Biodiversity Climate change

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Climate change effects on soil biota in the UK

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Summary

- There is much evidence that climate change significantly impacts the abundance, diversity and activity of soil biota, but few consistent effects are reported in the literature, and effects vary strongly depending on environmental context.
- Elevated atmospheric CO_2 increases microbial biomass and the abundance of fungi (moderate confidence), the abundance and body size of most faunal groups (moderate confidence), and thus causes changes in the structure of the soil food web (high confidence). Elevated CO_2 has limited impacts on bacterial diversity (moderate confidence)
- Warming increases the abundance of bacteria and fungi (high confidence) and of most soil faunal groups (moderate confidence), resulting in changes in the structure of the soil food web (high confidence)
- Drought increases the abundance of fungi relative to bacteria (high confidence), but decreases the biomass and abundance of most microbial and soil faunal groups (high confidence)
- Very little is known on the effects of increased rainfall and flooding on soil biota, and reported effects are highly context dependent
- Changes in the abundance of soil organisms and the structure of the soil food web resulting from climate change will have consequences for soil functioning and the delivery of soil-based ecosystem services (high confidence). However, the relative importance of changes in soil biota compared to direct effects of climate change on soil functioning is unclear. Links between soil biota and soil functioning are context dependent, and specific processes and functional groups need further study. For example, the impact of climate change driven changes in soil biota on disease suppression, and the extent and consequences for soil functioning of invasive microbes, remain unexplored.

Introduction

Soil harbours an enormous diversity of life. A handful of soil can contain literally billions of bacterial cells, and tens of thousands of bacterial (Torsvik et al. 2002) and hundreds of fungal species (Read 1992). Soils also contain a vast diversity of animals, including microscopic nematodes, mites, Collembola, and larger fauna such as earthworms, beetles, and moles. Through using molecular techniques, it was discovered that upward of 2000 thousand taxonomic units of soil fauna can be found in even the most species poor ecosystems, such as arctic tundra (Wu et al. 2011a). The scale of belowground diversity is such that it is has been estimated that it could represent as much as 25% of the total amount of described living species worldwide (Decaens et al. 2006), although it has been suggested that we only know about 1% of the bacteria and fungi that live in soil (Decaens 2010).

Together, the organisms that inhabit the soil make up the soil food web: a tight web of organisms with different feeding habits that feed on dead organic matter, plant roots and on each other (Figure 1). This web of organisms is of crucial importance for the functioning of terrestrial ecosystems, as its primary role is to recycle unused organic matter derived from the above-ground, plant-based food web (Coleman et al. 2004, Bardgett 2005). By decomposing organic material, soil organisms release carbon back into the atmosphere, and liberate nutrients, such as nitrogen and phosphorus, for plant growth, thus influencing the functioning of terrestrial ecosystems. Soil food webs consist of root, fungal, and bacterial

energy channels: the root channel consists of symbiotic microbes and root-associated fauna, whereas the fungal and bacterial energy channels consist of organisms that derive their energy from detritus (Moore and Hunt 1988) (Fig. 1). These channels differentially affect nutrient and carbon cycling in the soil: bacterial-based food webs occur in more disturbed systems and are associated with fast and leaky nutrient (e.g. nitrogen) and carbon cycles, whereas fungal-based soil food webs slow down rates of nutrient and carbon cycling, and thus promote carbon and nutrient retention in soil (Wardle et al. 2004, De Vries and Bardgett 2012).

Soil food webs, and the interactions within them, not only affect processes of carbon and nutrient cycling, but also a range of other processes that underpin the functioning of terrestrial ecosystems. At the base of the soil food web are the primary consumers, which include the microorganisms (bacteria, fungi, actinomycetes, and algae) that are primarily responsible for breaking down and mineralising complex organic substances in soil, thereby controlling nutrient cycling and release of greenhouse gases from soil. Moreover, there is a whole suite of microorganisms, including mycorrhizal fungi and nitrogen fixing bacteria, that form symbiotic associations with plant roots, thereby affecting the performance of plants directly (Wardle et al. 2004). Next, are the secondary and higher-level consumers, which include a myriad of soil fauna of varying body size and life history strategies that feed on microorganisms, on each other, and on organic matter. These fauna are often broadly characterised on the basis of their body size, and include the microfauna, which are < 100 µm (e.g. protozoa and nematodes), mesofauna, which are < 2mm (microathropods and enchytraid worms), and the macrofauna (e.g .earthworms, ants, millipedes, and insect larvae) (Bardgett 2005). The functional roles of soil fauna most likely matches their tremendous diversity, but in broad terms they impact soil biogeochemical processes through their feeding on soil microorganisms and each other, through fragmenting and macerating organic matter, through direct interactions with plant roots, and through modifying soil structure and the physical soil environment (Bardgett 2005). Thus, the activities of soil organisms play a major role in controlling the processes that underpin the delivery of a range of ecosystem services, such as the production of food and fibre, climate regulation, disease and pest regulation, and soil formation and nutrient cycling (Wall et al. 2012).

