in disentangling the relative contributions of direct invertebrate-mediated changes in soil nutrient cycling (e.g. Joly et al., 2020) from those driven by shifts in microbial communities (Des Marteaux et al., 2020; Bray et al., 2019). However, what is becoming clearer is the vital role that invertebrate-microbial partnerships (rather than either group in isolation) play in driving decomposition and the importance of these interdependent processes for plants.

**Non-trophic effects of invertebrate movement and nest building**

The indirect effects of invertebrate decomposers, via their movement through the soil and translocation of soil particles, alters soil physical structure (Tuma et al., 2019) and nutrient status (Dangerfield et al. 1998), with consequences for plant survival (e.g. Ashton et al. 2019; Pathway 3, Fig. 2). Earthworm movement, for example, causes extensive bioturbation, modifying the soil structure by increasing soil aggregate carbon stability (Bossuyt et al., 2005) and it is well established that the presence of earthworms have consistent positive effects on soil fertility and plant growth (Scheu, 2003). Additionally, it was recently shown that earthworm burrowing and casting activities can enhance the biocontrol potential of entomopathogenic nematodes against root-feeding pests by facilitating nematode movement through the restructuring the soil physicochemical environment (Fattore et al., 2020).

In the tropics and subtropics, termites alter soil abiotic properties through tunnelling, creating above-ground protective layers (‘sheeting’, Tuma et al., 2019) and nest building - which influence plant diversity, growth and survival via changes to soil physical and chemical properties. For example, termite mounds are known to be nutrient hotspots (Dangerfield et al., 1998) displaying elevated N, P and K compared with surrounding soil with the enriched termite mound soil frequently used by smallholder farmers in parts of Southern Africa as an alternative NPK fertiliser (Chisanga et al., 2020). The vegetation growing on termite mounds has higher foliar N and P content (Davies et al., 2016), different vegetation communities to the surrounding matrix and can host higher plant biomass and diversity (David, 2014). The effect of termite mound soils on vegetation communities may be driven by enriched soils, changes in soil composition (Chisanga et al., 2020), higher soil moisture (Dangerfield et al., 1998) or a combination of these factors. Termites can also increase agricultural yields by increasing soil water infiltration (Evans et al., 2011), as well as increasing soil nitrogen fixation, through the action of their symbiotic bacteria (Ohkuma et al., 1999). Finally, the presence of termites has also been shown to increase the heterogeneity of plant-available nutrients and confer benefits for plant survival during periods
of drought in rainforest, possibly by elevating soil moisture through construction of their protective sheeting (Ashton et al., 2019).

IV. Outlook

Human activity, including climate change, land-use change, biological invasions and nutrient deposition are leading to changes in soil fauna diversity, abundance and distributions (Geisen et al., 2019). Shifts in any part of complex soil food-webs could affect the ecosystem processes carried out by invertebrate decomposers, with cascading consequences for plants. Given that direct evidence for which soil invertebrate activities affect plants is so incomplete, we have limited capacity to predict the consequences of loss in below-ground biodiversity for ecosystem functioning. However, in light of the evidence we present here, which shows that soil invertebrates can 1) chemically degrade dead plant material (Joly et al., 2020; 2) enhance nutrient cycling and plant available nutrients (Yang and Li 2020; Joly et al., 2018; Bray et al., 2019) and 3) positively influence plant nutrient status, growth and survival (Ashton et al., 2019; Xiao et al., 2018; Setälä and Huhta 1991), intact soil faunal communities are likely to be essential for safeguarding ecosystem processes and resilient plant communities in the present era of rapid environmental change (e.g. Ashton et al., 2019).

