11

Climate Change in the Underworld: Impacts for Soil-Dwelling Invertebrates

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Summary

Increasing concentrations of atmospheric CO_2 and associated changes in climate are undoubtedly impacting communities and ecosystem functioning. Despite the importance of soil ecosystem services, little is known on how these changes will affect soil-dwelling communities. In this chapter, we review and discuss the impact of elevated atmospheric CO_2 and climatic changes on three of the functionally most important invertebrate taxa in soil ecosystems: nematodes, insects, and earthworms. Elevated atmospheric CO_2 concentrations are mostly impacting these three groups indirectly (e.g., plant-mediated mechanisms), whereas climatic changes (elevated temperature and altered precipitation) are both directly and indirectly affecting soil invertebrates. Earthworms are ~~mostly~~ positively affected by elevated atmospheric CO_2 and climate change; these effects are however mostly indirect and more subtle than those observed in the other two taxa discussed. Chemical ecology underpins biotic interactions belowground. Plant secondary metabolites patterns and their diffusion in soil are influenced by climate change; therefore belowground chemical interactions are likely to be influenced too. Soil ~~ecosystems~~ are at high risk and better comprehending the effect of the rapid changes occurring will help to protect these highly complex ecosystems.

11.1 Introduction

Climate fluctuations have occurred over millions of years and have shaped ecosystems throughout this period. The greenhouse gases carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) concentrations have increased of 40%, 150%, and 20%, respectively, from 1970 to 2010 (IPCC, 2013b). The combined average temperature of the atmosphere and oceans is increasing together with changes in both the amount and patterns of precipitation (IPCC, 2013b). The rapid pace of the recent changes is alarming and likely to have serious impacts on ecosystems and biological communities therein (Newman et al., 2011).

Most contemporary research on climate change has focused on aboveground communities to the comparative neglect of belowground ecosystems. This is paradoxical since soils are at high risk with, for example, ca. 11 ha of arable soil sealed (e.g., concreted or paved upon) every hour in Europe (FAO, 2015; Wall ~~et al.~~, 2015). It is therefore essential to take up the challenge and assess the impact

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of climate change on soil communities before irremediable damage is done to the wealth of ecological services that soils confer.

The effects of climate and atmospheric CO_2 change (from here on, climate change encompasses atmospheric changes and variations in CO_2, warming and altered precipitations) on soil abiotic conditions vary and numerous biotic feedbacks occur. For example, elevated atmospheric CO_2 concentrations (eCO_2) decrease plant stomatal conductance and consequently increase soil moisture (Cowan ~~et al.~~, 1977), whereas higher temperatures reduce soil moisture by increasing plant evapotranspiration (Norby ~~et al.~~, 2004; Dermody et al., 2007). These variations in soil abiotic conditions arising from climate change are likely to shape soil invertebrate communities (e.g., Blankinship et al., 2011; Newman et al., 2011; Lang et al., 2014; García-Palacios et al., 2015; Nielsen ~~et al.~~, 2015a), which will have impacts at a global scale (Lavelle et al., 1997).

11.1.1 Soil Community Responses to Climate Change

The response of a diverse group of organisms, such as soil invertebrates, to eCO_2 cannot be easily generalised and will vary for different members of the community. For example, in a greenhouse experiment, earthworm biomass was ca. 50% greater at 700 ppm than a 350 ppm $CO_{2,}$ whereas eCO_2 treatment reduced some nematode communities (Yeates et al., 1997). In the field, eCO_2 did not affect the abundance of invertebrate grazers (i.e., nematodes, mites and springtails) but large omnivorous and predacious nematodes were fewer, possibly because of the changes in the soil structure and particularly in the aggregate and pore sizes (Yeates et al., 2002; Niklaus et al., 2003).

Similarly, the consequences of warming and altered precipitation on soil invertebrates are also highly variable, though changes in precipitation patterns are likely to have the strongest effect on the abundance of soil biota (Blankinship et al., 2011) since arthropods are highly dependent on soil moisture (e.g., Chikoski et al., 2006; Kardol et al., 2011; Sylvain et al., 2014; Williams et al., 2014). The response of invertebrate communities appears to be largely idiosyncratic (Blankinship et al., 2011). Yet, there is evidence that taxonomy, ecosystem type and the direction of the environmental change are determinant factors that influence the response of soil-dwelling invertebrates to climate change. The response of soil biota to climate change may also depend on the body size of the organisms as well as on their trophic or functional grouping (Blankinship et al., 2011; A'Bear et al., 2014). In addition, as suggested by the trophic dynamic theory (Lindeman, 1942), trophic levels differ in limitations and thus climate and atmospheric change affect them differently. Moreover, the consequences of climate change at any trophic level will have cascading effects up and down the food web (e.g., Scheu, 2002; Xiao et al., 2005; Lang et al., 2014).

11.1.2 Scope of the Chapter

In this chapter we discuss in further detail the impact of eCO_2, warming and altered precipitation on three broad taxonomic and functional groups mentioned in a community context above: (1) nematodes, (2) insects, and (3) earthworms. These groups represent major components of the soil ecosystem. Nematodes are the most abundant soil invertebrates, represent several trophic groups (i.e., fungivores, bacterivores, herbivores and predators) and play an essential role in C and nutrient cycling (Yeates et al., 2009a). Many soil-dwelling insects are herbivores and devastate crops, which impact human societies through yield decreases (Johnson & Murray, 2008); therefore an understanding of how climate change will affect their pest status is essential. Some insects are like earthworms in that they too are ecosystem engineers (Jones et al., 1994) and provide ecosystem services, and might be used in climate change adaptation (Johnson et al., 2015). As ecosystem engineers, earthworms are pivotal in belowground processes such as bioturbation and the incorporation of organic matter to the mineral fraction of soil. Mitigating the impact of climatic changes on this group is therefore likely to be essential to ensure a sustainable use of soils as a natural resource. In closing, we discuss aspects of belowground ecology in the context of climate change.

11.2 Effect of Climate Change on Nematodes, Omnipresent Soil Invertebrates

Nematodes are ubiquitous in soils and the most numerous multicellular soil-dwelling animals in most ecosystems (Fierer et al., 2009). They represent at least five distinct trophic groups and a multitude of feeding guilds. Plant parasitic nematodes and microbial grazers, however, typically dominate soil nematode communities (Nielsen ~~et al.~~, 2004; Nielsen et al., 2014). The plant parasites affect carbon (C) and nutrient cycling directly by feeding on root biomass, and they can have substantial negative impacts on plant biomass production in both natural and managed ecosystems, including agriculture and horticulture. Microbial grazers stimulate the turnover of microbial biomass and moderate microbial activities, which in turn influence ecosystem processes including decomposition, mineralization and nutrient cycling. Other nematode trophic groups, including omnivores and predators, similarly influence C and nutrient cycling, but their impacts occur mostly indirectly through predation or control of plant pathogens. The true extent of the roles of nematodes in ecosystem functioning is not well quantified (Bardgett et al., 1999; Hunt ~~et al.~~, 2002; Nielsen et al., 2015b), but given their known impacts on ecosystems, soil nematode community responses to climate change may have far-reaching effects.

In this section we discuss the observed and potential soil nematode community responses to climate change (Fig. 11.1) and how this might influence ecosystem functioning more broadly. Evidence from field surveys indicates that nematode community composition is strongly related to climate suggesting that predicted changes in temperature and precipitation might have substantial long-term effects (Nielsen et al., 2014). There is less evidence to suggest that eCO_2 should influence soil nematode communities directly but indirect effects may theoretically be expected. These observations are now being supported by in situ climate change manipulations, and we provide an overview of the observed effects under field conditions. We focus first on the effects of eCO_2, which is expected to influence nematode communities mostly mediated by vegetation responses (Nielsen et al., 2015), and then discuss the effects of altered precipitation regimes and increased temperatures (warming) as these two global change drivers are likely to have the strongest direct impact on soil nematode communities. It is worth noting that the realized effects of climate change will be moderated by interactions between eCO_2, warming, and altered precipitation regimes as these rarely change in isolation. Yet, very few studies have investigated the interactive effects of these global change drivers on soil nematode communities. Potential broader impacts of soil nematode community responses to climate change on ecosystems are briefly discussed at the end of the section.

11.2.1 Nematode Responses to eCO_2

Carbon dioxide concentrations are much higher in soil than in the atmosphere, and therefore, eCO_2 is unlikely to substantially influence soil nematode communities directly. However, indirect effects are likely to occur due to changes in root exudates and litter input associated with altered vegetation structure and composition (Nielsen et al., 2015b). For instance, C:N ratio in plant tissue has been shown to increase under eCO_2 (Pendall et al., 2004b; Milchunas et al., 2005), which may influence their quality as a food source for belowground herbivores including plant parasitic nematodes with

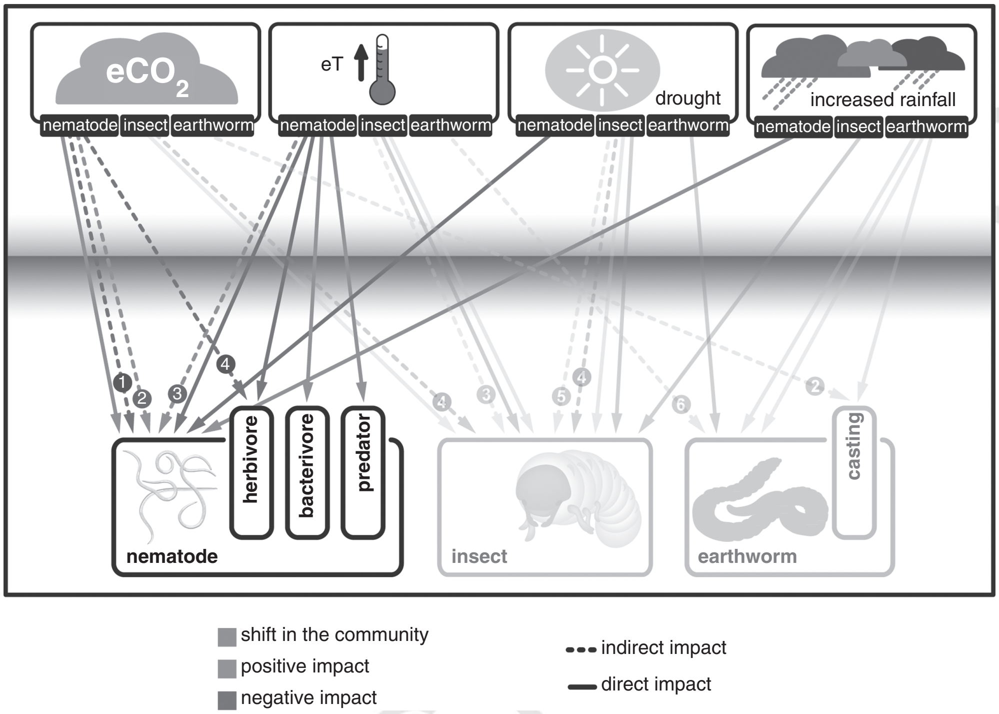


Figure 11.1 Direct and indirect effect of climate change on nematodes. The solid arrows indicate direct effects, while dashed arrows indicate indirect effects. Blue arrows represent shift in the community whereas green arrows indicate a positive impact and red arrows a negative impact on the community. Indirect effects are mediate by (1) changes in the soil structure, (2) increased soil moisture resulting from lower stomatal conductance, (3) shifts in the plant community, (4) a reduction of plant quality (often reflected by higher C:N ratio), and (5) decreased population of predators and/or parasitoids, and (6) a higher N rhizodeposition. Details and references in the text. (Drawings: I. Hiltpold, WSU, Australia)

cascading impacts on the soil food web more broadly. Along the same lines, Frederiksen et al. (2001) found that wheat litter grown under eCO$_2$ showed reduced decomposition rates and supported lower abundances of bacterial grazers including nematodes in situ indicating indirect effects of eCO$_2$ on ecosystem processes. Moreover, eCO$_2$ has been shown to enhance fine root growth and distribution (e.g., Rogers et al., 1996; Curtis ~~et al.~~, 1998; Pendall et al., 2004a; Prior et al., 2012; Madhu ~~et al.~~, 2013; Pacholski et al., 2015). Root architecture plays a role in the ability of entomopathogenic nematodes to find and infect insect hosts in the rhizosphere (Demarta et al., 2014). Indeed, entomopathogenic nematodes appeared to be more infectious in the presence of root systems or structure mimicking root systems (Ennis et al., 2010; Demarta et al., 2014), but increased root complexity results in a lower infectiousness of entomopathogenic nematodes (Demarta et al., 2014). In this context, eCO$_2$ can potentially lessen successful implementation of entomopathogenic nematodes in pest control strategies. More broadly, it is often observed that eCO$_2$ reduces evapotranspiration with cascading effects on soil moisture, which could benefit nematode communities as these are limited by soil moisture availability at least in some ecosystem types. Furthermore, there is some evidence that suggests that eCO$_2$ may influence soil aggregation, which might in turn influence nematode communities through a reduction in soil pore neck diameters (Niklaus et al., 2003).