There is growing concern that global change is affecting soil food webs and their functioning. Soil communities are under threat from a wide range of global change drivers, including land use change, and pollution, habitat fragmentation and disruption, invasive species, soil sealing and climate change (Gardi et al. 2013). Much research has been done on the impacts of these drivers on soil food webs, but most research into effects of climate change have focussed on aboveground organisms. On a global scale, climate change is causing increased temperatures and an increased frequency of extreme events, such as drought and heat waves, and excessive rainfall; these changes are already affecting the functioning of terrestrial ecosystems (IPCC 2014). For example, climate change is considered to be a major driver of earlier greening, leaf emergence, and fruiting in temperate and boreal trees, and to increased invasion of alien plant species (IPCC 2014). It is becoming evident that climate change also significantly impacts soil food webs, both directly by affecting the activity and mortality of soil organisms, and indirectly through effects on plant growth and plant community composition (Bardgett et al. 2008). Moreover, these climate change induced changes in soil food webs can have significant implication for their functioning, with potential

detrimental consequences for the functioning of terrestrial ecosystems and the ecosystem services they deliver.
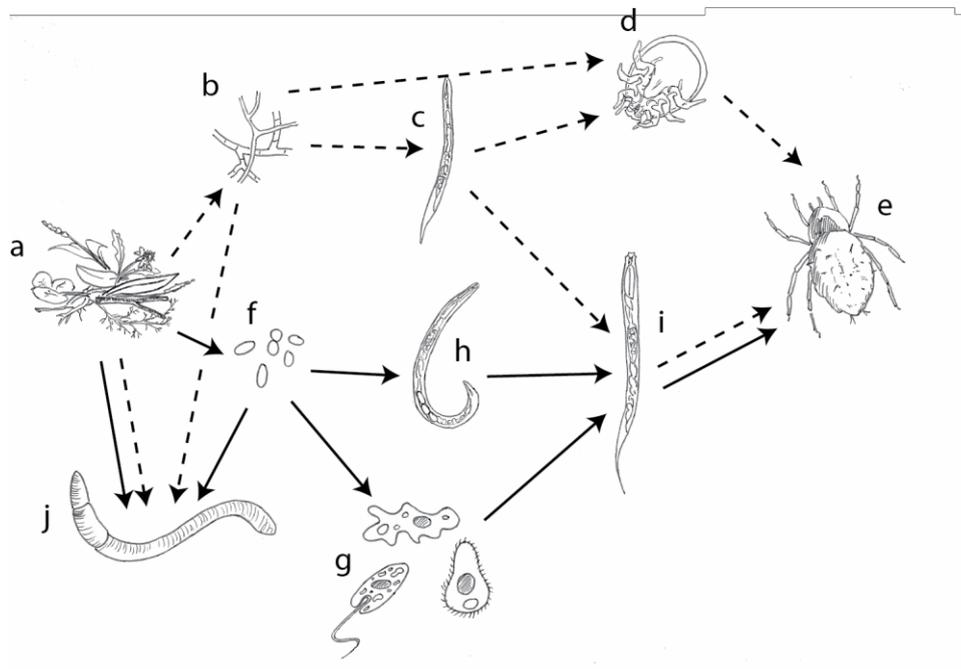
Fig. 1. A simplified example of a soil food web, with detritus (a), fungi (b), fungal-feeding nematodes (c), ominvorous nematodes (i), oribatid mites (d), predatory mites (e), bacteria (f), protozoa (g), bacterial-feeding nematodes (h), and earthworms (j). Dashed arrows represent the fungal energy channel, solid lines represent the bacterial energy channel. Drawing by Franciska de Vries.