Decomposer organisms are largely missing from Earth System Models (Filser et al., 2016), which are generally parameterised using coarse spatial-temporal information (e.g. latitudinal gradients in water availability, temperature, vegetation productivity) and therefore cannot account for fine-scale variability in decomposer abundance and activity. These gaps in knowledge are maintained by the siloization of ecological research into microbial and invertebrate fields. To redress this, key future research areas include expanding our understanding of which soil fauna are true decomposers and deepening knowledge of the mechanisms by which their direct and indirect activity influences plant communities (see Box 2 Future directions). It is important that these questions are addressed by integrating emerging technologies with traditional field-based manipulations of soil fauna composition and diversity (see Box 2 Future directions), so that we can develop a real-world understanding of these complex processes. There remain large uncertainties surrounding the contributions of soil invertebrates to carbon and nutrient cycling. Consequently, we have limited understanding of how these processes shift with environmental change. A more interdisciplinary approach is necessary to understand the complex partnerships between soil microbes and invertebrates, and the consequences of these for plant nutrition, growth and survival in our era of rapid global change.
Acknowledgements

We are grateful to the three reviewers and editor, Amy Austin, who provided valuable feedback that greatly improved the manuscript. We also thank the funding body that financially supported this work: The Leverhulme Trust, research grant: RPG-2017-271 awarded to CLP, and Mike Boyle for helpful comments on the manuscript.

References

Ashton LA, Griffiths HM, Parr CL, Evans TA, Didham RK, Hasan F, Teh YA, Tin HS, Vairappan CS, Eggleton P. 2019. Termites mitigate the effects of drought in tropical rainforest. Science 363: 174-177.

Ayuso-Fernández I, Rencoret J, Gutiérrez A, Ruiz-Dueñas FJ, Martínez AT. 2019. Peroxidase evolution in white-rot fungi follows wood lignin evolution in plants. Proceedings of the National Academy of Sciences 116: 17900-17905.

Bardgett RD, Chan KF. 1999. Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. Soil Biology and Biochemistry 31: 1007-1014.

Baskaran P, Hyvönen R, Berglund SL, Clemmensen KE, Ågren GI, Lindahl BD, Manzoni S. 2017. Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. New Phytologist 213: 1452-1465.

Bishop T, HM Griffiths, LA Ashton, PE Eggleton, JS Woon, Parr C. 2020. Clarifying Terrestrial Recycling Pathways. Trends in Ecology & Evolution 36: 9-11.

Bossuyt H, Six J, Hendrix PF. 2005. Protection of soil carbon by microaggregates within earthworm casts. Soil Biology and Biochemistry 37: 251-258.

Bradford MA, Berg B, Maynard DS, Wieder WR, Wood SA. 2016. Understanding the dominant controls on litter decomposition. Journal of Ecology 104: 229-238.

Bradford MA, Veen GC, Bonis A, Bradford EM, Classen AT, Cornelissen JHC, Crowther TW, Jonathan R, Freschet GT, Kardol P. 2017. A test of the hierarchical model of litter decomposition. Nature Ecology & Evolution 1: 1836-1845.
Bray N, Kao-Kniffin J, Frey SD, Fahey T, Wickings K. 2019. Soil macroinvertebrate presence alters microbial community composition and activity in the rhizosphere. *Frontiers in Microbiology* **10**: 256.

Briones MJ. 2018. The serendipitous value of soil fauna in ecosystem functioning: the unexplained explained. *Frontiers in Environmental Science* **6**: 149.

Chang WH, Lai AG. 2018. Mixed evolutionary origins of endogenous biomass-depolymerizing enzymes in animals. *BMC Genomics* **19**: 1-10.

Chisanga K, Mbega ER, Ndakidemi PA. 2020. Prospects of using termite mound soil organic amendment for enhancing soil nutrition in Southern Africa. *Plants* **9**: 649.

Chomel M, Lavallee JM, Alvarez-Segura N, De Castro F, Rhymes JM, Caruso T, de Vries FT, Baggs EM, Emmerson MC, Bardgett RD. 2019. Drought decreases incorporation of recent plant photosynthate into soil food webs regardless of their trophic complexity. *Global Change Biology* **25**: 3549-3561.

Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoo res B, Kurokawa H, Pérez-Harguindeguy N. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**: 1065-1071.

Cragg SM, Beckham GT, Bruce NC, Bugg TD, Distel DL, Dupree P, Etxabe AG, Goodell BS, Jellison J, McGeehan JE. 2015. Lignocellulose degradation mechanisms across the Tree of Life. *Current Opinion in Chemical Biology* **29**: 108-119.

Crowther TW, Van den Hoogen J, Wan J, Mayes MA, Keiser A, Mo L, Averill C, Maynard DS. 2019. The global soil community and its influence on biogeochemistry. *Science* **365**: eaav0550.

Dangerfield J, McCarthy T, Ellery W. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* **14**: 507-520.

David J-F. 2014. The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biology and Biochemistry* **76**: 109-118.

Davies AB, Levick SR, Robertson MP, van Rensburg BJ, Asner GP, Parr CL. 2016. Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales. *Oikos* **125**: 726-734.
Davies AB, Robertson MP, Levick SR, Asner GP, van Rensburg BJ, Parr CL. 2014. Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. *Journal of vegetation science* **25**: 1405-1416.

Des Marteaux LE, Kullik SA, Habash M, Schmidt JM. 2020. Terrestrial isopods *Porcellio scaber* and *Oniscus asellus* (Crustacea: Isopoda) increase bacterial abundance and modify microbial community structure in leaf litter microcosms: a short-term decomposition study. *Microbial Ecology* **80**: 690-702.

Eisenhauer N, Vogel A, Jensen B, Scheu S. 2018. Decomposer diversity increases biomass production and shifts aboveground-belowground biomass allocation of common wheat. *Scientific reports* **8**: 1-8.

Evans TA, Dawes TZ, Ward PR, Lo N. 2011. Ants and termites increase crop yield in a dry climate. *Nature communications* **2**: 262.

Fattore S, Xiao Z, Godschalx AL, Röder G, Turlings TC, Le Bayon R-C, Rasmann S. 2020. Bioturbation by endogeic earthworms facilitates entomopathogenic nematode movement toward herbivore-damaged maize roots. *Scientific reports* **10**: 1-11.

Filser J, Faber JH, Tiunov AV, Brussaard L, Frouz J, Deyn GD, Uvarov AV, Berg MP, Lavelle P, Loreau M. 2016. Soil fauna: key to new carbon models. *SOIL* **2**: 565-582.

Fujii S, Cornelissen JH, Berg MP, Mori AS. 2018. Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. *Functional Ecology* **32**: 840-852.

García-Palacios P, Maestre FT, Kattge J, Wall DH. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters* **16**: 1045-1053.

Geisen S, Wall DH, van der Putten WH. 2019. Challenges and opportunities for soil biodiversity in the Anthropocene. *Current Biology* **29**: R1036-R1044.

Griffiths HM, Ashton LA, Evans TA, Parr CL, Eggleton P. 2019. Termites can decompose more than half of deadwood in tropical rainforest. *Current Biology* **29**: R118-R119.

Griffiths HM, Eggleton P, Hemming-Schroeder N, Swinfield T, Woon JS, Allison SD, Coomes DA, Ashton LA, Parr CL. 2021. Carbon flux and forest dynamics: Increased deadwood
decomposition in tropical rainforest tree-fall canopy gaps. Global Change Biology 27: 1601-1613.

Guerra CA, Heintz-Buschart A, Sikorski J, Chatzinotas A, Guerrero-Ramirez N, Cesarz S, Beaumelle L, Rillig MC, Maestre FT, Delgado-Baquerizo M. 2020. Blind spots in global soil biodiversity and ecosystem function research. Nature communications 11: 1-13.

Guo C, Tuo B, Ci H, Yan ER, Cornelissen JH. 2021. Dynamic feedbacks among tree functional traits, termite populations and deadwood turnover. Journal of Ecology 109: 1578-1590.

