

THE RELATIONSHIP BETWEEN PLANTS AND SOIL INVERTEBRATES - A BRIEF REVIEW

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Abstract. Following their death, plants and animals decompose into organic substances that reach the soil in different proportion. The relationships between plants and animals are complex, soil invertebrates playing an important role in soil fertility, nutrient turnover and other processes at the soil level. The decomposing organic matter in the soil provides nutrients vital for plant growth. Decomposition and nutrient cycling by soil invertebrates comprise both direct (affecting the structure and activity of microbial populations) and indirect (excreting nutrients into the soil solution) components and augment the pool of available nutrients for root up-take thus benefiting the plants. Our paper focuses on our previous experience and studies as well as on different articles published in international journals accessed from the internet. This preliminary literature study will be developed further in the future as more relevant publications are identified.

Keywords: plants, soil invertebrates, relationship.

Rezumat. Relația plante-nevertebrate din sol – o scurtă trecere în revistă. După moartea plantelor și animalelor, acestea devin substanțe organice care ajung în sol în diferite proporții. Relația între plante și animale este complexă, nevertebratele de sol având un rol important în fertilitatea solului, circuitul nutrienților și alte procese la nivelul solului. Materia organică în descompunere furnizează nutrienți vitali pentru creșterea plantelor. Descompunerea și ciclarea nutrienților de către nevertebratele de sol sunt accelerate fie direct (în raport de structura și activitatea populațiilor microbiene), fie indirect (prin excreția nutrienților în soluția solului) și determinând astfel o creștere a rezervelor de nutrienți disponibili plantelor prin preluare de către rădăcini. Lucrarea se bazează pe experiența și cercetările noastre anterioare, precum și pe consultarea unor articole publicate în reviste internaționale cu acces liber pe internet. Mai există publicații privind subiectul de studiu care vor fi analizate în viitor și astfel vom îmbunătăți cunoștințele actuale.

Cuvinte cheie: plante, nevertebrate din sol, relații.

INTRODUCTION

Biodiversity loss is the result of global changes and negatively affects ecosystem sustainability and human well-being (GOREAU et al., 2014). In the context of environmental changes, biodiversity interactions between above-ground and below-ground biota have been a major concern in recent years (XU et al., 2020). An important driver of plant community processes is the feedback between individual plants and the soil communities where they grow (VAN DER STOEL et al., 2002). The coexistence of species in the same ecological space has been already explained for some organisms (BONANOMI et al., 2005). The diversity of soil organisms is explained both by the combination of their own varied life history tactics, phenology and by the heterogeneity of soil types that enable so many species to co-exist (COLE et al., 2008). BEZEMER & VAN DAM (2005) state that there are studies suggesting a strong research and societal bias against soil (below-ground) invertebrates in favour of more “charismatic” organisms (plants, above-ground invertebrates, and vertebrates). However, even though all these groups of organisms are separated in space, they influence each other, either directly (i.e. predators living above-ground), or indirectly (i.e. the plant species from vegetation cover have changed biomass and nutritional quality). For the extraordinarily diverse community of soil organisms connected by highly complex interactions in terrestrial ecosystems, the main source of matter and energy is the input of above- and below-ground plant-litter (HÄTTENSCHWILER et al., 2005). Sometimes scientists have tried to use above-ground mechanisms for understanding multitrophic interactions of the below-ground organisms. Because of the limited mobility of most soil organisms, the interactions in the soil generally occur over much smaller spatial scales than interactions above ground (VAN DER PUTTEN et al., 2001).

For several hundred million years, plants, invertebrates and microorganisms have coevolved within soils. They have developed highly complex and intimate interactions that give high resistance and resilience to the soils, affecting soil properties and their influence on the availability of resources for other organisms (WARDLE et al., 2004; LAVELLE et al., 2006).