A recent meta-analysis by A'Bear et al. (2014) found an overall negative effect of eCO_2 on nematode abundances except for plant parasitic nematodes. However, plant parasitic nematodes may still respond to eCO_2. For instance, a study investigating the effects of eCO_2 at three grassland sites found no effect on total abundance of plant parasites, but the abundance of Anguinidae increased at one site and Hoplolaimidae decreased at another (Ayres et al., 2008) indicating changes in community structure. In another study, eCO_2 increased the abundance of the plant parasitic Trichodoridae and reduced the abundance of bacterial feeding Rhabditidae in low nitrogen (N) soil, whereas the abundance of predators/omnivores increased in high N soil due to an increase in Dorylaimida and the abundance of bacterial feeding Cephalobidae decreased (Hoeksema et al., 2000). Hence, it is clear that eCO_2 can influence both nematode abundances and community composition although some studies have found limited effects (Allen et al., 2005; Ayres et al., 2008; Eisenhauer et al., 2013). However, ecosystem level implications of these changes are not well established.

11.2.2 Nematode Responses to Warming

Nematodes are likely to respond to warming through both direct and indirect effects. Most regions are predicted to become warmer under future climates (IPCC, 2013b). While soil temperatures will be buffered to some degree compared to surface air temperatures, even moderate increases in soil temperatures are likely to enhance nematode activity and metabolic rates, and through this reproduction, provided that other environmental variables such as soil moisture are not limiting. Moreover, indirect effects are likely through shifts in plant community composition, microbial biomass and composition, and edaphic variables including potential increased stress associated with decreased soil moisture under elevated temperature (e.g., Nielsen et al., 2015b). However, the number of studies reporting the effects of warming on soil nematode communities is still surprisingly limited and results are often idiosyncratic. For instance, two years of increased soil temperature (+1.7°C and +3.4°C) had no effect on total or trophic group abundances in a temperate-boreal forest ecotone, although there was an increase in microbial feeders relative to plant parasites (Thakur et al., 2014) suggesting an overall shift in community composition. By contrast, 1°C soil warming in a heath was found to reduce the abundance of nematodes including root herbivores and interestingly there was shift towards longer-lived species perhaps due to longer growing seasons (Stevnbak et al., 2012). Similarly, in a subarctic heath and a fell field, summer warming was shown to influence nematode community structure with an observed increase in abundance of *Aphelenchoides* and *Filenchus*, both species with rapid life cycles and high fecundity, whereas the abundance of species with slower reproductive cycles, specifically *Eudorylaimus* and *Teratocephalus*, decreased (Ruess et al., 1999). Finally, warming has been observed to influence soil nematode community composition at least in some vegetation types and bare soil in temperate semiarid ecosystems (Bakonyi et al., 2007) as well as nematode diversity in maize fields (Dong et al., 2013). Collectively, these results suggest that warming can have strong effects on soil nematode community composition even when total nematode abundance is not affected.

A couple of meta-analyses aimed to synthesize the effects of warming on soil nematode communities. One of the first meta-analyses of studies that investigated belowground effects of climate change suggested that increased temperature consistently increase nematode abundances (Blankinship et al., 2011), but this was not confirmed by a more recent meta-analysis (A'Bear et al., 2014). The latter paper found no strong directional effect of increased temperature on total nematode abundance, but instead showed that plant parasitic nematodes respond negatively, and fungal feeding and predatory nematodes respond positively, to increased temperatures (A'Bear et al., 2014). Such divergent trophic level responses to warming indicate whole soil food web level responses to warming and suggest broader impacts on ecosystem functioning. However, it is clear that responses are context dependent and further research is required to establish general patterns and to further our understanding of potential feedbacks of warming driven nematode community responses to the ecosystem.

11.2.3 Nematode Responses to Altered Precipitation Regimes

Soil nematodes are effectively aquatic animals that rely on water films for movement and feeding (Vandegehuchte et al., 2015). Thus, any climate change that influences soil moisture availability is likely to affect soil nematode communities. Water is a limiting resource in many ecosystems and increased precipitation is theoretically expected to have a positive effect on soil nematodes. By extension, reduced precipitation could be expected to have negative effects on soil nematodes, whereas the effects of changes in seasonality or event size and frequency are more difficult to predict (Nielsen ~~et al.~~, 2015~~a~~). Most field studies investigating the effect of altered precipitation regimes to date have focused on increased or reduced precipitation, the latter often in terms of a drought event, while very few studies have manipulated event size and frequency.

The effect of altered precipitation regimes has been summarized in two meta-analyses. The earlier meta-analysis found no consistent effect of reduced precipitation on soil nematode abundances (Blankinship et al., 2011), but given new data a more recent paper found that drought significantly reduces the abundance of plant parasites and bacterial feeders (A'Bear et al., 2014). For instance, summer drought imposed for eight years in a heath negatively affected nematode abundances and all other decomposer biota measured (Stevnbak et al., 2012). These results suggested a substantial reduction in C flow through the decomposer community, which in turn indicate significant ecosystem responses to summer drought. Also, reduced precipitation has been found to influence soil nematode community composition with more pronounced effects in bare soils than under poplar, and no effects in fescue grassland and a temperate semi-arid shrubland (Bakonyi et al., 2007). Another study found that nematode families responded differentially to a one-year imposed drought in pine woodland with Plectidae being highly sensitive to drought conditions whereas drought had no effect on Cephalobidae and Qudsianematidae (Landesman et al., 2011). Hence, there may be taxonomically specific responses to reduced precipitation and responses are often context-dependent (Sylvain et al., 2014; Vandegehuchte et al., 2015). In particular, nematode communities in dryland soils appear to be very robust to altered precipitation regimes with limited observed responses to reduced precipitation (Vandegehuchte et al., 2015), at least in the short term. The capacity of nematodes to tolerate reduced precipitation in dryland ecosystems is likely due to their adaptation to already low soil moistures, and their capacity to enter stress tolerant life stages such as anhydrobiosis (Nielsen ~~et al.~~, 2015~~a~~). However, longer-term exposure to reduced precipitation may have stronger effects.

The meta-analysis by A'Bear et al. (2014) further showed that increased precipitation has a strong positive effect on soil nematode abundances, although these results are based on a relatively small number of studies (n=7). For instance, irrigation to simulate a 100% increase in precipitation had a strong positive effect on nematode abundances in a pineland after a years manipulation (Landesman et al., 2011), and another study, that investigated the effect of rainfall event size (2 mm versus 25 mm weekly), eCO_2, and warming in an artificial grassland community, showed that the effect of increased soil moisture availability was much greater than that of eCO_2 or warming (Kardol et al., 2010). However, increased water availability has been observed to have no effect on total and trophic group abundances in desert ecosystems (Darby et al., 2011; Sylvain et al., 2014), although increased abundance of plant parasites (Freckman et al., 1987; Vandegehuchte et al., 2015) and reduced abundances (Sylvain et al., 2014) have been observed elsewhere. Studies investigating belowground effects of changes in precipitation are increasing; however, more research is needed to establish general patterns, and the effects of changes in event size and frequency need to be considered more explicitly (Nielsen et al., 2015a).

It is worth noting here that while rainfall is predicted to increase in some areas around the world, these increases are often predicted to be accompanied by warmer temperatures that may cause increased evapotranspiration and therefore no net increase in soil moisture (IPCC, 2013a). This interaction between precipitation regime and warming is crucial in understanding climate change effects. Moreover, changes in precipitation may also interact with other global change drivers. For instance, a recent study found that increased precipitation had a slight positive effect on total nematode densities in a temperate forest but when N was added to simulate increased N deposition, a strong negative effect was observed (Sun et al., 2013). Finally, even though relatively small effects of altered precipitation regimes are observed in trophic or total nematode abundances in some studies there may be ecologically relevant shifts in community composition. This is illustrated by recent findings that suggest that functional guild abundances are more sensitive to climate changes than trophic groups and therefore a better indication of potential shifts in food web structure and ecosystem functioning (Cesarz et al., 2015). It is therefore important that responses are quantified at appropriate taxonomic levels.

11.2.4 Ecosystem Level Effects of Nematode Responses to Climate Change

As discussed above, there is strong evidence that soil nematode communities show climate change responses that are moderated by ecosystem characteristics such as vegetation type and nutrient levels (Smolik et al., 1983; Klironomos et al., 1996; Niklaus et al., 2003). However, we need more experimental data to build a robust framework to make generalizations, particularly if we want to understand potential feedbacks on ecosystem functioning. This is very important given the substantial impact trophic groups such as plant parasites might have on plant productivity. For instance, Yeates et al. (2009b) found that nine years of eCO_2 substantially increased the abundance of a dominant plant parasite in a grazed pasture (*Longidorus elongatus* increased 3.48-fold) and a follow-up pot experiment indicated that eCO_2 could result in increased belowground root herbivory by nematodes. This, in turn, could have cascading effects on the soil food web more broadly by inducing plant chemical responses. Similarly, *Phleum pratense* and *Poa pratensis* showed greater reduction in root biomass due to the plant parasite *Pratylenchus penetrans* when grown at eCO_2 (650 ppm) compared with plants grown at 350 ppm (Wilsey, 2001), indicating that global changes may moderate belowground interactions between plants and herbivorous nematodes. While such data are very insightful there is a need for more in-depth studies on how useful nematode communities are as bioindicators of ecosystem state and food web complexity, and to more accurately measure how great a role they play in C and nutrient cycling. In particular, developing new techniques that can assess the degree to which the activity of soil nematodes moderate microbial activity and functioning would be insightful in understanding ecosystem functioning and potential responses to global changes.

11.3 Effect of Climate Change on Insect Root Herbivores: the Grazers of the Dark

Soil-dwelling insects that feed on roots are usually the juvenile stages of insects that live aboveground as adults (Brown et al., 1990). These soil invertebrates can reach astonishing densities, with root-feeding cicadas of deciduous forests of North America having the largest collective biomass per unit area of any terrestrial animal (Karban, 1980). While the agricultural importance of root-feeding

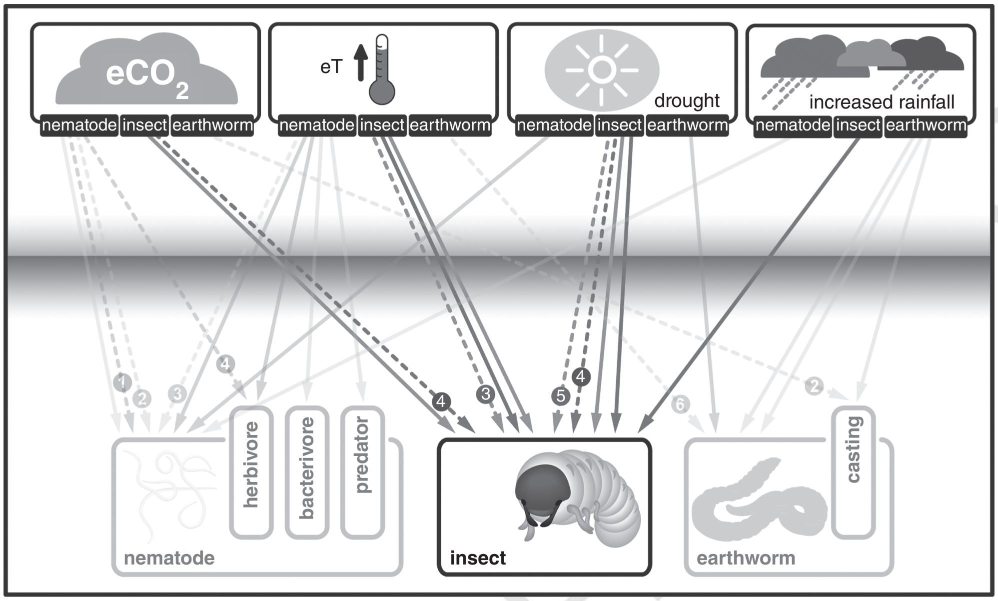


Figure 11.2 Direct and indirect effect of climate change on insects. The solid arrows indicate direct effects, while dashed arrows indicate indirect effects. Blue arrows represent shift in the community whereas green arrows indicate a positive impact and red arrows a negative impact on the community. See Figure 11.2 for nature of the indirect effects. Details and references in the text.

insects has long been known (Blackshaw ~~et al.~~, 2008), it is increasingly recognised that they also affect numerous above- (Johnson et al., 2012a; Soler et al., 2012; Johnson et al., 2013a) and belowground organisms (Johnson ~~et al.~~, 2015b). Root-feeding insects therefore represent important components of many ecosystems, and while far less is understood about how climate change affects this trophic group than their aboveground counterparts (Fig. 11.2), research in the field is undoubtedly increasing (Staley ~~et al.~~, 2008; McKenzie et al., 2013).