Hända IT, Aerts R, Berendse F, Berg MP, Bruder A, Butenschoen O, Chauvet E, Gessner MO, Jabiol J, Makkonen M. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509: 218-221.

Harmon ME, Fasth BG, Yatskov M, Kastendick D, Rock J, Woodall CW. 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. Carbon balance and management 15: 1-21.

Hättenschwiler S, Tiunov AV, Scheu S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology Evolution and Systematics 36: 191-218.

Ji R, Brune A. 2005. Digestion of peptidic residues in humic substances by an alkali-stable and humic-acid-tolerant proteolytic activity in the gut of soil-feeding termites. Soil Biology and Biochemistry 37: 1648-1655.

Joly F-X, Coq S, Coulis M, David J-F, Hättenschwiler S, Mueller CW, Prater I, Subke J-A. 2020. Detritivore conversion of litter into faeces accelerates organic matter turnover. Communications biology 3: 1-9.

Joly FX, Coq S, Coulis M, Nahmani J, Hättenschwiler S. 2018. Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition. Functional Ecology 32: 2605-2614.

Jones JM, Heath KD, Ferrer A, Dalling JW. 2020. Habitat-specific effects of bark on wood decomposition: Influences of fragmentation, nitrogen concentration and microbial community composition. Functional Ecology 34: 1123-1133.

Lehmann J, Kleber M. 2015. The contentious nature of soil organic matter. Nature 528: 60-68.
Li H, Yang X-R, Wang J, Zhou G-W, Zhang Y-S, Lassen SB, Zhu Y-G, Su J-Q. 2020. Earthworm gut: An overlooked niche for anaerobic ammonium oxidation in agricultural soil. *Science of the Total Environment* **752**: 141874.

Lustenhouwer N, Maynard DS, Bradford MA, Lindner DL, Oberle B, Zanne AE, Crowther TW. 2020. A trait-based understanding of wood decomposition by fungi. *Proceedings of the National Academy of Sciences* **117**: 11551-11558.

Makkonen M, Berg MP, Handa IT, Hättenschwiler S, van Ruijven J, van Bodegom PM, Aerts R. 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters* **15**: 1033-1041.

Marhan S, Scheu S. 2006. Mixing of different mineral soil layers by endogeic earthworms affects carbon and nitrogen mineralization. *Biology and Fertility of Soils* **42**: 308-314.

Ohkuma M, Noda S, Kudo T. 1999. Phylogenetic diversity of nitrogen fixation genes in the symbiotic microbial community in the gut of diverse termites. *Applied and Environmental Microbiology* **65**: 4926-4934.

Pausas JG, Bond WJ. 2020. On the Three Major Recycling Pathways in Terrestrial Ecosystems. *Trends in Ecology & Evolution* **35**: 767-775.

Scharf ME. 2015. Termites as targets and models for biotechnology. *Annual Review of Entomology* **60**: 77-102.

Scheu S. 2003. Effects of earthworms on plant growth: patterns and perspectives: The 7th international symposium on earthworm ecology· Cardiff· Wales· 2002. *Pedobiologia* **47**: 846-856.

Scrivener A, Slaytor M, Rose H. 1989. Symbiont-independent digestion of cellulose and starch in Panesthia cribrata Saussure, an Australian wood-eating cockroach. *Journal of Insect Physiology* **35**: 935-941.

Setälä H, Huhta V. 1991. Soil fauna increase Betula pendula growth: laboratory experiments with coniferous forest floor. *Ecology* **72**: 665-671.

Shelomi M, Wipfler B, Zhou X, Pauchet Y. 2020. Multifunctional cellulase enzymes are ancestral in Polyneoptera. *Insect Molecular Biology* **29**: 124-135.
Srivastava DS, Cardinale BJ, Downing AL, Duffy JE, Jouseau C, Sankaran M, Wright JP. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90: 1073-1083.