Plant growth depends on light, moisture and available nutrients in inorganic form, released from decomposing organic matter in soil; thus they are dependent on the rate at which mineralisation occurs in the soil (LAMBERS et al., 2008). Nutrient mineralisation is a result of the activity of soil microflora, while soil fauna populations increase nutrient release by fragmentation of litter, grazing of microflora and improvement of soil structure (REICHLE, 1977; SETALA & HUHTA, 1991; BARDGETT & CHAN, 1999). All nutrients absorbed by plants have to pass through the rhizosphere, a region of intense interactions between roots and soil organisms (microorganisms, invertebrates) (BONKOWSKI, 2004). Soil fertility depends on the different proportions of soil nutrients resulting from these processes.

At the plant level, soil invertebrates play a key role in increasing soil fertility (aiding organic substances to reach plants) and are a key factor in vegetation change. Some of the soil organisms depend on particular species of plant. Soil organisms may directly or indirectly alter plant community composition and influence plant life histories,

plant performance, growth and competitiveness (SETALA & HUHTA, 1991; BLOSSEY & HUNT-JOSHI, 2003; CIFUENTES-CROQUEVIELLE et al., 2020). Plants benefit from the activities of soil fauna increasing the pool of available nutrients for root uptake, especially in soils with limited nutrient supply (N and P) (SETALA & HUHTA, 1991; CARILLO et al., 2011).

Plant species diversity is positively correlated with invertebrate diversity and modifies local environmental conditions (light incidence, temperature, soil moisture and substrate chemical quality that becomes later incorporated as detritus) (CIFUENTES-CROQUEVIELLE et al., 2020). Soil organisms can be important drivers of vegetation changes at the local scale (KARDOL et al., 2006).

At the ecosystem level, soil invertebrates perform a wide range of functions that contribute to ecosystem health, through the maintenance of nutrient cycling, water storage and primary productivity (CIFUENTES-CROQUEVIELLE et al., 2020). During decomposition, recycling of carbon and nutrients is a fundamentally important ecosystem process that has major influences over the carbon cycle, nutrient availability and, consequently, plant growth and community structure. Soil animals can enhance decomposition and nutrient-cycling rates both directly, by excreting nutrients into the soil solution or indirectly, by affecting the structure and activity of microbial populations (SETALA & HUHTA, 1991; HÄTTENSCHWILER et al., 2005; LAMBERS et al., 2008).

In terms of human well-being, soil invertebrates are very important because they contribute to soil functions by regulating key ecosystem services: litter decomposition, nutrient cycling, plant nutrient uptake and climate regulation (i.e. CO₂ fluxes) (BASTIDA et al., 2020). Around 75% of CO₂ in soil is the result of the respiration of living plant roots together with fungi, bacteria, and soil invertebrates (GOREAU et al., 2014).

In agriculture, successful crop production requires knowledge and skill when farmers prepare the soil, selecting inputs, planting the crop, and then managing the crop from emergence to harvest. The application of basic principles of soil fertility and plant nutrition changes over time as procedural practices can then be adapted to new products, systems of crop management procedures, and plant genetics (BENTON JONES, 2012).

In the context of these themes, the purpose of this paper is to briefly review the existing scientific articles regarding the relationship between soil invertebrates and plants, and to highlight the most important studies developed on this subject.

MATERIALS AND METHODS

The present brief review focussed on highlighting the relationship between plants and soil invertebrates, and comprised a structured internet search using three main tools (Research Gate, Google Academic, E-nformation). The search used the same key words listed in this article (and its title): plants-soil invertebrate relationship, soil invertebrates. Only open-access articles were obtained and included within this preliminary review. The relationship between plants and soil invertebrates has been a core theme for the research team behind this paper and hence several papers from our own work were included in the review.

RESULTS AND DISCUSSION

As part of an analysis of temperate forest ecosystems, EDWARDS et al. (1973) published a complex chapter based on reviewing past research projects regarding the role of soil invertebrates in the turnover of organic matter and nutrients. They highlighted how soil organisms contribute to the turnover of plant organic matter to the rate of breakdown of litter, woody materials and roots (biomass of organic material that reaches the temperate forest floor) and to soil formation (Table 1).

Table 1. Soil type, organic/organisms content and the contribution of the soil invertebrates to organic matter breakdown (after EDWARDS et al., 1973).