For the UK, climate change projections indicate rising mean temperatures (between 2.4 and 4 degrees for 2080), rising minimum and maximum temperatures (in summer and winter), increasing incidence of hot summers and droughts, and a greater proportion of rainfall may fall in intense events (UKCP09). It is also expected that summers in the UK will get drier and winters will get wetter on average, and that sea levels will continue to rise at a faster rate than observed over the last century (UKCP09). All these climate change phenomena (increased temperature, increased rainfall, decreased rainfall, drought, and heat waves) have been shown to significantly affect soil biota. In addition, elevated atmospheric levels of CO_2, which is the major cause of these changes in global climate, can also indirectly affect soil communities by influencing the growth of plants. Here, we review and summarise recent evidence for impacts of climatic drivers on soil communities relevant to the UK, and predict the consequences for the processes they perform, which underpin a range of ecosystem services. Climate change can impact soils and their biota via a wide variety of mechanisms (Bardgett and Wardle 2010), including indirect impacts of changing land use and sea level rise. But we mainly focus here on the direct and indirect effects of the primary climate change drivers on soils, namely impacts on soil biota of warming, altered precipitation, including drought and flooding, and elevated atmospheric carbon dioxide.

Climate change effects on soil communities

Climate change drivers predicted for the UK have the potential to impact soil biota directly, through increased and decreased precipitation, and/or warming, and indirectly, through changes in plant growth and physiology and vegetation structure, due to altered precipitation, warming, and elevated atmospheric CO_2. Changes in precipitation, including drought and flooding, affect soil biota directly by changing soil water availability, but also indirectly by changes in the soil habitat, for instance as result of shrinkage and swelling of clay rich soils. Little is known about the impact on flooding on soil organisms, but immediate effects of drought on soil communities are well documented and can be severe, with declines in microbial biomass and activity, and even death of larger soil organisms, being observed (Liiri et al. 2002, Gordon et al. 2008, De Vries and Shade 2013). Climate change can also impact soil biota by increasing water and wind erosion of soil, especially where the frequency and intensity of extreme rainfall events increases and where climate-change driven changes in land use make soils more vulnerable to erosion (Nearing et al. 2004).

The impact of warming on soil biota, in contrast, is more gradual, causing stimulation of physiological processes, and hence rates of microbial respiration and nutrient mineralisation (Dorrepaal et al. 2009, Wu et al. 2011b, Zhou et al. 2012). Drought and warming can also indirectly affect soil biota through their impact on the growth of individual plants and plant community structure, which alters the supply of organic matter to soil from plant litter and root exudates, and through changes in root growth and exudation which can modify soil structure, thereby affecting soil water and gas fluxes, and the movement of soil organisms through soil (Bardgett et al. 2013). Likewise, the effects of elevated atmospheric CO_2 on soil biota are indirect, through changes in plant physiological processes and carbon allocation, and changes in plant community composition (Bardgett et al. 2013). In particular, elevated CO_2 typically increases plant photosynthesis and growth, and the amount of carbon pumped into the soil by plant roots, which in turn strongly modifies the growth and activity of soil biota (de Graaff et al. 2006, Drake et al. 2011, Phillips et al. 2011, Phillips et al. 2012). Similarly, recent work shows that warming can stimulate the exudation of carbon from plant roots, thereby stimulating the activity of soil biota (Yin et al. 2013). Such stimulation of microbial activity under elevated carbon dioxide has been shown, in some situations, to increase organic matter decomposition and soil N supply, which in turn sustains the growth response of trees (Phillips et al. 2011, Phillips et al. 2012). Root exudates are also known to increase aggregate stability in soil, because they contain polysaccharides and proteins that act like glue, bonding soil particles together (Czarnes et al 2000). Moreover, these compounds form hydrophobic coatings on soil particles, which act as a water repellent, thereby reducing wetting rates and slaking of soil (Hallett et al. 2009). Although largely unexplored, changes in root exudation resulting from elevated atmospheric CO_2 are therefore likely to impact on soil physical properties, with potential consequences for both water and gas flux through soil, and on soil organisms by altering the habitable pore space of soil.