Swift MJ, Heal OW, Anderson JM, Anderson J. 1979. *Decomposition in terrestrial ecosystems*. Oxford, UK: Blackwell.

Tuma J, Fleiss S, Eggleton P, Frouz J, Klimes P, Lewis OT, Yusah KM, Fayle TM. 2019. Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation. *Applied Soil Ecology* 144: 123-133.

Van der Drift J. 1951. Analysis of the animal community in a beech forest floor. *Tijdschrift voor Entomologie* 94: 1-168.

Van Groenigen JW, Lubbers IM, Vos HM, Brown GG, De Deyn GB, Van Groenigen KJ. 2014. Earthworms increase plant production: a meta-analysis. *Scientific reports* 4: 6365.

Wall DH, Bradford MA, St John MG, Trofymow JA, Behan-Pelletier V, Bignell DE, Dangerfield JM, Parton WJ, Rusek J, Voigt W. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14: 2661-2677.

Watanabe H, Noda H, Tokuda G, Lo N. 1998. A cellulase gene of termite origin. *Nature* 394: 330-331.

Winck B, Chauvat M, Coulibaly S, Santonja M, de Sá ELS, Forey E. 2020. Functional collembolan assemblages induce different plant responses in Lolium perenne. *Plant and Soil* 452: 347-358.

Xiao Z, Wang X, Koricheva J, Kergunteuil A, Le Bayon R-C, Liu M, Hu F, Rasmann S. 2018. Earthworms affect plant growth and resistance against herbivores: A meta-analysis. *Functional Ecology* 32: 150-160.

Yang X, Li T. 2020. Effects of terrestrial isopods on soil nutrients during litter decomposition. *Geoderma* 376: 114546.

Zellweger F, De Frenne P, Lenoir J, Rocchini D, Coomes D. 2019. Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution* 34: 327-341.
Figure 1. The fate of plant matter through the decomposition process. This can be conceptualised as removing different layers of an onion. The initial stages of decomposition involve leaching and multiple organisms (microbial and invertebrate) that can digest simple compounds: carbohydrates, peptides and fats (the red layer of the onion). After this stage multiple organisms can catabolise lignocellulose (the yellow and green parts of the onion). This can be microbes alone, invertebrates alone (using endogenous cellulases, but generally not endogenous lignin-modifying enzymes), or a partnership between endogenous invertebrate cellulases and (mostly) gut symbiont cellulases (‘digestomes’). The result of these progressive decomposition processes is the creation of organic matter that becomes smaller in molecular size and is increasingly protected from further breakdown by interaction with mineral surfaces and incorporation into soil aggregates (Lehmann & Kleber, 2015 defined here as stable or protected soil organic matter; the blue part of the onion). This protected organic matter is then consumed by a range of organisms, including microbes, soil-feeding termites, and endogeic earthworms. These soil-feeding invertebrates often break down clay-complexed peptides and are thought to be important sources of plant-available nitrogen, key bioavailable parts of the nitrogen cycle (Ji & Brune, 2005).

Figure 2. The trophic effects of decomposition caused by feeding and enzymatic breakdown of dead organic material (solid lines: pathway 2) and non-trophic effects of movement and nest building (dashed lines: pathway 3) of soil invertebrates, showing the consequences for soil properties and the concomitant consequences for plants. The dotted line (pathway 1) shows the consequences that the presence of invertebrates can have on plants, but highlights that evidence of causal mechanisms, via changes in the soil environment, is often lacking. Numbers next to each process are examples of studies demonstrating each effect: 1Yang & Li (2020); 2David (2014); 3Joly et al. (2020); 4Joly et al. (2018); 5Des Marteaux et al. (2020); 6Bray et al. (2019); 7Tuma et al. (2019); 8Chisanga et al. (2020); 9Dangerfield et al. (1998); 10Ashton et al. (2019); 11Setälä & Huhta (1991); 12Xiao et al. (2018); 13Wink et al. (2020); 14Eisenhauer et al. (2018) 15Davies et al. (2014).