Soil type	Organic/organisms content	Contribution of soil invertebrates
acid raw humus	plant residues with well-preserved cellular structure	increase the surface area available for bacterial and fungal action
	< animals	
	> fungi	
less acid raw humus (mor soil)	>animals (mainly collembolans and oribatid mites)	disintegrate plant and animal tissues and make them more easily invaded by microorganisms
	some plant residues with cellular structures may still be discerned	
moder soil	plant remains converted into animal faeces or other residues but some cellular structures may still be discerned	the production of humic substances has not proceeded very far; mineral matter, animal faeces and organic residues form a fairly loose mixture
	>animals (mostly mites and collembolans)	
mull humus form	No plants residues the larger arthropods and invertebrates increase in numbers	selectively decompose and chemically change parts of organic residues, transform plant residues into humic substances; ingest mineral substances with their food, and soil aggregates begin to be formed (although much of the upper soil is still only a mechanical mixture)
true mull humus	No plants residues numerous and varied fauna	soil aggregates are completely formed during passage through the intestines of animals, the humus and clay fractions have become inseparable, all plant structures have been destroyed

Soil fertility is determined by the combination of properties: physical (texture, structure, profile depth, water-holding capacity, drainage, etc.), chemical (pH, level of available essential plant elements, cation/anion exchange capacities, mineral and organic matter content, etc.) and biological (type of soil organisms, their abundance-dominance, their relationship among themselves and with plant species). A fertile soil may be defined either on the basis of its own properties, or based on plant growth, performance and yield (BENTON JONES, 2012).

The review by WOLTERS (1991) emphasised some key issues in understanding the descriptive and functional aspects of soil zoology that stem from the close interrelationships between all the components of the soil ecosystem. These issues were associated with the cryptic life of soil biota and the way such organisms are specifically adapted to the soil habitat. Different soil invertebrates influence soil processes at different spatio-temporal scales which are themselves quantified differently.

The chemical composition of plants and both soil mesofauna and macrofauna communities affects the processes of litter and soil organic matter decomposition (CARILLO et al., 2011). This study also found that the community structure in a mineral soil may determine how the chemical composition of the surface litter influences the nitrogen dynamics.

The trophic level expresses the importance of organisms in terms of either density (numbers/unit area), biomass (dry weight/unit area) (MANU et al., 2017b) or, occasionally, the energy output by the population through respiration (Table 2). Earthworms (Oligochaeta), represent the large decomposers that dominate mull soils, but in other habitats Isoptera, Isopoda or Diplopoda are more numerous, although their relative incidence may vary greatly. The total metabolic activity of soil animals is remarkably constant regardless of their body size. Nematoda are more common in mineral soils. Parasitic mites are the dominant predatory species in all types of soils. Chilopoda are large active predators in most woodland ecosystems, and spiders are more important in grasslands (EDWARDS et al., 1973).

Table 2. The invertebrate populations of soil and litter in three temperate forests: beech in Japan, oak and beech in Europe (after EDWARDS et al., 1973).

	Herbivores	Large decomposers	Small decomposers	Predators
BELOW-GROUND	Nematoda	Oligochaeta	Nematoda	Parasitic mites
		Diplopoda	Enchytraeidae	
		Isopoda	Oribatidae	
		Coleoptera larvae	Collembola	
			Diptera larvae	
ABOVE-GROUND	Coleoptera	Diplopoda	Diptera larvae	Araneae
	Diptera	Isopoda		Phalangida
	Lepidoptera	Mollusca		Chilopoda
	Mollusca			Diptera
	Hemiptera			Coleoptera