11.3.1 Insect Root Herbivore Responses to eCO$_2$

To our knowledge, CO$_2$ is the only greenhouse gas to be investigated in the context of its impact on root-feeding insects (Staley ~~et al.~~, 2008). Moreover, changes in CO$_2$ are likely to affect root-herbivores purely via indirect (e.g., plant-mediated, Fig. 11.2) mechanisms since, like nematodes and earthworms, they are already exposed to much higher concentrations in the rhizosphere than is the case aboveground (Payne ~~et al.~~, 1988). While the effects of eCO$_2$ on aboveground insect herbivores are relatively well studied, and several reviews and meta-analyses are now available (e.g., Stiling ~~et al.~~, 2007; DeLucia et al., 2012; Robinson et al., 2012; Zavala et al., 2013), studies involving root herbivores are scarce, by comparison, and seem to reach contrasting conclusions.

In an early study, Salt et al. (1996) reported that eCO$_2$ had no effect on the root-feeding aphid, *Pemphigus populi-transversus*, despite increasing root biomass in aphid-free plants. eCO$_2$ often increases root biomass relative to shoot mass (Rogers et al., 1994; Rogers et al., 1996) and also leads to more branched root systems that are generally shallower (Gregory, 2006). Staley ~~et al.~~ (2008) speculated that this increase in root biomass and architecture could promote the performance of some root herbivores, but it was more likely to affect root chewing herbivores that are limited by the quantity rather than quality of their host roots. Indeed, root quality might be anticipated to decrease in response to eCO_2; a meta-analysis of over 100 studies reported that while both C and N increased in both roots and shoots, C increased far more than N leading to an average increase in C:N ratios of 11%, effectively reducing nitrogen concentrations in both roots and shoots (Luo et al., 2006), either by dilution or reallocation (DeLucia et al., 2012). Given the importance of N in insect herbivore diets (Mattson, 1980), we might reasonably assume this would negatively affect root herbivores. There is recent evidence for this, with the body mass of root-feeding Argentine scarab (*Sericesthis nigrolineata*) decreasing by 24% under eCO_2, despite consuming 118% more root tissue when feeding on the grass *Microlaena stipoides* (Johnson et al., 2014a). Compensatory feeding by folivores is a common response to increased C:N in the foliage of plants grown under eCO_2 (Stiling ~~et al~~., 2007; DeLucia et al., 2012), so it seems probable that such tactics might be employed belowground too. Like folivores, which typically fail to redress this deterioration in host plant quality (Stiling ~~et al.~~, 2007), it seems that the *S. nigrolineata* could not maintain performance levels even with compensatory feeding (Johnson et al., 2014a). Interestingly, when *S. nigrolineata* fed on a C_4 grass, *Cymbopogon refractus*, its performance was typically lower than when feeding on *M. stipoides*, but performance did not decline further under eCO_2. This was likely due to the fact that the C:N ratio in root tissue did not increase under eCO_2 (Johnson et al., 2014a). Unchanged C:N ratios in C_4 plants grown under eCO_2 is often reported (Wand et al., 1999) because Rubisco, the initial enzyme facilitating CO_2 assimilation into carbohydrates, operates close to its maximum capacity at ambient atmospheric concentration of CO_2 (aCO_2), so C_4 plants have less capacity to respond to eCO_2 than C_3 plants (Ainsworth et al. 2004; DeLucia et al., 2012). Hence, belowground responses to eCO_2 will be moderated by plant species functional type.

Secondary metabolites in shoots are frequently altered in response to eCO_2, and this too can affect herbivores aboveground (Ode et al., 2014). While it usually follows that eCO_2-induced increases in plant secondary metabolite concentrations diminish herbivore performance (Zavala et al., 2013; Ode et al., 2014), this may not always be the case for root herbivores which appear to respond quite differently to plant defences expressed belowground (Johnson et al., 2016). For instance, vine weevils (*Otiorhynchus sulcatus*) feeding on blackcurrant grown under eCO_2 performed much worse (33% and 23% declines in abundance and body mass, respectively) than when feeding on plants grown at aCO_2 concentrations. Plants had 16% lower root growth under eCO_2 and this most likely drove this decline in herbivore performance but, surprisingly, root phenolic compounds were positively correlated with abundance and body mass. Vine weevils induced increases in root phenolic compounds under aCO_2 concentrations but not at eCO_2 (Johnson et al., 2011).

While there is a general trend for host plant quality for herbivores to decline under eCO_2 (Robinson ~~et al.~~, 1996; Stiling ~~et al~~., 2007; Ode et al., 2014), this isn't necessarily true for all plant taxa. In particular, leguminous plants will often increase rates of root nodulation (Ryle et al., 1992) and biological nitrogen fixation under eCO_2 (Soussana ~~et al.~~, 1996), which is accomplished via their association with nitrogen fixing bacteria. While this increase in ~~nitrogen~~ availability can promote populations of shoot herbivores, especially aphids (Guo et al., 2013; Guo et al., 2014; Johnson et al., 2014b; Ryalls et al., 2015), it has also been shown to affect root herbivores (Johnson ~~et al.~~, 2010). In particular, the clover root weevil (*Sitona lepidus*) were 38% more abundant under eCO_2, which the authors linked to the doubling in root nodules in white clover (*Trifolium repens*) under these conditions (Johnson ~~et al.~~, 2010). The larvae of *S. lepidus* are particularly dependent on root nodules (Gerard, 2001) and it appears that the increased abundance of root nodules under eCO_2 promoted weevil populations. Warmer air temperatures, which are anticipated to increase in tandem with eCO_2, tend to have opposite effects on nodulation in legumes because higher temperatures are inhibitory to many ~~nitrogen~~ fixing bacteria (Zahran, 1999). In a study combining eCO_2 and air temperature, root nodulation in lucerne (*Medicago sativa*) increased and decreased, respectively, under these treatments. Emergence success of *S. lineatus* was positively correlated with these patterns of nodulation, so eCO_2 promoted emergence whereas elevated temperatures diminished it (Ryalls et al., 2013). Further studies, preferably those involving multiple environmental changes, are clearly needed before we can determine any patterns in root herbivore responses to atmospheric change.

11.3.2 Insect Root Herbivore Responses to Warming

The soil is buffered, to some extent, from fluctuating temperatures and so soil dwelling invertebrates might be affected less by predicted rises in air temperature than those living aboveground (Bale et al., 2002). However, many root herbivores are affected by soil temperature (see Barnett ~~et al.,~~ 2013 for a full account), and especially those feeding close to the soil surface. Leatherjacket larvae (Tipulidae) represent shallow feeders and reciprocal soil core transfer experiments using these insects showed that warmer temperatures increased rates of development such as time to pupation (Coulson et al., 1976). Using historical records, it was shown that UK spring (specifically May) temperatures were highly correlated with emergence of Tipulids and for every 1°C increase, Tipulids would emerge, on average, 7 days earlier (Pearce-Higgins et al., 2005). Tipulid emergence was predicted to advance by 12 days by 2100 (Pearce-Higgins et al., 2005), which could affect the numerous bird species that depend on them to feed their young (see Thomas et al., this volume). The carrot root fly (*Delia radicum*) is another root herbivore to receive attention in respect to global warming; simulation models predict that an increase of 3°C in soil temperatures would advance and prolong emergence in Spring and create a larger third generation in late summer. A 5°C increase in soil temperature would even result in a fourth generation in southern UK (Collier et al., 1991).

In addition to these direct effects, rising temperatures are likely to impact root herbivores via plant-mediated mechanisms (Staley ~~et al.~~, 2008; Barnett ~~et al.~~, 2013). Plants respond in extraordinarily diverse ways to increased temperatures, which cannot be easily summarised or generalised. Extrapolating from the meta-analysis of Zvereva et al. (2006), which focuses on *foliar* responses to elevated temperature and eCO_2, we might anticipate a general decline in root quality for herbivores. When elevated temperature and CO_2 acted in tandem, elevated temperature negated the eCO_2 induced increase in leaf carbohydrates, but amplified decreases in leaf N, causing the leaf C:N ratio to increase overall (Zvereva et al., 2006). Decreases in root quality can trigger compensatory feeding in root herbivores (Johnson et al., 2014a), and given that warmer temperatures directly accelerate insect metabolism we could see sharp increases in rates of root herbivory and damage in the future.

11.3.3 Insect Root Herbivore Responses to Altered Precipitation

Altered patterns of precipitation are highly likely to affect root-feeding insects since soil moisture is amongst the most important abiotic factors affecting their physiology and behaviour (Barnett ~~et al.,~~ 2013; Erb ~~et al.,~~ 2013b). Numerous studies characterise how water availability affects root-feeding insects, and several reviews cover this in some depth (Brown ~~et al.,~~ 1990; Villani ~~et al.,~~ 1990; Barnett ~~et al.,~~ 2013; Erb et al., 2013a). In this section, we therefore focus primarily on extended periods of drought, since climate change models predict this will occur more frequently in many parts of the world.

Dry conditions usually affect soil-dwelling herbivores adversely because they often possess permeable cuticles that make them prone to desiccation (Brown ~~et al.,~~ 1990). Indeed, there are several examples of rainfall manipulation experiments that link reduced precipitation to population decline (see Staley ~~et al.~~, 2008 for details). Despite this, many soil-dwelling insects have evolved physiological and behavioural strategies for coping with decreased water availability (Barnett ~~et al.~~, 2013). Physiological adaptations include the production of metabolic water, a by-product of the oxidative catabolism of fats and carbohydrates (Wharton, 1985) and the formation of physical spiracle plastrons and hydrofugic hairs for water retention (Villani et al., 1999). Behavioural adaptations are probably more effective and at the simplest level include movement down the soil profile from dry regions to damper soils (Villani ~~et al.~~, 1990). In other cases, root-feeding scarabs manipulate the microclimate by constructing earthen chambers in which they encase themselves, allowing them to endure periods of drought (Villani et al., 1999). In contrast, seasonal declines in rainfall can benefit some root-feeding insects. African black beetle (*Heteronychus arator*) populations, for instance, are often supressed by early summer rainfall (Matthiessen ~~et al.~~, 1991), because first instar larvae cope badly with high soil moistures (King et al., 1981). In periods of seasonal drought, the larval populations are no longer suppressed by the normally high moisture content, resulting in damaging outbreaks (Matthiessen ~~et al.~~, 1991).

In addition to the direct impacts of water availability on root-feeding insects, plant-mediated effects are likely to be very important (Barnett ~~et al.~~, 2013; Erb ~~et al.~~, 2013b). Generally speaking, periods of drought decrease growth and nutritional quality of the roots (Erb et al., 2013a) and there is evidence for it increasing concentrations of root defensive compounds too (Zhang et al., 2008). It might reasonably be expected that many root herbivores will be adversely affected via such plant-mediated impacts. While periods of drought might adversely affect root herbivores via bottom-up (i.e., plant-mediated) drivers, they could benefit from less effective top-down (i.e., natural enemies) control. Preisser ~~et al.~~ (2004), for instance, showed that lupine ghost moth (*Hepialus californicus*) larvae escaped control by entomopathogenic nematodes under dry conditions, which resulted in population outbreaks of the moth. Seasonal shifts in rainfall, or increased frequency of extreme events, could therefore cause temporal mismatches in such predator–prey cycles simply because nematodes are so sensitive to prevailing soil water conditions.

11.3.4 Soil-Dwelling Insects as Modifiers of Climate Change Effects

The plant-mediated effects of environmental change on invertebrates is well represented in the literature, but the effects of invertebrates on plant responses to environmental change, has received relatively little attention. Two groups of soil-dwelling insect, in particular, have the capacity to modify how plants respond to climatic and atmospheric change: herbivores and detritivores.