Box 1 Glossary
Decomposition: The process of breaking down dead organic (in this case) plant material into smaller fragments and/or molecules (Lehmann & Kleber, 2015) either by abiotic agents (e.g. photodegradation) or decomposer organisms through catabolism by microbial enzymes (most importantly cellulases) and/or invertebrate endogenous enzymes in concert with microbial symbionts.

Digestome: The whole set of enzymes found in an invertebrate gut: the endogenous enzymes, mostly produced in the mid gut and/or salivary glands, and the exogenous enzymes produced by symbionts in the hind gut (or farmed externally, in the case of fungus-growing termites). The combined digestome is the agent of invertebrate decomposition.

Endogenous cellulase: Cellulases produced by organisms within their own tissues, as opposed to exogenous cellulases, which are produced by symbionts.

Invertebrate functional classifications: There are many functional classifications of soil fauna. Here we concentrate on decomposers, defined as any group that ingests dead plant material leading to changes in physiochemical composition, contributing to a reduction in the size of fragments and/or molecules and facilitating the interaction with mineral surfaces in soil aggregates, therefore stabilising and protecting organic material from further degradation (Fig. 1). Animals that feed on animal carcasses are also decomposers and make nutrients available to plants.

Mutualistic symbionts: Organisms living with another organism each of which conferring benefits to the other. Here, we predominantly focus on the gut biota of invertebrates.

Plant chemistry and decomposability: Plants have interior cell chemicals similar to other organisms (i.e. sugars, fats and proteins, most of which are easy to metabolise by nearly all organisms). However, all plants have cell walls made of cellulose, a complex polymer which is a linear chain of several hundred to many thousands of β linked D-glucose units (Cragg et al., 2015). It is much harder to metabolise cellulose and far fewer organisms have the enzymes that can depolymerise it. The cellulose fibres are, in turn, linked by hemicellulose chemical cross linkages. In addition, many plants, especially woody plants, have a substantial amount of lignin – a cross-linked phenolic polymer, which is catabolised by relatively few organisms (all are fungi or bacteria, most efficiently by white rot fungi).
Soil biota classifications according to body size: Size is commonly used to classify soil biota, with organisms being split into microbiota (<200μm: most microbes, nematodes, protists), mesofauna (0.2-2mm width: mites, Collembola) and macrofauna (>2mm: earthworms, millipedes, centipedes, snails, woodlice, termites, beetles).

Soil fertility refers to the availability of soil nutrients and is often used in agricultural contexts (e.g. how well a particular crop grows in a soil).

Box 2 Future directions

Understanding which invertebrates have endogenous cellulases. While our knowledge is improving, there remain large gaps in our understanding of which invertebrate taxa can be considered ‘true’ decomposers (with endogenous cellulases), how ubiquitous they are, and how these properties work in partnership with symbiotic microorganisms (i.e. the digestome).

Field-based manipulations of invertebrate decomposers replicated at high spatial resolution are needed to assess their effects on vegetation decay rates with contrasting traits across a range of environments. This will fill major gaps in understanding of invertebrate contribution to the hierarchy of controls of decomposition (Hättenschwiler et al., 2005; Cornwell et al., 2008; Makkonen et al., 2012; Bradford et al., 2016; Bradford et al., 2017) and enable quantification of how small-scale heterogeneity in soil fauna, microbes and microclimate shape decay rates and biogeochemical cycling. Furthermore, rather than focussing on litter quality within the same class of substrate, manipulations using different substrate types (e.g. wood, litter, dung), will allow a more complete understanding of the role that different agents of decomposition play for different substrates. These data are essential to accurately parameterise Earth System Models incorporating real-world heterogeneity in biotic communities and ecological processes.