The influence of soil invertebrates upon plants. Nutrient uptake by plants takes place in the rhizosphere, which is characterised by complex interactions between roots, micro-organisms and animals. In the rhizosphere, competition for nutrients is increased. The interaction between roots, root exudates and micro-organisms can only be understood in relation to the faunal activity in the soil. Thus, soil fauna has an important function in regulating the microbial processes of rhizosphere and significantly affects plant growth (NEAGOE et al., 2014). In the rhizosphere, bacteria are strongly “top-down” regulated by protozoa and nematodes via grazing. The important impact on bacterial turnover in the rhizosphere is indicated by the high abundance, biomass and, in particular, turnover in the soil of the bacterivores (BONKOWSKI et al, 2000). The interactions between plants, bacteria and protozoan grazers in the rhizosphere have been described from a gross nutrient perspective as forming a “microbial loop in soil”: plant exudates stimulate bacterial growth; protozoa graze bacteria and release nutrients which stimulate plant growth (BONKOWSKI, 2004). Bacterivores are well known for their plant growth-promoting properties. Plant performance is strongly influenced by: a) density of fungivores, which (together with higher trophic levels) depends in large part on root-derived carbon; b) root herbivores by their influence on bottom-up and top-down control of above-ground invertebrate herbivores with important consequences for plant community composition; and c) a complexity of interactions with soil macrofauna. At higher trophic levels, predators regulate population densities of fungivores; predation being a major factor influencing the structure and function of rhizosphere bacterial community (BONKOWSKI et al, 2009).

By controlling decomposition and nutrient availability, as well as affecting root grazing and plant nutrient uptake, soil biota have very important roles in modulating primary production (DE DEYN et al., 2007; ZHANG et al., 2019). Some articles report studies that have used the microcosm to test hypotheses. SETALA & HUHTA, 1991 performed experiments in which they grew birch seedlings in enclosed microcosms containing a coniferous forest soil mixture that had been partially sterilised and subsequently inoculated with soil microbes, either with or without soil micro- and mesofauna. The results of the study demonstrated that the soil fauna has a positive impact on nutrient uptake. In addition, the net production of birch seedlings growing in microcosms simulating the coniferous forest floor increased.

Short term (<1 year in duration) studies highlight that plant species richness influences the effects of invertebrate herbivory on plant communities across a landscape. Long term studies regarding the effects on plant productivity might be quite variable and subtle and might be influenced by the inter-annual variation in rainfall patterns and temperature. Invertebrate herbivores can affect ecosystem processes under field conditions and the size of the effect might depend on the species diversity of the plant community. Above-ground biomass does not necessarily show the influence of herbivores on a plant community composition but instead on the plant functional groups in the community (STEIN et al., 2010).

In laboratory experiments, ENDLWEBER & SCHEU (2006, 2007) studied the fauna-induced changes in root architecture. They investigated the effect of collembolan on the growth and competition between *Cirsium arvense* (creeping thistle) and *Epilobium adnatum* (willow herb) and between clover (*Trifolium repens*) and the grass *Lolium perenne*. The authors hypothesised that in the presence of collembola, roots grew longer and thinner and had more root tips. Collembola did not affect total root biomass but produced changes in root morphology due to collembola-mediated changes in nutrient availability and distribution. Studies on tomato plants showed that, influenced by bacterial-feeding nematodes, they developed a highly branched root system with longer and thinner. Above- and below-ground invertebrate herbivores may facilitate root-feeding rather than decomposer nematodes driving shifts in plant species composition (DE DEYN et al., 2007).

Soil macro-invertebrates have important soil- and plant-mediated impacts on above-ground invertebrate communities, soil properties (physical, chemical, other soil biota (micro- and macro-organisms)) and plant communities (READER & SOUTHWOOD, 1981; WURST et al., 2018).