Root herbivores have a distinctive ecology that makes them particularly damaging to plants (Zvereva et al., 2012; Johnson et al., 2016). Root herbivores can: (i) decrease nutrient and water uptake, (ii) cause disproportionate resource losses by severing roots, (iii) divert assimilates below-ground for root re-growth and (iv) impair photosynthesis by imposing water deficits (Johnson ~~et al.~~, 2008; Zvereva et al., 2012). Plant biomass of C_3 plants is predicted to increase by 10–20% under eCO_2 and C_4 plants by 0–10% (Newman et al., 2011), yet this crucially depends on plants increasing rates of photosynthesis to accomplish this growth. While some foliar chewing herbivores stimulate rates of photosynthesis (Nykänen ~~et al.~~, 2004), presumably as the plant attempts compensatory growth to tolerate attack, root herbivory has the exact opposite effect causing significant declines of around 12% (Zvereva et al., 2012). So while any kind of herbivory has the potential to reduce the positive effects of eCO_2, it seems that soil-dwelling herbivores have the capacity to completely negate these effects. Indeed, this is exactly what happened when root herbivores attacked a brassica (*Cardamine pratensis*) (Salt et al., 1996) and seedling eucalypts (Johnson ~~et al.~~, 2013b). In both cases, plant growth was restrained and plants grown under eCO_2 had similar biomass to those grown under aCO_2. Legumes possibly cope better and root herbivory did not diminish the fertilising impacts of eCO_2 (Johnson ~~et al.~~, 2010; Ryalls et al., 2013).

In contrast, soil-dwelling detritivores such as dung beetles may mitigate the negative impacts of environmental change. In addition to consuming animal faeces, dung beetles disperse and incorporate it into the soil via burrowing activities. Most recently, dung beetles have been shown to mitigate the effects of simulated drought on plants by increasing soil permeability to water and reducing surface runoff (Johnson et al., 2016). Considered as ecosystem engineers, those species of dung beetle that build networks of tunnels in the soil beneath the dung pad (the paracoprids) are most likely to be beneficial in this respect (Johnson et al., 2015a), and field trials in Southern Australia showed that dung beetles improved pasture productivity for up to a decade due, in large part, to improved access to water (Doube et al., 2014). Moreover, Doube et al. (2014) make a convincing argument that dung beetles promote carbon sequestration, so these invertebrates may reduce atmospheric change (and therefore its impact) directly, at least as much as other carbon sequestration measures (e.g., conservation tillage).

11.4 Effect of Climate Change on Earthworms, the Crawling Engineers of Soil

In 1881, Charles Darwin wrote: “It may be doubted whether there are many other animals which have played so important part of the history of the world, as these lowly organized creatures [earthworms].” (Darwin, 1881). This quotation embraces the importance of these ecosystem engineers in our contemporary natural and agro-ecosystems. Indeed, these ubiquitous soil invertebrates incessantly burrow galleries, mix organic and mineral matter, and produce casts. Earthworms are essential to the formation of humic matter, are key players in nutrient cycling, alter soil hydrology and drainage, or still affect plant population dynamic and community composition (i.e., dissemination of seeds) (Lal, 1991; Thompson et al., 1993; Jones et al., 1994). In addition to modifying soil structure (Shipitalo et al., 2004; Amossé et al., 2015), earthworms impact biota composition and soil processes (Edwards et al., 1996; Eisenhauer, 2010; Blouin et al., 2013). Because they are a crucial component of soil fertility and promote agricultural productivity (van Groenigen et al., 2014), understanding the effect of climate change on earthworms will help to ensure food security. Yet, knowledge on the impact of climate change on earthworm communities is still very scarce (Fig. 11.3).

11.4.1 Earthworm Responses to eCO_2

Few studies report the effects of eCO_2 on earthworm density, biomass, or diversity. Milcu et al. (2011) observed an increased earthworm biomass of *Lumbricus terrestris* in microcosms with high plant diversity (eight species) under eCO_2, probably due to higher N rhizodeposition. Conversely, Chevallier et al. (2006) did not record any effect of eCO_2 on earthworm biomass (*Lumbriscus rubellus* and *Aporrectodea caliginosa*) in grazed pastures in New Zealand. The effect of eCO_2 on earthworm fitness, especially on cocoon production, incubation and hatching, are neglected (Butt et al., 1992). Earthworms may even contribute modestly to global warming (Lubbers et al., 2013); while being widely beneficial, they also increase soil CO_2 emissions by 33% through aerobic respiration and N_2O emission by 37% via their intestinal bacteria, as compared to emissions from soil where they are absent (Lubbers et al., 2013).

Moving in the soil matrix, mixing, ingesting and excreting soil and organic matter particles (bioturbation), earthworms create biogenic structures such as burrows and casts (Lavelle et al., 1997). These newly formed habitats are enriched in organic matter and nutrients and act as hotspots of biological activity (Fonte et al., 2007; Le Bayon et al., 2009; Chapuis-Lardy et al., 2011). On a pasture in

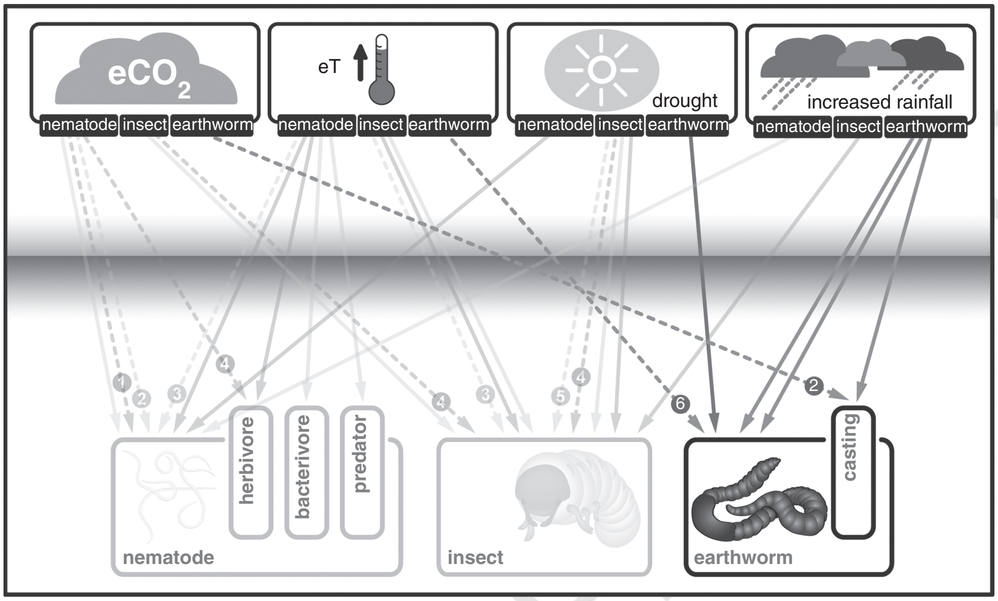


Figure 11.3 Direct and indirect effect of climate change on earthworms. The solid arrows indicate direct effects, while dashed arrows indicate indirect effects. Blue arrows represent shift in the community whereas green arrows indicate a positive impact and red arrows a negative impact on the community. See Figure 11.2 for nature of the indirect effects. Details and references in the text.

Switzerland, annual production of earthworm surface-casts was 35% greater under eCO$_2$ (610 μl l^{-1}) due to a 10% increase in soil moisture (Arnone ~~et al.~~, 1997). In a second study, the stimulatory effect of eCO$_2$ on cast production was not observed when plant species diversity decreased from 31 to 12 and five species (Arnone et al., 2013). Conversely, Chevallier et al. (2006) did not detect any direct effect of eCO$_2$ on earthworm (*L. rubellus* and *A. caliginosa*) casting in a grazed pasture in New Zealand. However, cast available N was lower under eCO$_2$ suggesting that N concentrations in casts reflect N cycle processes (Chevallier et al., 2006). This impact of earthworms on nutrient biogeochemical cycles in a context of climate change is reinforced in a review by Blouin et al. (2013) which highlighted the crucial role of earthworms in C sequestration both in their burrow linings and in casts.

The variable distribution of organic matter patchiness in soil determines how earthworms influence plant response to nutrient heterogeneity. Thus, under eCO$_2$, lower shoot and root biomass of *Lolium perenne* were found in heterogeneous *vs.* homogeneous treatments when epigeic earthworms (*Eisenia foetida*) were present (Garcia-Palacios et al., 2014). The authors suggested that earthworms foraging from patches of *L. perenne* shoots stimulate microbial N mobilization thus decreasing N availability for plants. Under eCO$_2$, earthworms may therefore mediate plant biomass responses to nutrient patchiness by affecting N capture (Garcia-Palacios et al., 2014).

As reviewed by Norby et al. (2001), eCO$_2$ influence on litter quality is not yet entirely clarified and several experimental artefacts render a general interpretation of the refereed literature difficult. Because of resorption of nutrients to perennial tissues during senescence, the decline in leaf litter N concentration under eCO$_2$ is lower than N concentration measured in green leaves of plants grown in the similar atmospheric conditions. This may suggest that indirect effect of eCO$_2$ would be greater on soil herbivores, consuming live tissues, than on decomposers, such as earthworms, consuming mainly senescent material.

11.4.2 Earthworm Responses to Warming and Altered Precipitations

Hackenberger ~~et al.~~ (2014) demonstrated that earthworm species composition, the ratio of ecological categories (epigeics, endogeics and anecics) and juvenile:adult ratio changed along a transect of varying climate types and elevations. This suggests that temperature influences the species composition of communities, possibly impacting the ecosystem services provided by these same communities. As earthworm populations are regulated in a density-dependent manner, inter- and intra-specific interactions may strongly affect species response and thereby structure and functioning of lumbricid communities (Uvarov, 2009) with further consequence on soil processes.

Zaller ~~et al.~~ (1999b) noticed that elevated rainfall increased earthworm density, and consequently casting activities. However, they did not record any impact on aboveground net primary production (ANPP) of graminoids. Conversely, the same authors further demonstrated that increasing earthworm activities stimulates shoot growth (Zaller ~~et al.~~, 1999a) and enhances ANPP (Zaller et al., 2013). To unravel these conflicting results, the authors conducted a third experiment focussing on earthworms' impact on plant roots (Arnone ~~et al.,~~ 2014). At low earthworms density (37 individuals m^{-2}), plants produced more deep roots to compensate for lower nutrient availability in shallow soils resulting from reduced casting activities. Whereas at high earthworm densities (114 and 169 individuals m^{-2}), large amounts of casts and greater nutrient availability compensated for physical disruption of roots by worms and induced a shift in the higher carbon allocation toward ANPP (Arnone ~~et al.,~~ 2014). These successive studies underlined the essential and integrative role of earthworms on plant communities' aboveground *vs.* belowground biomass allocation under climate change, possibly impacting other functional and trophic groups in the ecosystem in addition to agricultural yield. Earthworm bioturbation activity depends on both soil temperature (Whalen et al., 2004) and moisture (Edwards ~~et al.,~~ 1996), and are therefore likely to influenced by climate change.

11.4.3 Climate Change Modification of Earthworm–Plant–Microbe Interactions

Because earthworms impact soil seed banks (Forey et al., 2011), mainly by dispersing and feeding on seeds (Eisenhauer et al., 2010), changes in their community composition or behaviour caused by climate change will probably affect plant communities. Indeed, earthworms play a role in seed transport and translocation into deep soil layers, acceleration or deceleration of seed germination and seedling establishment. Eisenhauer et al. (2010) found that the selective ingestion of seeds depends on several variables: earthworm body size, species specific habits and mode of digestion (e.g., depending on gut enzyme activities and gizzard contraction) (Eisenhauer et al., 2010). Plants that are highly reliant on earthworms for propagation will either benefit or suffer from climate change impact on these organisms, depending on the direction of the effect. eCO_2 ~~impacts~~ the quality of plants (C:N ratio) (Korner, 2000), as well as starch storage, lignin concentrations (Coûteaux ~~et al.,~~ 2000), and in allocation of photosynthates within the plant (Young, 1998). This effect on plants in turn results in an increased consumption of litter by earthworms to compensate for N (Coûteaux et al., 1991). Root biomass either increases (Zaller et al., 2013) or remains stable (Eisenhauer et al., 2009) in the presence of earthworms, therefore, disentangling the effects of climate change in this particular context is challenging.

An increasing number of studies focus on the ~~impact~~ of climate change on earthworm and soil microbe interactions (Zirbes et al., 2012). Niklaus et al. (2003) showed that soil microbial communities are not affected by eCO_2 while Cesarz et al. (2015) highlight that the decomposer community may switch from a bacterial-dominated to a fungal-dominated system at eCO_2, indicating shifts in the microbial community as well as the functional structure of belowground food-webs. Earthworms have a dramatic impact on microorganism communities and therefore on the ecological services provided by soil microbes. For instance, *A. caliginosa* mucus enhanced the mineralization and humification of plant residues through the activation of microorganisms (Bityutskii et al., 2012). Earthworms and mycorrhizal fungi, especially arbuscular (AMF), are commonly co-occurring and interacting. These interactions depend on earthworm and plant species and are, generally speaking, beneficial for soil ecosystems as they result in increased soil aggregate stability (Kohler-Milleret et al., 2013), dispersal of non-pathogenic fungal spores and increased AMF colonization of plant roots by 140% (Zaller et al., 2013; Trouvé et al., 2014). Earthworms may also moderate plant performance by disrupting the interactions between plants and their AMF symbionts (Grabmaier et al., 2014). For instance, anecic earthworms (i.e., *L. terrestris*) reduced seedling emergence and diversity in the presence of AMF (*Glomus* sp.) indicating that their feeding reduced the effect of AMF on the seeds and seedlings (Zaller et al., 2011).