Deepening our understanding of the interdependent interactions between soil fauna, microbes and plants can be achieved using physical exclusion or chemical suppression experiments (García-Palacios et al., 2013; Handa et al., 2014; Bray et al., 2019) that allow access either to microbes and invertebrates, or microbes only. Crucially, these experiments must go
beyond assessing litter mass loss and also assess the concomitant impacts on soil nutrient status, physical structure, microbial communities and consequences for plant growth and survival. Fruitful avenues include using isotope tracers to follow the fate and assimilation rate of carbon and nitrogen from dead organic matter through the soil food web (e.g. David, 2014; Chomel et al., 2019) and the consequences of this for plants.

**Contributions of invertebrates to biogeochemical cycles and incorporation into Earth System Models.** Reductions in decomposer diversity (both microbes and soil invertebrates) tend to have negative effects on rates of decomposition (Srivastava et al., 2009; Handa et al., 2014). Despite this, and although incorporation of soil fauna has been shown to fundamentally affect the predictive outcome of soil organic matter models (explored in Filser et al., 2016), invertebrate contribution to decomposition is not currently incorporated into Earth System modelling. Therefore, quantifying the contribution of animal decomposers to nutrient and carbon cycling and incorporation of these data into Earth System Models is a research priority that represents a major challenge. Implementation requires a synthesis of emerging technologies and traditional field experimentation to combine: 1) remote sensing techniques, which are increasingly able to detect, map and predict land-scape scale variability in vegetation as well as microclimatic conditions at the land-air interface (Zellweger et al., 2019); 2) detailed field experiments that partition the role of invertebrates in biomass degradation, biogeochemical cycling, carbon flux and plant growth and survival. Field experiments should ideally be carried out with a high levels of spatial replication within focal ecosystems to capture biogeochemical responses to fine-scale environmental heterogeneity; 3) high-throughput DNA sequencing to provide high resolution taxonomic information on which of the soil organisms are driving soil processes and plant responses observed in field manipulations; and 4) Earth System modelling, able to process and integrate the huge volumes of data generated from these disparate research fields. This interdisciplinary approach will allow us to model and predict the consequences of interdependent changes in biotic communities and abiotic conditions for terrestrial degradation pathways and the biogeochemical cycles that underpin vegetation communities and regulate global climate.

**Distribution of decomposers in a changing world.** Anthropogenic driven distribution shifts in soil fauna are likely to change biogeochemical processing in ecosystems. Advances in molecular techniques will make mapping the relationships between changes in decomposer distributions, decomposition, carbon and nutrient cycling and plant responses more easily quantifiable, and should be a research priority. Field-based experiments that simulate anthropogenic impacts such as drought are necessary to underpin modelling efforts to understand how changes to
decomposer fauna will shift under climate change. To date there has been a focus on agricultural ecosystems and earthworms in temperate zones, but more work on other soil invertebrates in other ecosystems would provide insight into their roles in ecosystem function and how this will be altered by environmental change.
Figure 1
Tansley Insight 35032
Dead organic material
Plant-available nutrients
Formation of mineral-protected/stable organic matter
Simple carbohydrates, fats, proteins
Lignin
Increasingly stable decomposition products
Mineral-protected organic matter
Cellulose
Endogenic earthworms, soil-feeding termites and microbes
The decomposition onion
Decay strips layers off the ‘onion’, making nutrients available to plants at each stage and leaving increasingly stable/mineral-protected organic matter
Decomposer invertebrates

Trophic effects (decomposition)
- Plant available nutrients
- Input of faecal matter
- Accelerated C and N cycling
- Change in microbial community

Non-trophic effects (movement)
- Bioturbation
- Change in particle composition
- Change in soil nutrient status
- Soil moisture

Consequences for soil properties
- Survival
- Biomass
- Nutrition
- Change in resource allocation (e.g., roots vs. shoots)
- Change in community composition

Consequences for plants
- Change in soil properties

This article is protected by copyright. All rights reserved