In temperate regions, the fragmentation of litter appears mainly achieved by earthworms (particularly *Lumbricus terrestris*), enchytraeid worms, diplopods, isopods, dipteran larvae, collembolans and oribatid mites. If this fragmentation is retarded experimentally, the whole process of decomposition is slowed down (EDWARDS et al., 1973). Earthworms are important in soil structure and fertility acting as vectors of the mycorrhizal fungi and ingesting mostly organic matter in decay (GANGE & BROWN., 2002). They create important regeneration niches for plant seedlings and seedling establishment by a variety of earthworm-mediated mechanisms: a) selective seed ingestion and digestion; b) acceleration or deceleration of germination; c) seed transport (droppings deposited on the soil surface and the entrances of earthworm burrows often contain viable seeds); d) spreading nutrients; and e) providing easy passage for root growth (FOREY et al., 2011; GOREAU et al., 2014). Earthworms have no direct effect on the nematode population size, but throughout their presence, root biomass is not affected by nematodes, thus increasing photosynthesis (BLOUIN et al., 2005; JOUQUET et al., 2006). Plant production increases with increased earthworm species biomass (SPAIN et al. 1992). The composition of earthworm communities (i.e. the proportional abundance of surface- vs deep-dwelling species) can strongly influence nitrogen availability and rates of nitrogen leaching in the surface soil of some grain-crop agro-ecosystems, at least in the short-term (SUBLER et al., 1997). Some researchers studied the interactive effects of soil invertebrates (i.e. earthworms *Aporrectodea caliginosa*) and summer drought upon plant communities (i.e. those containing *Hordeum vulgare*, *Capsella bursa-pastoris*, *Senecio vulgaris*), and how such effects then influenced populations of the aphid *Rhopalosiphum padi* and its parasitoid, *Aphidius ervi*. The results illustrated that reduced summer rainfall (i.e. climate change), interacts with soil decomposers affecting both plants and herbivore-parasitoid populations above ground, and producing interactions between different components of the above- and below-ground communities (JOHNSONS et al., 2011; ROBINSON et al., 2018).

FOREY et al. (2011) reviewed the importance of earthworms for the composition and structure of plant communities, finding evidence that interactions between earthworms and seeds are of primary importance for both plant community structure and earthworm performance. Indeed, interactions between earthworms and seeds are a central driver in the dynamics of soils seed banks, and thus on the development of plant communities derived from these seed-banks. This link appears to stem from co-evolutionary processes. Earthworms can also affect N mineralisation, either directly through N release from their metabolic products (faeces, urine, mucus) and dead tissues, or indirectly, through altering soil physical properties, break-up of organic material, and via their interactions with other soil biota (ARAUJO et al., 2004). Earthworm vigour and population may also be limited by nitrogen availability (TIUNOV & SCHEU, 2004). BLOUIN et al. (2005) conducted an experiment in which an 82% decrease in the production of plants was suppressed when earthworms were present. The role of earthworms is usually considered important in long-term processes such as decomposition of litter materials. It would be incorrect, however, to assume that earthworms solely affect plant growth and performance by enhanced release of nutrients (ARNONE & ZALLER, 2014). For example, humus compounds released from earthworm worked soils have been shown to exert hormone-like effects and recent studies provide convincing evidence that earthworms can induce subtle host-mediated changes that determine the vulnerability of plants to herbivore attack (BONKOWSKI et al., 2009). The diversity of below-ground herbivorous invertebrates has a positive effect on plant species diversity, plant species richness and evenness (STEIN et al., 2010). For instance, during summer drought, the total biomass of plant communities decreased by around 25% but increased by over 11% in the presence of earthworms (JOHNSON et al., 2011).

The effect of plants upon soil invertebrates. The successional development of the ecosystems and the plants species involved can themselves influence the effects of soil organisms. Thus, when model systems of plants and soils from different successional stages are investigated, the plant-soil feedbacks are: a) negative for early-successional plant

species; b) neutral for mid-successional species; and c) positive for late-successional species (KARDOLL et al., 2006; MANU & ONETE, 2013; MANU et al., 2018a; c).

SANDERSON et al. (2020) sought to determine the invertebrate diversity and composition in upland plots cut (i.e. land-use change) over five years. They employed pitfall traps and sweep nets to guarantee that invertebrates with a representative range of behavioural characteristics were sampled. They compared invertebrate abundance both within the cut vegetation plots, and along the boundaries between plots of different ages in order to assess whether there was evidence of an edge effect between habitats. The results of this study showed that vegetation cutting could be used to create a mosaic of habitats that could support both a high taxonomic diversity and abundance of invertebrates. This in turn would benefit other species within the ecosystem, notably birds.

Invasive plants represent an economic problem and threats to the conservation of natural ecosystems. The success of their invasion arises in part from escaping the depredations of their natural enemies. In some invaded ecosystems soil biota may promote 'exotic' invasion, and plant–soil feedback processes (CALLAWAY et al., 2004).