These interactions are species-specific and/or context dependent and general patterns are hard to draw but it has to be emphasised that climate change may dramatically modify these systems with unpredictable consequences at the ecosystem level.

11.4.4 Influence of Climate Change on Earthworms in Belowground Food Webs

In the context of belowground multitrophic interactions, several studies focus on tritrophic interactions in the presence of earthworms. Earthworms increase the incorporation of plant residues deep in the soil, which generally stimulate microbial activity but could also cause changes in the microbial communities that induce plant defences (Coûteaux et al., 1991; Wurst, 2010). However, earthworms with disparate life history traits may differ in their effects on aboveground herbivore performance, with impacts mediated by plant responses, while earthworms and root herbivores interact either directly, over the trophic web, or indirectly through the plants or changes in soil characteristics (Wurst, 2010). Regarding root-feeding nematodes, earthworms have a direct trophic effect (digestion) or indirect effects through the modification of soil properties (structure, water regime, nutrient cycling) (Yeates, 1981). Thus earthworms counteract the negative effects of root-feeding nematodes on plant performance (Blouin et al., 2005; Lohmann et al., 2009; Wurst, 2010). However, these effects depend on the community composition (Wurst, 2010) that inevitably may vary under climatic changes. There is increasing evidence that earthworms also play a role in the dispersion of beneficial entomopathogenic nematodes (Poinar ~~et al.~~, 1975; Shapiro et al., 1993; Shapiro et al., 1995; Campos-Herrera et al., 2006; Shapiro-Ilan ~~et al.~~, 2013). Whether climate change will have an impact on such interactions (and the dependent trophic cascades) remains unknown but it is likely that any impact of climate on earthworm behaviour will cascade to upper and lower levels of the complex soil food webs.

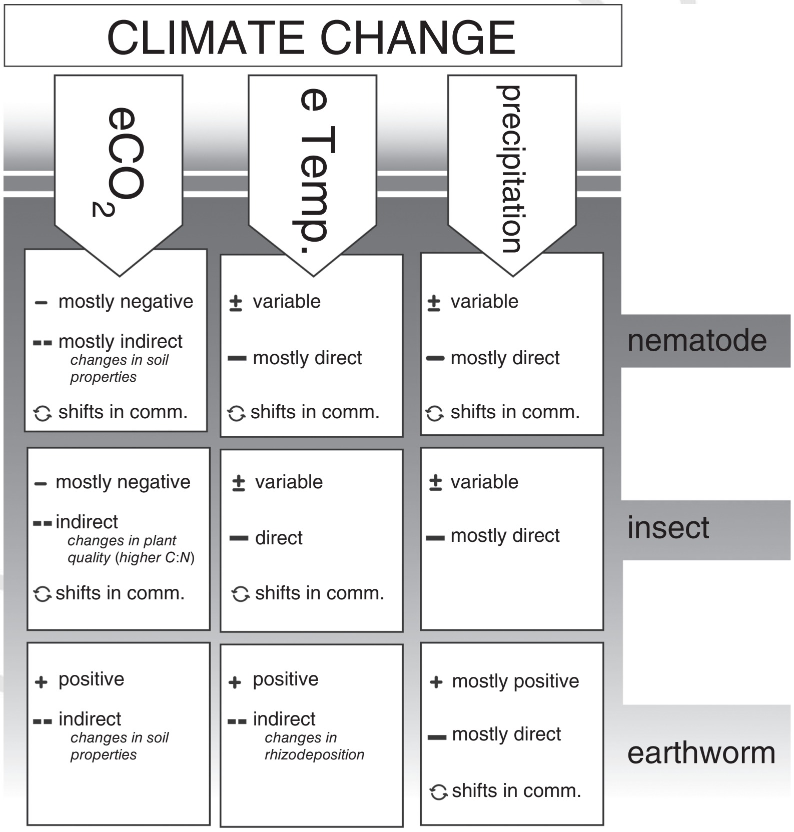
11.4.5 Influence of Climate Change on Earthworm Colonization of New Habitats

Climate change induces migration of species, and earthworms ~~are important~~ invasive species with severe above- and belowground consequences on native ecosystems. As revealed by Uvarov (2009), in regions rich in native earthworm communities (i.e., Australia, New Zealand), the invasion of peregrine earthworms may largely impact the functioning of natural and agroecosystems (Baker et al., 2006). In areas devoid of earthworms, lumbricid invasions may cause substantial changes in ecosystem structure and functioning (Frelich et al., 2006) with important implications for climate change. Suárez et al. (2006) found that the invasions follow a successional sequence (epigeic then anecic and finally endogeic species) and that the activities of the previous group facilitated the habitat exploration by the following ~~group~~. Changes in plant communities may also be induced by earthworm invasive species as vectors of seeds (Forey et al., 2011). In ~~n~~orth America, Frelich ~~et al.~~ (2010) highlighted the role of exotic earthworms as drivers of "savannification" of the forest through increasing soil bulk density, decreasing N availability and removing the organic layer, thus inhibiting the establishment of tree seedlings. In addition to such shifts in plant communities, the extended range expansion of macro-detritivores, including earthworms (*L. rubellus*) into subarctic environments, will probably result in a positive ecosystem feedback mechanism for climate change via increased CO_2 release in the atmosphere (van Geffen et al., 2011).

11.5 Conclusions and Future Perspectives

Climate change impacts on soil invertebrate communities are mostly idiosyncratic although some general patterns can be hypothesised (sections 11.2-11.4 and Table 11.1). Because several effects of climate change on soil-dwelling invertebrate communities are indirect, often mediated by plants,

Table 11.1 Summary of the Impact of Climate Change on Nematodes, Insects and Earthworms.



CLIMATE CHANGE

	eCO_2	e Temp.	precipitation
nematode	– mostly negative -- mostly indirect *changes in soil properties* ⟳ shifts in comm.	± variable ▬ mostly direct ⟳ shifts in comm.	± variable ▬ mostly direct ⟳ shifts in comm.
insect	– mostly negative -- indirect *changes in plant quality (higher C:N)* ⟳ shifts in comm.	± variable ▬ direct ⟳ shifts in comm.	± variable ▬ mostly direct
earthworm	+ positive -- indirect *changes in soil properties*	+ positive -- indirect *changes in rhizodeposition*	+ mostly positive ▬ mostly direct ⟳ shifts in comm.

it is very difficult to encompass the consequences on soil invertebrate communities, and cascading effects on soil processes and ecological services. We have identified gaps in our current knowledge on the effect of climate change on soil invertebrate communities. Experimental time scale needs further attention given that most studies to date are relatively short-term. Such studies may be well equipped to elucidate the potential effects of extreme events such heavy rainfall, high temperatures or drought, but are unlikely to realistically reflect responses to longer-term impacts such as altered precipitation regimes, increased temperature or eCO_2. This is illustrated in studies that collect samples across years. For instance, Sonnemann ~~et al.~~ (2005) found that root hair feeding nematodes showed a strong response to moderate increases in atmospheric CO_2 after one year but this effect was not apparent in the second or third years, whereas predators were suppressed by eCO_2 in the first year and enhanced in the second. Consequently, different conclusions will often be made depending on the length of the study. There is a great need for studies that evaluate both short- and long-term responses to climate change drivers.

In addition, very few studies have experimentally investigated the effects of changes in precipitation, increased temperatures and eCO_2 simultaneously. This is not surprising given logistical constraints and substantial variability in climate change scenarios between regions and even between models. However, climate change drivers are unlikely to change in isolation and their interactions need to be considered to understand belowground community responses in detail. Moreover, the effect of climate change will be moderated by other global change drivers such as land use and N deposition further complicating the matter. On a positive note, there is evidence that an increasing number of studies are addressing this issue.

Chemical ecology plays a particularly important role in soil invertebrate trophic interactions since the soil environment precludes other sensory mechanisms (i.e., visual and acoustic cues, e.g., Rasmann et al., 2012b; Hiltpold et al., 2013); yet, to date this field of research is mostly neglected in the context of climate change. Insect root herbivores use plant secondary metabolites to identify and locate palatable root systems (e.g., Johnson ~~et al.~~, 2006; Johnson ~~et al.~~, 2012b; Hiltpold et al., 2013). Plant parasitic nematodes also rely on root exudates to find hosts (Ali et al., 2011; Rasmann et al., 2012a) and entomopathogenic nematodes exploit volatiles emitted by insect damaged roots to locate their host (Boff et al., 2002; Rasmann et al., 2005; Ali et al., 2010; Hiltpold et al., 2010; Hiltpold et al., 2011; Rasmann et al., 2011; Laznik ~~et al.~~, 2013). The impact of root exudates in soil food webs highly depends on the concentration of the released metabolites (e.g., Hiltpold et al., 2015) and changes in exudate quality and quantity at eCO_2 (e.g., Tarnawski ~~et al.~~, 2006) will possibly severely impact invertebrate communities (e.g., Drigo et al., 2010). Changes in abiotic factors such as temperature, soil moisture, and rainfall patterns will also interfere with plant chemical signalling. Indeed, Hiltpold ~~et al.~~ (2008) showed a negative correlation between soil moisture and the diffusion of root volatiles in the ground. Despite this example, the impact of climate change on belowground chemical ecology has so far been largely overlooked.

Filling these gaps in our knowledge is likely to be the next boundary to expand and will provide us with a more holistic comprehension of the impact of climate change on belowground invertebrate communities and soil ecosystem services.

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References

A'Bear, A.D., Jones, T.H. & Boddy, L. (2014) Potential impacts of climate change on interactions among saprotrophic cord-forming fungal mycelia and grazing soil invertebrates. *Fungal Ecology*, **10**, 34–43.

Ainsworth, E.A., Rogers, A., Nelson, R. & Long, S.P. (2004) Testing the "source–sink" hypothesis of down-regulation of photosynthesis in elevated [CO_2] in the field with single gene substitutions in *Glycine max*. *Agricultural and Forest Meteorology*, **122**, 85–94.

Ali, J.G., Alborn, H.T. & Stelinski, L.L. (2010) Subterranean herbivore-induced volatiles released by citrus roots upon feeding by *Diaprepes abbreviatus* recruit entomopathogenic nematodes. *Journal Of Chemical Ecology*, **36**, 361–368.

Ali, J.G., Alborn, H.T. & Stelinski, L.L. (2011) Constitutive and induced subterranean plant volatiles attract both entomopathogenic and plant parasitic nematodes. *Journal of Ecology*, **99**, 26–35.

Allen, M.F., Klironomos, J.N., Treseder, K.K. & Oechel, A.W.C. (2005) Responses of soil biota to elevated CO_2 in a chaparral ecosystem. *Ecological Applications*, **15**, 1701–1711.

Amossé, J., Le Bayon, R.-C. & Gobat, J.M. (2015) Are urban soils similar to natural soils of river valleys? *Journal of Soils and Sediments*, **15**, 1716–1724.

Arnone, J.A.I. & Zaller, J.G. (1997) Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO_2. *Oecologia*, **111**, 249–254.

Arnone, J.A.I. & Zaller, J.G. (2014) Earthworm effects on native grassland root system dynamics under natural and increased rainfall. *Frontiers in Plant Science*, **5**, 152.

Arnone, J.A.I., Zaller, J.G., Hofer, G., Schmid, B. & Körner, C. (2013) Loss of plant biodiversity eliminates stimulatory effect of elevated CO_2 on earthworm activity in grasslands. *Oecologia*, **171**, 613–622.

Ayres, E., Wall, D.H., Simmons, B.L., Field, C.B., Milchunas, D.G., Morgan, J.A. & Roy, J. (2008) Belowground nematode herbivores are resistant to elevated atmospheric CO_2 concentrations in grassland ecosystems. *Soil Biology and Biochemistry*, **40**, 978–985.

Baker, G.H., Brown, G., Butt, K., Curry, J.P. & Scullion, J. (2006) Introduced earthworms in agricultural and reclaimed land: their ecology and influences on soil properties, plant production and other soil biota. *Biological Invasions*, **8**, 1301–1316.

