Tansley insight

The impact of invertebrate decomposers on plants and soil

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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.

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

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(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, 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.)

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, for 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 that 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 that 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 (<200 μm: most microbes, nematodes, protists), mesofauna (0.2–2 mm width: mites, Collembola) and macrofauna (>2 mm: 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).

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.*,
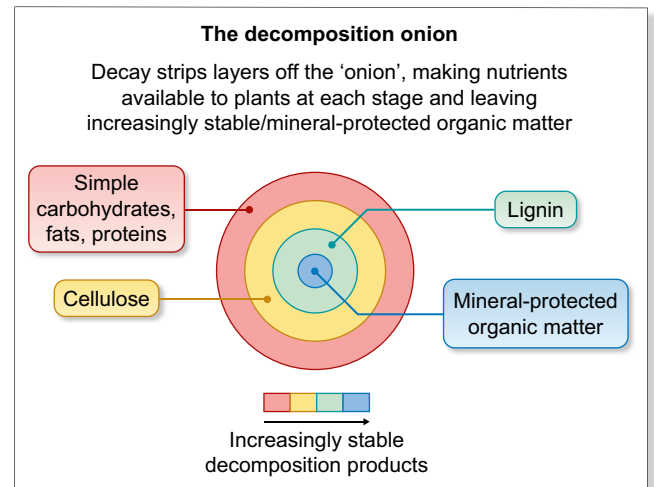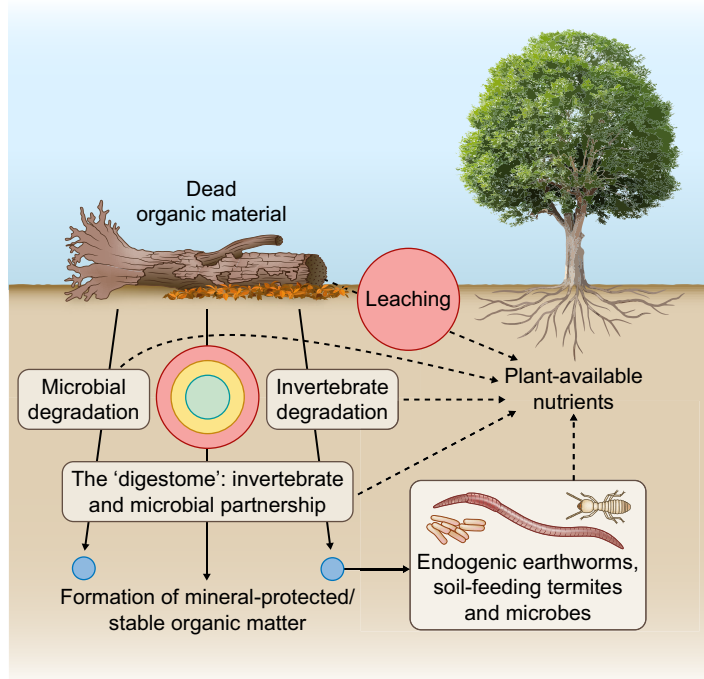
Fig. 1 The fate of plant matter through the decomposition process. This can be conceptualised as removing different layers of an onion. The initial stages of decomposition involve leaching and multiple organisms (microbial and invertebrate) that can digest simple compounds: carbohydrates, peptides and 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).