Studies regarding the impact of exotic plant invasions on soil communities and nutrient cycling processes were conducted through experiments using exotic invasive plant detritus (residues). These experiments found that plant detritus stimulates the growth of nematodes, particularly bacterial feeders. Bacteria have great ability to colonise detritus-enriched habitats. In decomposing litter, the generic diversity of nematodes was reduced (indicating that a few genera become dominant) and the nematode communities have altered (including increase in nematode abundance, the decreases in taxonomic diversity, maturity index and structure index, and the alterations of community structure). The results obtained here suggest that the invasion of an exotic plant is likely to alter ecosystem functions indirectly through exerting its effect on soil decomposer communities such as nematodes (CHEN et al., 2007).

The mechanisms involved in the expansion of exotic plant species and their influence of soil invertebrates (CALLAWAY et al., 2004; DAWSON & SCHRAMA, 2016) have been tested through comparative biogeographical experiments. Their research showed that the rapid expansion of a highly invasive plant may be linked to a switch from negative plant–soil microbial feedback in natural habitats to positive plant–soil feedbacks in invaded habitats. Invasive plants may disrupt the interactions between soil communities and the native flora, thus accelerating the success of the invasion. The litter and the rhizosphere associated with invasive plants affects different soil biota trophic groups to different degrees and/or directions, which could then reinforce the overall impact of plant invasion on the abundances/biomass of particular components of the soil communities (ZHANG et al., 2019).

ROSTÁS & HILTPOLD (2017) report new findings and concepts on grassland–invertebrate interactions in semi-natural and improved grasslands with emphasis on the effects of climate change, invasive species, and sustainable control methods of invasive pests. Their work experimentally tested several hypotheses: a) increasing soil temperature α -diversity of plants and invertebrates decreases; b) species turnover of plants and invertebrates increases; c) the mean body mass of invertebrates declines at the community- and population-levels; d) percentage cover of vegetation; and e) the total abundance and biomass of invertebrates decrease at the community-level, with variable effects at the population-level. Invertebrate species richness was not affected by increasing temperature and no significant correlation was found between temperature and any other measured environmental variables (pH, moisture, total carbon, or total nitrogen).

The growth of human population increased land use change all over the world (LI et al. 2018). Areas maintained by artificial irrigation expanded, mainly through transforming natural habitats into arable or afforested land. The assessment of soil biodiversity shows that it is affected by various land-use strategies, each representing historical land-use regimes. The researchers sampled dominant functional groups of soil biota, covering multiple trophic levels: a) macrofauna consumers (predators and insect herbivores); b) mesofauna decomposers (Oribatida and Collembola); and c) microbial decomposers (bacteria and fungi). These biota were surveyed in six distinct land uses in China with different management strategies: non-irrigated natural grasslands, scrub of *Haloxylon ammodendron* in sandy ground, plantations of *Populus gansuensis*, irrigated plantations and arable lands. The results highlighted that changes in land use eliminated or reduced the abundance of some taxa adapted to natural grasslands, and stimulated the appearance of exotic species better suited to anthropogenic habitats. Community composition shifted in all six functional groups, directly correlated with land conversion. The land-use strategies affected the diversity and structure of the below-ground communities differentially, which in turn influenced ecosystem functioning differently (MANU et al., 2018b).

A cross-biome survey that included 83 locations across six continents was conducted to increase the knowledge of both the ecological preferences and vulnerabilities of nematodes, arachnids and rotifers i.e. covering the diversity of dominant and functionally important soil invertebrate taxa (BASTIDA et al., 2020). The results of this major survey suggested that declines in forest cover and plant diversity, as well as reductions in plant productivity associated with increased aridity, can result in reductions of the diversity of soil invertebrates in a drier and more intensively managed and regulated world.

Potential for usage. Soil invertebrates might be used as bioindicators. Bioindicators are defined as taxa/functional groups which reflect the state of the environment, either: a) acting as early warning indicators of any environmental change (environmental indicator) (GERLACH et al., 2012; BRAY & WICKINGS, 2019); b) used to monitor a specific ecosystem stress (ecological indicator) (PAOLETTI et al., 1996; MANU et al., 2016; ȘTEFĂNUȚ et al., 2018); or c) to indicate the levels of taxonomic diversity at a site (biodiversity indicator) (BÁLDI, 2003; MANU et al., 2013; MANU & ONETE, 2014a; b; 2015). Bioindicators may also be used to prioritise conservation action

(assessments using spatial comparisons of site value), monitoring of ecosystem recovery, or response to management (GERLACH et al., 2013).