Bakonyi, G., Nagy, P., Kovács-Láng, E., Kovács, E., Barabás, S., Répási, V. & Seres, A. (2007) Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. *Applied Soil Ecology*, **37**, 31–40.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.

Bardgett, R.D., Denton, C.S. & Cook, R. (1999) Below-ground herbivory promotes soil nutrient transfer and root growth in grassland. *Ecology Letters*, **2**, 357–360.

Barnett, K. & Johnson, S.N. (2013) Living in the Soil Matrix: Abiotic Factors Affecting Root Herbivores. *Advances in Insect Physiology*, **45** (eds S.N. Johnson, I. Hiltpold & T.C.J. Turlings), pp. 1–52. Academic Press, Oxford, UK.

Bityutskii, N.P., Maiorov, E.I. & Orlova, N.E. (2012) The priming effects induced by earthworm mucus on mineralization and humification of plant residues. *European Journal of Soil Biology*, **50**, 1–6.

Blackshaw, R.P. & Kerry, B.R. (2008) Root herbivory in agricultural ecosystems. *Root Feeders – an ecosystem perspective* (eds S.N. Johnson & P.J. Murray), pp. 35–53. CABI, Wallingford, UK.

Blankinship, J.C., Niklaus, P.A. & Hungate, B.A. (2011) A meta-analysis of responses of soil biota to global change. *Oecologia*, **165**, 553–565.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D. & Brun, J.-J. (2013) A review of earthworm impact on soil function and ecosystem services. *European Journal of Soil Science*, **64**, 161–182.

Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.-T., Laffray, D., Reversat, G., Pando, A., Tondoh, J. & Lavelle, P. (2005) Belowground organism activities affect plant aboveground phenotype, inducing plant tolerance to parasites. *Ecology Letters*, **8**, 202–208.

Boff, M.I.C., van Tol, R.H.W.M. & Smits, P.H. (2002) Behavioural response of *Heterorhabditis megidis* towards plant roots and insect larvae. *Biocontrol*, **47**, 67–83.

Brown, V.K. & Gange, A.C. (1990) Insect herbivory below ground. *Advances in Ecological Research*, **20**, 1–58.

Butt, K.R., Frederickson, J. & Morris, R.M. (1992) The intensive production of *Lumbricus terrestris* L. for soil amelioration. *Soil Biology & Biochemistry*, **24**, 1321–1325.

Campos-Herrera, R., Trigo, D. & Gutiérrez, C. (2006) Phoresy of the entomopathogenic nematode *Steinernema feltiae* by the earthworm *Eisenia fetida*. *Journal Of Invertebrate Pathology*, **92**, 50–54.

Cesarz, S., Reich, P.B., Scheu, S., Ruess, L., Schaefer, M. & Eisenhauer, N. (2015) Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors. *Pedobiologia*, **58**, 23–32.

Chapuis-Lardy, L., Le Bayon, R.-C., Brossard, M., López-Hernández, D. & Blanchart, E. (2011) Role of Soil Macrofauna in Phosphorus Cycling. *Phosphorus in Action*, **26** (eds E. Bünemann, A. Oberson & E. Frossard), pp. 199–213. Springer, Berlin Heidelberg.

Chevallier, A.J.T., Lieffering, M., Carran, R.A. & Newton, P.C.D. (2006) Mineral nitrogen cycling through earthworm casts in a grazed pasture under elevated atmospheric CO_2. *Global Change Biology*, **12**, 56–60.

Chikoski, J.M., Ferguson, S.H. & Meyer, L. (2006) Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment. *Acta Oecologica*, **30**, 203–211.

Collier, R.H., Finch, S., Phelps, K. & Thompson, A.R. (1991) Possible impact of global warming on cabbage root fly (*Delia radicum*) activity in the UK. *Annals of Applied Biology*, **118**, 261–271.

Coulson, J.C., Horobin, J.C., Butterfield, J. & Smith, G.R.J. (1976) Maintenance of annual life-cycles in two species of *Tipulidae* (Diptera): field study relating development, temperature and altitude. *Journal of Animal Ecology*, **45**, 215–233.

Coûteaux, M.-M. & Bolger, T. (2000) Interactions between atmospheric CO_2 enrichment and soil fauna. *Plant And Soil*, **224**, 123–134.

Coûteaux, M.-M., Mousseau, M., Célérier, M.-L. & Bottner, P. (1991) Increased atmospheric CO_2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos*, **61**, 54–64.

Cowan, I.R. & Farquhar, G.D. (1977) Stomatal function in relation to leaf metabolism and environment. *Symposia of the Society for Experimental Biology*, **31**, 471–505.

Curtis, P.S. & Wang, X. (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. *Oecologia*, **113**, 299–313.

Darby, B.J., Neher, D.A., Housman, D.C. & Belnap, J. (2011) Few apparent short-term effects of elevated soil temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna. *Soil Biology and Biochemistry*, **43**, 1474–1481.

Darwin, C.R. (1881) *The Formation of Vegetable Mould through the Action of Worms*. John Murray, London.

DeLucia, E.H., Nabity, P.D., Zavala, J.A. & Berenbaum, M.R. (2012) Climate change: resetting plant–insect interactions. *Plant Physiology*, **160**, 1677–1685.

Demarta, L., Hibbard, B.E., Bohn, M.O. & Hiltpold, I. (2014) The role of root architecture in foraging behavior of entomopathogenic nematodes. *Journal Of Invertebrate Pathology*, **122**, 32–39.

Dermody, O., Weltzin, J.F., Engel, E.C., Allen, P. & Norby, R.J. (2007) How do elevated [CO_2], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem? *Plant And Soil*, **301**, 255–266.

Dong, Z., Hou, R., Chen, Q., Ouyang, Z. & Ge, F. (2013) Response of soil nematodes to elevated temperature in conventional and no-tillage cropland systems. *Plant And Soil*, **373**, 907–918.

Doube, B. & Marshall, T. (2014) *Dung down under: dung beetles for Australia*. Dung Beetle Solutions Australia, Bridgewater, South Australia, Australia.

Drigo, B., Pijl, A.S., Duyts, H., Kielak, A.M., Gamper, H.A., Houtekamer, M.J., Boschker, H.T.S., Bodelier, P.L.E., Whiteley, A.S., Van Veen, J.A. & Kowalchuk, G.A. (2010) Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 10938–10942.

Edwards, C.A. & Bohlen, P.J. (1996) *The Biology and Ecology of Earthworms*. Springer, London.

Eisenhauer, N. (2010) The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, **53**, 343–352.

Eisenhauer, N., Butenschoen, O., Radsick, S. & Scheu, S. (2010) Earthworms as seedling predators: Importance of seeds and seedlings for earthworm nutrition. *Soil Biology & Biochemistry*, **42**, 1245–1252.

Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K. & Reich, P.B. (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 6889–6894.

Eisenhauer, N., Schuy, M., Butenschoen, O. & Scheu, S. (2009) Direct and indirect effects of endogeic earthworms on plant seeds. *Pedobiologia*, **52**, 151–162.

Ennis, D.E., Dillon, A.B. & Griffin, C.T. (2010) Simulated roots and host feeding enhance infection of subterranean insects by the entomopathogenic nematode *Steinernema carpocapsae*. *Journal Of Invertebrate Pathology*, **103**, 140–143.

Erb, M., Huber, M., Robert, C.A.M., Ferrieri, A.P., Machado, R.A.R. & Arce, C.C.M. (2013a) The Role of Plant Primary and Secondary Metabolites in Root-Herbivore Behaviour, Nutrition and Physiology. *Advances in Insect Physiology*, **45** (eds S.N. Johnson, I. Hiltpold & T.C.J. Turlings), pp. 53–95. Academic Press, Oxford, UK.

Erb, M. & Lu, J. (2013b) Soil abiotic factors influence interactions between belowground herbivores and plant roots. *Journal of Experimental Botany*, **64**, 1295–1303.

FAO (2015) Nothing dirty here: FAO kicks off International Year of Soils 2015. Food and Agriculture Organization of the United Nations, Rome. Retrieved from http://www.fao.org/news/story/en/item/270812/icode/

Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A. & Cleveland, C.C. (2009) Global patterns in belowground communities. *Ecology Letters*, **12**, 1238–1249.

Fonte, S.J., Kong, A.Y.Y., van Kessel, C., Hendrix, P.F. & Six, J. (2007) Influence of earthworm activity on aggregate-associated carbon and nitrogen dynamics differs with agroecosystem management. *Soil Biology & Biochemistry*, **39**, 1014–1022.

Forey, E., Barot, S., Decaëns, T., Langlois, E., Laossi, K.-R., Margerie, P., Scheu, S. & Eisenhauer, N. (2011) Importance of earthworm–seed interactions for the composition and structure of plant communities: A review. *Acta Oecologica-International Journal of Ecology*, **37**, 594–603.

Freckman, D.W., Whitford, W.G. & Steinberger, Y. (1987) Effect of irrigation on nematode population dynamics and activity in desert soils. *Biology and Fertility of Soils*, **3**, 3–10.

Frederiksen, H.B., Rønn, R. & Christensen, S. (2001) Effect of elevated atmospheric CO_2 and vegetation type on microbiota associated with decomposing straw. *Global Change Biology*, **7**, 313–321.

Frelich, L.E., Hale, C.M., Scheu, S., Holdsworth, A.R., Heneghan, L., Bohlen, P.J. & Reich, P.B. (2006) Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, **8**, 1235–1245.

Frelich, L.E. & Reich, P.B. (2010) Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America? *Frontiers in Ecology and the Environment*, **8**, 371–378.

Garcia-Palacios, P., Maestre, F.T., Bradford, M.A. & Reynolds, J.F. (2014) Earthworms modify plant biomass and nitrogen capture under conditions of soil nutrient heterogeneity and elevated atmospheric CO_2 concentrations. *Soil Biology & Biochemistry*, **78**, 182–188.

García-Palacios, P., Vandegehuchte, M.L., Shaw, E.A., Dam, M., Post, K.H., Ramirez, K.S., Sylvain, Z.A., de Tomasel, C.M. & Wall, D.H. (2015) Are there links between responses of soil microbes and ecosystem functioning to elevated CO_2, N deposition and warming? A global perspective. *Global Change Biology*, **21**, 1590–1600.

Gerard, P.J. (2001) Dependence of *Sitona lepidus* (Coleoptera: Curculionidae) larvae on abundance of white clover *Rhizobium* nodules. *Bulletin of Entomological Research*, **91**, 149–152.

Grabmaier, A., Heigl, F., Eisenhauer, N., van der Heijden, M.G.A. & Zaller, J.G. (2014) Stable isotope labelling of earthworms can help deciphering belowground–aboveground interactions involving earthworms, mycorrhizal fungi, plants and aphids. *Pedobiologia*, **57**, 197–203.

Gregory, P.J. (2006) *Plant roots – growth, activity and interaction with soils*. Blackwell Publishing, Oxford, UK.

Guo, H., Sun, Y.C., Li, Y., Liu, X., Zhang, W. & Ge, F. (2014) Elevated CO_2 decreases the response of the ethylene signaling pathway in *Medicago truncatula* and increases the abundance of the pea aphid. *New Phytologist*, **201**, 279–291.

Guo, H., Sun, Y.C., Li, Y., Tong, B., Harris, M., Zhu-Salzman, K. & Ge, F. (2013) Pea aphid promotes amino acid metabolism both in *Medicago truncatula* and bacteriocytes to favor aphid population growth under elevated CO_2. *Global Change Biology*, **19**, 3210–3223.

Hackenberger, D.K. & Hackenberger, B.K. (2014) Earthworm community structure in grassland habitats differentiated by climate type during two consecutive seasons. *European Journal of Soil Biology*, **61**, 27–34.

Hiltpold, I., Bernklau, E., Bjostad, L.B., Alvarez, N., Miller-Struttmann, N.E., Lundgren, J.G. & Hibbard, B.E. (2013) Nature, Evolution and Characterisation of Rhizospheric Chemical Exudates Affecting Root Herbivores. *Advances in Insect Physiology*, **45** (eds S.N. Johnson, I. Hiltpold & T.C.J. Turlings), pp. 97–157. Academic Press, Oxford, UK.

Hiltpold, I., Erb, M., Robert, C.A.M. & Turlings, T.C.J. (2011) Systemic root signalling in a belowground, volatile-mediated tritrophic interaction. *Plant Cell and Environment*, **34**, 1267–1275.

Hiltpold, I., Jaffuel, G. & Turlings, T.C.J. (2015) The dual effects of root-cap exudates on nematodes: from quiescence in plant-parasitic nematodes to frenzy in entomopathogenic nematodes. *Journal of Experimental Botany*, **66**, 603–611.