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, 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 that 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.*,
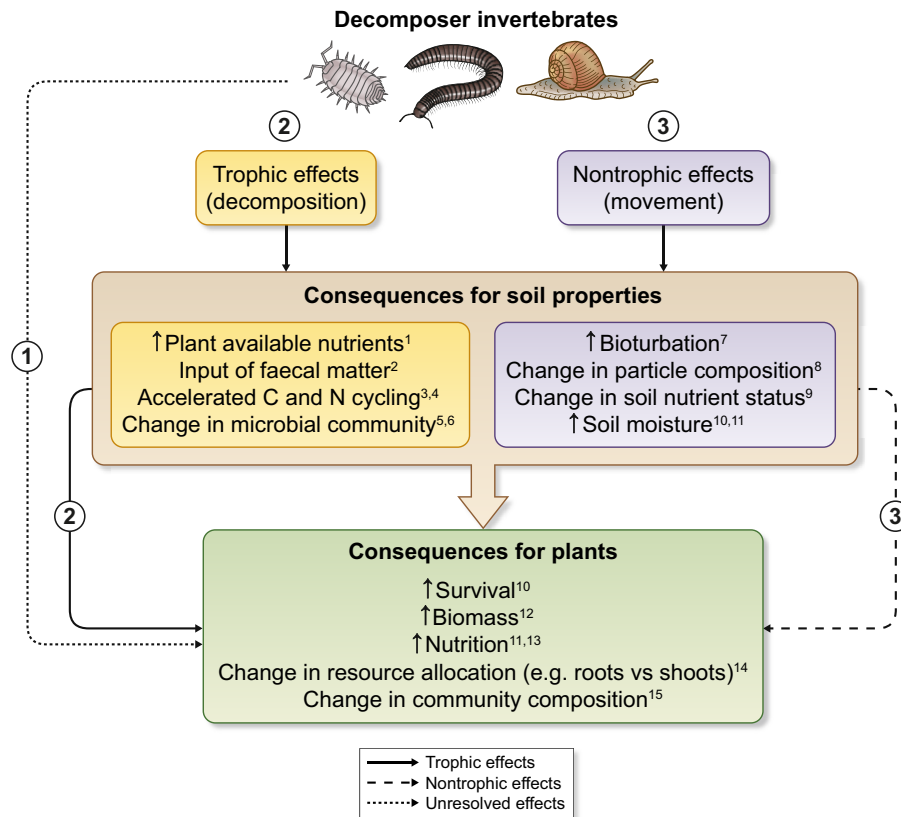
Fig. 2 The trophic effects of decomposition caused by feeding and enzymatic breakdown of dead organic material (solid lines: pathway 2) and nontrophic effects of movement and nest building (dashed lines: pathway 3) of soil invertebrates, showing the consequences for soil properties and the concomitant 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: [1]Yang & Li (2020); [2]David (2014); [3]Joly *et al*. (2020); [4]Joly *et al*. (2018); [5]Des Marteaux *et al*. (2020); [6]Bray *et al*. (2019); [7]Tuma *et al*. (2019); [8]Chisanga *et al*. (2020); [9]Dangerfield *et al*. (1998); [10]Ashton *et al*. (2019); [11]Setälä & Huhta (1991); [12]Xiao *et al*. (2018); [13]Wink *et al*. (2020); [14]Eisenhauer *et al*. (2018); [15]Davies *et al*. (2014).

2018; Griffiths *et al*., 2019, 2021; Yang & Li, 2020; 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 has 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 for example Joly *et al*., 2018; Joly *et al*., 2020; Winck *et al*., 2020); and/or via nontrophic effects resulting from movement and nest building, which alters soil structure (soil particle distribution, aeration, soil moisture status: for example Ashton *et al*., 2019; Tuma *et al*., 2019) and can in turn influence soil chemical status (Dangerfield *et al*., 1998).

Trophic and nontrophic 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, this is likely to be through increased availability of phosphate in earthworm casts and labile carbon in earthworm mucus stimulating microbial communities (Marhan & Scheu, 2006). However, studies focussing on the effect of invertebrate decomposers on plants tend to look at just one aspect of these multitrophic 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,

Box 2 Future directions.

Describing which invertebrates have endogenous cellulases is essential to understand their impacts on plans and soils. 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 landscape 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.

Fig. 2). Setälä & 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 in which soil fauna were absent. This suggests that soil fauna facilitate more efficient root nutrient uptake, possibly due to enhanced nutrient mobilisation (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 focussed 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 above-ground 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 presence of crop residue, earthworm density and the type and rate of fertilisation, 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 (Bray *et al.*, 2019; Des Marteaux *et al.*, 2020). 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.

Nontrophic 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 (Joly *et al.*, 2018; Bray *et al.*, 2019; Yang & Li, 2020); and (3) positively influence plant nutrient status, growth and survival (Setälä & Huhta, 1991; Xiao *et al.*, 2018; Ashton *et al.*, 2019), 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 siloisation 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 a 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.

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