Anthropogenic activities (human disturbance) create qualitative and quantitative environmental changes seen in the response of soil invertebrates, plants, and, more generally, ecological communities. It is very difficult to make accurate and distinct generalisations about the response of invertebrate populations to direct and indirect environmental stresses because many variables can interact e.g. particular invertebrate species and/or the developmental stage exposed to the stress, or the particular environmental stress due to different pollutants (IORDACHE et al., 2010; MANU et al., 2015; 2017a; c; 2019), and also the physical environmental factors, which sometimes interact in complex patterns (PAOLETTI et al., 1996; COLE et al., 2008). Many past studies not only contribute to a better understanding of how land-use change affects diversity and community composition within soil food-webs but also provide ideas to landscape managers for the development of management strategies for different types of ecosystems to mitigate the negative impact of land-use change on biodiversity and ecosystem services (HOOPER et al., 2000; SPURGEON et al., 2013; ROSTÁS & HILTPOLD, 2017). Such research outputs underpin the creation and implementation of sustainable control methods for climate change and invasive species (LI et al., 2018).

In urban systems, the community structure and function of soil invertebrates (MANU et al., 2018c) have high importance under some circumstances but may also vary considerably both within and among different urban habitats (e.g. lawns, gardens, vacant lots and green roofs), and also present a challenge for assessing and predicting ecosystem services that are linked to soil invertebrates (BRAY & WICKINGS, 2019).

The ability to predict the responses of below-ground communities to environmental change based on information about plant communities might be enhanced by also studying the diversity associations of plants and soil fauna that are dependent on plant life form and are largely driven by rare taxa along an elevational gradient (XU et al., 2020).

CONCLUSIONS

This brief review revealed some of the most outstanding studies in open-access literature regarding the direct and/or indirect interactions both below-ground between soil fauna, rhizosphere microorganisms and plant roots and above-ground with other invertebrates and plant biomass, productivity and also food webs of herbivores and their predators.

It was once believed that there are “direct” feeding relationships between plant roots and herbivores, but modern research shows that the relationships are not so simple and straightforward. The connection between plants and rhizosphere fauna is far more complex than simply that of resource and consumer. The relationship between plants, their below-ground decomposers, herbivores and predator invertebrates, together with the soil microbial community is likely to be dynamic, depending on plant growth stage, the degree of herbivory and predatory and the life-cycle of the soil invertebrates. Microbial turnover, carbon transfer and nutrient recycling in soils are enhanced by the biomass of microbivores with significant feedbacks on root growth and plant performance. There is a very extensive literature on this topic as a result of numerous experiments that emphasise the importance of the interaction between plants and invertebrates. Such experimental studies are most appropriate where the approach is closely linked to working hypotheses with measurable and relevant variables.

The information found in various scientific papers might be used for: a) improving the management of nutrients availability in soils; and b) increasing crop resistance to agricultural pests (the study of natural plant defence systems has a practical application). In the light of these results, we stress that it is necessary to approach the study of rhizosphere ecology as a multidisciplinary task to improve plant breeding efforts, primary production and productivity, etc. In urban systems it is not known how altered invertebrate communities interact with soil microbiomes and affect microbial community structure and function, hence targeted investigations are required.

For a better understanding of plant-soil invertebrate relationships, it is necessary to deepen our knowledge on: I) the role and importance of soil invertebrates; II) the interactions and synergistic effects of soil populations; III) whether the effect of below-ground herbivores is driven by their preference for particular plant species or by plant abundance, etc.

Future studies should be long-term because effects can be subtle and may be influenced by inter-annual variation in temperature and rainfall patterns; they should also include more measures of ecosystem functioning and not just above-ground biomass. Information about the genes important in root-fauna communication remains very poor because of the lack of focus on this topic by scientists. The present brief review is preliminary but has identified key themes; it will be extended by the research team in the future.

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