Hiltpold, I., Toepfer, S., Kuhlmann, U. & Turlings, T.C.J. (2010) How maize root volatiles influence the efficacy of entomopathogenic nematodes in controlling the western corn rootworm? *Chemoecology*, **20**, 155–162.

Hiltpold, I. & Turlings, T.C.J. (2008) Belowground chemical signalling in maize: when simplicity rhymes with efficiency. *Journal Of Chemical Ecology*, **34**, 628–635.

Hoeksema, J.D., Lussenhop, J. & Teeri, J.A. (2000) Soil nematodes indicate food web responses to elevated atmospheric CO_2. *Pedobiologia*, **44**, 725–735.

Hunt, H.W. & Wall, D.H. (2002) Modelling the effects of loss of soil biodiversity on ecosystem function. *Global Change Biology*, **8**, 33–50.

IPCC (2013a) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC (2013b) Summary for Policymakers. *Climate change 2013: The Physical Science Basis. Summary for policymakers. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds T.F. Stocker, D. Qin, G.-K. Plattner, M.M.B. Tignor, S.K. Allen, A. Nauels, Y. Xia, V. Bex & P.M. Midgley). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Johnson, S.N., Barton, A.T., Clark, K.E., Gregory, P.J., McMenemy, L.S. & Hancock, R.D. (2011) Elevated atmospheric carbon dioxide impairs the performance of root-feeding vine weevils by modifying root growth and secondary metabolites. *Global Change Biology*, **17**, 688–695.

Johnson, S.N., Clark, K.E., Hartley, S.E., Jones, T.H., McKenzie, S.W. & Koricheva, J. (2012a) Aboveground-belowground herbivore interactions: A meta-analysis. *Ecology*, **93**, 2208–2215.

Johnson, S.N., Erb, M. & Hartley, S.E. (2016) Roots under attack: contrasting plant responses to below- and aboveground insect herbivory. *New Phytologist*, **210**, 413–418.

Johnson, S.N. & Gregory, P.J. (2006) Chemically-mediated host-plant location and selection by root-feeding insects. *Physiological Entomology*, **31**, 1–13.

Johnson, S.N., Lopaticki, G., Barnett, K., Facey, S.L., Powell, J.R. & Hartley, S.E. (20~~15a~~) An insect ecosystem engineer alleviates drought stress in plants without increasing plant susceptibility to an aboveground herbivore. *Functional Ecology*, ~~doi:10.1111/1365-2435.12582~~.

Johnson, S.N., Lopaticki, G. & Hartley, S.E. (2014a) Elevated atmospheric CO_2 triggers compensatory feeding by root herbivores on a C_3 but not a C_4 grass. *Plos One*, **9**, e90251.

Johnson, S.N. & McNicol, J.W. (2010) Elevated CO_2 and aboveground–belowground herbivory by the clover root weevil. *Oecologia*, **162**, 209–216.

Johnson, S.N., Mitchell, C., McNicol, J.W., Thompson, J. & Karley, A.J. (2013a) Downstairs drivers - root herbivores shape communities of above-ground herbivores and natural enemies via changes in plant nutrients. *Journal of Animal Ecology*, **82**, 1021–1030.

Johnson, S.N. & Murray, P.J. (2008) ~~*Root Feeders: An Ecosystem Perspective*~~. CABI Publishing, Wallingford, UK.

Johnson, S.N. & Nielsen, U.N. (2012b) Foraging in the dark – chemically mediated host plant location by belowground insect herbivores. *Journal Of Chemical Ecology*, **38**, 604–614.

Johnson, S.N. & Rasmann, S. (2015b) Root-feeding insects and their interactions with organisms in the rhizosphere. *Annual Review of Entomology*, **60**, 517–535.

Johnson, S.N. & Riegler, M. (2013b) Root damage by insects reverses the effects of elevated atmospheric CO_2 on eucalypt seedlings. *Plos One*, **8**, e79479.

Johnson, S.N., Ryalls, J.M.W. & Karley, A.J. (2014b) Global climate change and crop resistance to aphids: contrasting responses of lucerne genotypes to elevated atmospheric carbon dioxide. *Annals of Applied Biology*, **165**, 62–72.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Karban, R. (1980) Periodical cicada nymphs impose periodical oak tree wood accumulation. *Nature*, **287**, 326–327.

Kardol, P., Cregger, M.A., Campany, C.E. & Classen, A.T. (2010) Soil ecosystem functioning under climate change: Plant species and community effects. *Ecology*, **91**, 767–781.

Kardol, P., Reynolds, W.N., Norby, R.J. & Classen, A.T. (2011) Climate change effects on soil microarthropod abundance and community structure. *Applied Soil Ecology*, **47**, 37–44.

King, P.D., Mercer, C.F. & Meekings, J.S. (1981) Ecology of the black beetle, *Heteronychus arator* (Coleoptera, Scarabaeidae) – Influence of temperature on feeding, growth, and survival of the larvae. *New Zealand Journal of Zoology*, **8**, 113–117.

Klironomos, J.N., Rillig, M.C. & Allen, M.F. (1996) Below-ground microbial and microfaunal responses to *Artemisia tridentata* grown under elevated atmospheric CO_2. *Functional Ecology*, **10**, 527–534.

Kohler-Milleret, R., Le Bayon, R.C., Chenu, C., Gobat, J.-M. & Boivin, P. (2013) Impact of two root systems, earthworms and mycorrhizae on the physical properties of an unstable silt loam Luvisol and plant production. *Plant And Soil*, **370**, 251–265.

Korner, C. (2000) Biosphere responses to CO_2 enrichment. *Ecological Applications*, **10**, 1590–1619.

Lal, R. (1991) Soil conservation and biodiversity. *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture* (ed D.L. Hawksworth), pp. 89–103. CAB International, Wallingford.

Landesman, W.J., Treonis, A.M. & Dighton, J. (2011) Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. *Pedobiologia*, **54**, 87–91.

Lang, B., Rall, B.C., Scheu, S. & Brose, U. (2014) Effects of environmental warming and drought on size-structured soil food webs. *Oikos*, **123**, 1224–1233.

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. & Dhillion, S. (1997) Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, **33**, 159–193.

Laznik, Ž. & Trdan, S. (2013) An investigation on the chemotactic responses of different entomopathogenic nematode strains to mechanically damaged maize root volatile compounds. *Experimental Parasitology*, **134**, 349–355.

Le Bayon, R.-C. & Milleret, R. (2009) Effects of earthworms on phosphorus dynamics – a review. *Dynamic Plant, Dynamic Soil*, **3**, 21–27.

Lindeman, R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology*, **23**, 399–417.

Lohmann, M., Scheu, S. & Müller, C. (2009) Decomposers and root feeders interactively affect plant defence in *Sinapis alba*. *Oecologia*, **160**, 289–298.

Lubbers, I.M., van Groenigen, K.J., Fonte, S.J., Six, J., Brussaard, L. & van Groenigen, J.W. (2013) Greenhouse-gas emissions from soils increased by earthworms. *Nature Climate Change*, **3**, 187–194.

Luo, Y.Q., Hui, D.F. & Zhang, D.Q. (2006) Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecology*, **87**, 53–63.

Madhu, M. & Hatfeld, J.L. (2013) Dynamics of plant root growth under increased atmospheric carbon dioxide. *Agronomy Journal*, **105**, 657–669.

Matthiessen, J.N. & Ridsdill-Smith, T.J. (1991) Populations of African Black Beetle, *Heteronychus arator* (Coleoptera, Scarabaeidae) in a Mediterranean climate region of Australia. *Bulletin of Entomological Research*, **81**, 85–91.

Mattson, W.J.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.

McKenzie, S.W., Hentley, W.T., Hails, R.S., Jones, T.H., Vanbergen, A.J. & Johnson, S.N. (2013) Global climate change and above–belowground insect herbivore interactions. *Frontiers in Plant Science*, **4**, 412.

Milchunas, D.G., Mosier, A.R., Morgan, J.A., LeCain, D.R., King, J.Y. & Nelson, J.A. (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: Using a new ingrowth method. *Plant And Soil*, **268**, 111–122.

Milcu, A., Paul, S. & Lukac, M. (2011) Belowground interactive effects of elevated $CO_{2,}$ plant diversity and earthworms in grassland microcosms. *Basic And Applied Ecology*, **12**, 600–608.

Newman, J.A., Anand, M., Henry, H.A.L., Hunt, S. & Gedalof, Z. (2011) *Climate Change Biology*. CABI, Walingford, UK.

Nielsen, O. & Philipsen, H. (2004) Seasonal population dynamics of inoculated and indigenous steinernematid nematodes in an organic cropping system. *Nematology*, **6**, 901–909.

Nielsen, U.N., Ayres, E., Wall, D.H., Li, G., Bardgett, R.D., Wu, T. & Garey, J.R. (2014) Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. *Global Ecology and Biogeography*, **23**, 968–978.

Nielsen, U.N. & Ball, B.A. (2015a) Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. *Global Change Biology*, **21**, 1407–1421.

Nielsen, U.N., Wall, D.H. & Six, J. (2015b) Soil biodiversity and the environment. *Annual Review of Environment and Resources*, **40**, 63–90.

Niklaus, P.A., Alphei, J., Ebersberger, D., Kampichler, C., Kandeler, E. & Tscherko, D. (2003) Six years of in situ CO_2 enrichment evoke changes in soil structure and soil biota of nutrient-poor grassland. *Global Change Biology*, **9**, 585–600.

Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G. & Canadell, J.G. (2001) Elevated CO_2, litter chemistry, and decomposition: A synthesis. *Oecologia*, **127**, 153–165.

Norby, R.J. & Luo, Y. (2004) Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. *New Phytologist*, **162**, 281–293.

Nykänen, H. & Koricheva, J. (2004) Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos*, **104**, 247–268.

Ode, P.J., Johnson, S.N. & Moore, B.D. (2014) Atmospheric change and induced plant secondary metabolites — are we reshaping the building blocks of multi-trophic interactions? *Current Opinion in Insect Science*, **5**, 57–65.

Pacholski, A., Manderscheid, R. & Weigel, H.J. (2015) Effects of free air CO_2 enrichment on root growth of barley, sugar beet and wheat grown in a rotation under different nitrogen supply. *European Journal of Agronomy*, **63**, 36–46.

Payne, D. & Gregory, P.J. (1988) The soil atmosphere. *Russell's Soil Conditions and Plant Growth* (ed A. Wild), pp. 298–314. Longman, Harlow, UK.

Pearce-Higgins, J.W., Yalden, D.W. & Whittingham, M.J. (2005) Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia*, **143**, 470–476.

Pendall, E., Bridgham, S., Hanson, P.J., Hungate, B., Kicklighter, D.W., Johnson, D.W., Law, B.E., Luo, Y., Megonigal, J.P., Olsrud, M., Ryan, M.G. & Wan, S. (2004a) Below-ground process responses to elevated CO_2 and temperature: A discussion of observations, measurement methods, and models. *New Phytologist*, **162**, 311–322.

Pendall, E., Mosier, A.R. & Morgan, J.A. (2004b) Rhizodeposition stimulated by elevated CO_2 in a semiarid grassland. *New Phytologist*, **162**, 447–458.

Poinar, G.O. & Thomas, G.M. (1975) *Rhabditis pellio* Schneider (Nematoda) from earthworm, *Aporrectodea trrasmapezoides* Duges (Annelida). *Journal of Nematology*, **7**, 374–379.

Preisser, E.L. & Strong, D.R. (2004) Climate affects predator control of an herbivore outbreak. *The American Naturalist*, **163**, 754–762.

Prior, S.A., Runion, G.B., Torbert, H.A., Idso, S.B. & Kimball, B.A. (2012) Sour orange fine root distribution after seventeen years of atmospheric CO_2 enrichment. *Agricultural and Forest Meteorology*, **162-163**, 85–90.

Rasmann, S., Ali, J.G., Helder, J. & van der Putten, W.H. (2012a) Ecology and evolution of soil nematode chemotaxis. *Journal Of Chemical Ecology*, **38**, 615–628.

Rasmann, S., Erwin, A.C., Halitschke, R. & Agrawal, A.A. (2011) Direct and indirect root defences of milkweed (*Asclepias syriaca*): trophic cascades, trade-offs and novel methods for studying subterranean herbivory. *Journal of Ecology*, **99**, 16–25.

Rasmann, S., Hiltpold, I. & Ali, J. (2012b) The role of root-produced volatile secondary metabolites in mediating soil interactions. *Advances in Selected Plant Physiology Aspects* (eds G. Montanaro & B. Dichio), pp. 269–290. InTech, Rijeka, Croatia.

Rasmann, S., Köllner, T.G., Degenhardt, J., Hiltpold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J. & Turlings, T.C.J. (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*, **434**, 732–737.

Robinson, A.F. & Jaffee, B.A. (1996) Repulsion of *Meloidogyne incognita* by alginate pellets containing hyphae of *Monacrosporium cionopagum*, *M. ellipsosporum*, or *Hirsutella rhossiliensis*. *Journal of Nematology*, **28**, 133–147.

Robinson, E.A., Ryan, G.D. & Newman, J.A. (2012) A meta-analytical review of the effects of elevated CO_2 on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist*, **194**, 321–336.

Rogers, H.H., Prior, S.A., Runion, G.B. & Mitchell, R.J. (1996) Root to shoot ratio of crops as influenced by CO_2. *Plant And Soil*, **187**, 229–248.

Rogers, H.H., Runion, G.B. & Krupa, S.V. (1994) Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution*, **83**, 155–189.

Ruess, L., Michelsen, A. & Jonasson, S. (1999) Simulated climate change in subarctic soils: responses in nematode species composition and dominance structure. *Nematology*, **1**, 513–526.

Ryalls, J.M.W., Moore, B.D., Riegler, M., Gherlenda, A.N. & Johnson, S.N. (2015) Amino acid-mediated impacts of elevated carbon dioxide and simulated root herbivory on aphids are neutralised by increased air temperatures. *Journal of Experimental Botany*, **66**, 613–623.

Ryalls, J.M.W., Riegler, M., Moore, B.D., Lopaticki, G. & Johnson, S.N. (2013) Effects of elevated temperature and CO_2 on aboveground-belowground systems: a case study with plants, their mutualistic bacteria and root/shoot herbivores. *Frontiers in Plant Science*, **4**, 445.

Ryle, G.J.A., Powell, C.E. & Davidson, I.A. (1992) Growth of white clover, dependent on N_2 fixation, in elevated CO_2 and temperature. *Annals of Botany*, **70**, 221–228.

Salt, D.T., Fenwick, P. & Whittaker, J.B. (1996) Interspecific herbivore interactions in a high CO_2 environment: root and shoot aphids feeding on *Cardamine*. *Oikos*, **77**, 326–330.

Scheu, S. (2002) The soil food web: Structure and perspectives. *European Journal of Soil Biology*, **38**, 11–20.

Shapiro, D.I., Berry, E.C. & Lewis, L.C. (1993) Interactions between nematodes and earthworms – Enhanced dispersal of *Steinernema carpocapsae*. *Journal of Nematology*, **25**, 189–192.

Shapiro, D.I., Tylka, G.L., Berry, E.C. & Lewis, L.C. (1995) Effect of earthworms on the dispersal of *Steinernema* spp. *Journal of Nematology*, **27**, 21–28.

Shapiro-Ilan, D.I. & Brown, I. (2013) Earthworms as phoretic hosts for *Steinernema carpocapsae* and *Beauveria bassiana*: Implications for enhanced biological control. *Biological Control*, **66**, 41–48.

Shipitalo, M. & Le Bayon, R.C. (2004) Quantifying the effects of earthworms on soil aggregation and porosity. *Earthworm Ecology* (ed C.A. Edward), pp. 183–200. CRC Press LLC, Boca Raton.

Smolik, J.D. & Dodd, J.L. (1983) Effect of Water and Nitrogen, and Grazing on Nematodes in a Shortgrass Prairie. *Journal of Range Management*, **36**, 744–748.

Soler, R., van der Putten, W.H., Harvey, J.A., Vet, L.E.M., Dicke, M. & Bezemer, T.M. (2012) Root herbivore effects on aboveground multitrophic interactions: patterns, processes and mechanisms. *Journal of Chemical Ecology*, **38**, 755–767.

Sonnemann, I. & Wolters, V. (2005) The microfood web of grassland soils responds to a moderate increase in atmospheric CO_2. *Global Change Biology*, **11**, 1148–1155.

Soussana, J.F. & Hartwig, U.A. (1996) The effects of elevated CO_2 on symbiotic N_2 fixation: a link between the carbon and nitrogen cycles in grassland ecosystems. *Plant And Soil*, **187**, 321–332.

Staley, J.T. & Johnson, S.N. (2008) Climate change impacts on root herbivores. ~~*Root Feeders: An Ecosystem Perspective*~~ (eds S.N. Johnson & P.J. Murray), pp. 192–213. CABI Publishing, Wallingford, UK.

Stevnbak, K., Maraldo, K., Georgieva, S., Bjørnlund, L., Beier, C., Schmidt, I.K. & Christensen, S. (2012) Suppression of soil decomposers and promotion of long-lived, root herbivorous nematodes by climate change. *European Journal of Soil Biology*, **52**, 1–7.

Stiling, P. & Cornelissen, T. (2007) How does elevated carbon dioxide (CO_2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842.

Suárez, E.R., Fahey, T.J., Groffman, P.M., Yavitt, J.B. & Bohlen, P.J. (2006) Spatial and temporal dynamics of exotic earthworm communities along invasion fronts in a temperate hardwood forest in south-central New York (USA). *Biological Invasions*, **8**, 553–564.

Sun, X., Zhang, X., Zhang, S., Dai, G., Han, S. & Liang, W. (2013) Soil nematode responses to increases in nitrogen deposition and precipitation in a temperate forest. *Plos One*, **8**, e82468.

Sylvain, Z.A., Wall, D.H., Cherwin, K.L., Peters, D.P.C., Reichmann, L.G. & Sala, O.E. (2014) Soil animal responses to moisture availability are largely scale, not ecosystem dependent: Insight from a cross-site study. *Global Change Biology*, **20**, 2631–2643.

Tarnawski, S. & Aragno, M. (2006) The Influence of Elevated [CO_2] on Diversity, Activity and Biogeochemical Functions of Rhizosphere and Soil Bacterial Communities. *Managed Ecosystems and CO_2: Case Studies, Processes and Perspectives* **187** (eds J. Nösberger, S.P. Long, R.J. Norby, M. Stitt, G.R. Hendrey & H. Blum), pp. 393–412. Springer Berlin Heidelberg.

Thakur, M.P., Reich, P.B., Fisichelli, N.A., Stefanski, A., Cesarz, S., Dobies, T., Rich, R.L., Hobbie, S.E. & Eisenhauer, N. (2014) Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. *Oecologia*, **175**, 713–723.

Thompson, L., Thomas, C.D., Radley, J.M.A., Williamson, S. & Lawton, J.H. (1993) The effect of earthworms and snails in a simple plant community. *Oecologia*, **95**, 171–178.

Trouvé, R., Drapela, T., Frank, T., Hadacek, F. & Zaller, J.G. (2014) Herbivory of an invasive slug in a model grassland community can be affected by earthworms and mycorrhizal fungi. *Biology and Fertility of Soils*, **50**, 13–23.

Uvarov, A.V. (2009) Inter- and intraspecific interactions in lumbricid earthworms: Their role for earthworm performance and ecosystem functioning. *Pedobiologia*, **53**, 1–27.

van Geffen, K.G., Berg, M.P. & Aerts, R. (2011) Potential macro-detritivore range expansion into the subarctic stimulates litter decomposition: a new positive feedback mechanism to climate change? *Oecologia*, **167**, 1163–1175.

van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B. & van Groenigen, K.J. (2014) Earthworms increase plant production: a meta-analysis. *Scientific Reports*, **4**, 6365.

Vandegehuchte, M.L., Sylvain, Z.A., Reichmann, L.G., De Tomasel, C.M., Nielsen, U.N., Wall, D.H. & Sala, O.E. (2015) Responses of a desert nematode community to changes in water availability. *Ecosphere*, **6**, 44.

Villani, M.G., Allee, L.L., Diaz, A. & Robbins, P.S. (1999) Adaptive strategies of edaphic arthropods. *Annual Review of Entomology*, **44**, 233–256.

Villani, M.G. & Wright, R.J. (1990) Environmental influences on soil macroarthropod behavior in agricultural systems. *Annual Review of Entomology*, **35**, 249–269.

Wall, D.H. & Six, J. (2015) Give soils their due. *Science*, **347**, 695.

Wand, S.J.E., Midgley, G.F., Jones, M.H. & Curtis, P.S. (1999) Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology*, **5**, 723–741.

Whalen, J.K., Sampedro, L. & Waheed, T. (2004) Quantifying surface and subsurface cast production by earthworms under controlled laboratory conditions. *Biology and Fertility of Soils*, **39**, 287–291.

Wharton, G.W. (1985) Water balance of insects. *Comprehensive insect physiology, biochemistry and pharmacology*, **4** (eds G.A. Kerkut & L.I. Gibert), pp. 565–601. Pergamon Press, Oxford, UK.

Williams, R.S., Marbert, B.S., Fisk, M.C. & Hanson, P.J. (2014) Ground-dwelling beetle responses to long-term precipitation alterations in a Hardwood forest. *Southeastern Naturalist*, **13**, 138–155.

Wilsey, B.J. (2001) Effects of elevated CO_2 on the response of *Phleum pratense* and *Poa pratensis* to aboveground defoliation and root-feeding nematodes. *International Journal of Plant Sciences*, **162**, 1275–1282.

Wurst, S. (2010) Effects of earthworms on above- and belowground herbivores. *Applied Soil Ecology*, **45**, 123–130.

Xiao, G., Lui, W., Xu, Q., Sun, Z. & Wang, J. (2005) Effects of temperature increase and elevated CO_2 concentration, with supplemental irrigation, on the yield of rain-fed spring wheat in a semiarid region of China. *Agricultural Water Management*, **74**, 243–255.

Yeates, G.W. (1981) Soil nematode populations depressed in the presence of earthworms. *Pedobiologia*, **22**, 191–195.

Yeates, G.W., Dando, J.L. & Shepherd, T.G. (2002) Pressure plate studies to determine how moisture affects access of bacterial-feeding nematodes to food in soil. *European Journal of Soil Science*, **53**, 355–365.

Yeates, G.W., Ferris, H., Moens, T. & van der Putten, W.H. (2009a) The Role of Nematodes in Ecosystems. *Nematodes as Environmental Indicators* (eds M.J. Wilson & T. Kakouli-Duarte), pp. 1–44. CABI Publishing, Walingford, UK.

Yeates, G.W. & Newton, P.C.D. (2009b) Long-term changes in topsoil nematode populations in grazed pasture under elevated atmospheric carbon dioxide. *Biology and Fertility of Soils*, **45**, 799–808.

Yeates, G.W., Tate, K.R. & Newton, P.C.D. (1997) Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. *Biology and Fertility of Soils*, **25**, 307–315.

Young, I.M. (1998) Biophysical interactions at the root–soil interface: a review. *Journal of Agricultural Science*, **130**, 1–7.

Zahran, H.H. (1999) Rhizobium–legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiology and Molecular Biology Reviews*, **63**, 968–989.

Zaller, J.G. & Arnone, J.A.I. (1999a) Earthworm and soil moisture effects on the productivity and structure of grassland communities. *Soil Biology & Biochemistry*, **31**, 517–523.

Zaller, J.G. & Arnone, J.A.I. (1999b) Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO_2. *Ecology*, **80**, 873–881.

Zaller, J.G., Heigl, F., Grabmaier, A., Lichtenegger, C., Piller, K., Allabashi, R., Frank, T. & Drapela, T. (2011) Earthworm-mycorrhiza interactions can affect the diversity, structure and functioning of establishing model grassland communities. *Plos One*, **6**, e29293.

Zaller, J.G., Wechselberger, K.F., Gorfer, M., Hann, P., Frank, T., Wanek, W. & Drapela, T. (2013) Subsurface earthworm casts can be important soil microsites specifically influencing the growth of grassland plants. *Biology and Fertility of Soils*, **49**, 1097–1107.

Zavala, J.A., Nabity, P.D. & DeLucia, E.H. (2013) An emerging understanding of mechanisms governing insect herbivory under elevated CO_2. *Annual Review of Entomology*, **58**, 79–97.

Zhang, H., Schonhof, I., Krumbein, A., Gutezeit, B., Li, L., Stuezel, H. & Schreiner, M. (2008) Water supply and growing season influence glucosinolate concentration and composition in turnip root (*Brassica rapa* ssp *rapifera* L.). *Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde*, **171**, 255–265.

Zirbes, L., Thonart, P. & Haubruge, E. (2012) Microscale interactions between earthworms and microorganisms: a review. *Biotechnologie Agronomie Societe Et Environnement*, **16**, 125–131.
Zvereva, E.L. & Kozlov, M.V. (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a metaanalysis. *Global Change Biology*, **12**, 27–41.
Zvereva, E.L. & Kozlov, M.V. (2012) Sources of variation in plant responses to belowground insect herbivory: a meta-analysis. *Oecologia*, **169**, 441–452.