<u>Impacts of climate change on soil microbial communities</u>

The number of studies exploring the effects of climate change on soil microbial communities has increased sharply in recent years. A recent meta-analysis by Blankinship et al.(2011) summarised the effects of elevated CO_2, warming, and altered precipitation on soil biota, including total microbial biomass, and fungal and bacterial abundance. They found very few significant responses of these three parameters – only microbial biomass was significantly

increased by elevated CO_2, bacterial abundance was negatively affected by warming, and fungal biomass increased with increasing precipitation. However, the effects of climate change on specific microbial functional groups or taxa, or the diversity of these, were not assessed. In recent years, the study of microbial diversity has advanced significant through the use of molecular methods, which allow for assessment of changes in community composition and diversity of functional groups or taxa, as well as of functional genes, and thus for predictions about functionality. Here, we extend on the analysis of Blankinship et al. (2011) by exploring climate change driven changes in microbial community composition and the abundance of microbial functional groups (see Appendix for details on the literature search).

Table 1. Summary of climate change effects on microbial communities as reported in the literature. Upward pointing arrows designate that the majority of reviewed studies found a positive effect, downward pointing arrows designate that the majority found a negative effect, horizontal arrows designate an equal amount of studies that found a positive and a negative effect, and question marks mean either that we found a number of studies too small to draw a conclusion, or that the amount of studies reporting a negative effect was equal to the amount reporting a positive effect. Shade of colouring indicates the strength/amount of evidence available; a dark shade indicates a greater number of studies found to support the direction of the effect (high confidence), a light shade indicates a low number of studies (low confidence), and white cells indicate that no studies were found. For details on the literature ew and references see Appendix and Tables A1-A4 therein.

	Elevated CO_2	Warming	Drought	Wetting/flooding
Microbial diversity	→	→	↑	?
Bacterial diversity	→	↓	↓	?
Fungal diversity	→	→	→	?
Archaeal diversity	?	?	?	↑
Microbial abundance	↑	↑	→	↓
Fungal abundance	↑	↑	↑	↑
- AMF	↑	↓	?	?
- EMF	?	↑	?	?
Bacterial abundance	→	↑	↓	→
- Gram negative	↓	→	↑	↑
- Gram positive	?	?	↓	↑
- AOB	→	↓	→	→
- Methanotrophs	?	↑	?	↑
Archaeal abundance	↑	↓	?	?
- AOA	?	↓	→	→
- Methanogens	→	↓	?	↑
N-cycling genes	↑	↑	→	?
C-cycling genes	↑	↑	?	?

Climate change effects on soil microbial communities are highly variable, and despite the growing number of studies on the topic, few consistent trends emerge. The impacts of elevated atmospheric CO_2 and warming are the most studied (Table 1, Table A1, A2), with some consistent patterns emerging. Elevated CO_2, for example, has been shown to enhance the exudation of easily degradable sugars, organic acids and amino acids, from roots, which stimulates microbial activity and soil organic matter mineralisation (van Groenigen et al. 2014). It also increases microbial biomass, including that of arbuscular mycorrhizal (AM) and decomposer fungi, and the biomass of Archaea, but bacterial biomass seems to be unaffected (Table 1). The response to elevated CO_2 of specific bacterial taxa varies strongly, and has been addressed in only a few studies (Table A1). Notably, Beta-proteobacteria and Bacteroidetes, which are copiotrophic bacteria that preferentially consume labile organic C, and have high nutritional requirements and growth rates (Fierer et al. 2007), increase with elevated CO_2. In contrast, Acidobacteria, which are oligotrophic bacteria, which exhibit slow growth rates, and are able to outcompete copiotrophs when nutrient availability is low (Fierer et al. 2007) decrease (Table A1). In addition, a few studies that show that the abundance of C and N cycling genes is increased by elevated CO_2 (He et al. 2010, Kelly et al. 2013) (Table 1, Table A1).

Warming generally increases plant respiration and photosynthesis (Wu et al. 2011b), and results in increased soil microbial activity and rates of respiration from soil (Yuste et al. 2007, Dorrepaal et al. 2009). Warming affects soil microbial communities in a similar way to elevated CO_2: it increases microbial abundance, including that of fungi and bacteria (Table 1, Table A2). Very little is known, however, about the response of Archaea or specific taxonomic or functional groups of soil microorganisms to warming, and, as with elevated CO_2, data that are available indicate that impacts on soil microbial community composition are highly variable. Some studies, for instance, show that bacterial diversity decreases with warming (Sheik et al. 2011, Deslippe et al. 2012), whereas others show that fungal diversity is unaffected (Anderson et al. 2013). Finally, there is some evidence that the abundance of C and N cycling genes increases with warming, thereby stimulating rates of C and N cycling (Cantarel et al. 2012, Zhou et al. 2012).

Drought can severely affect soil microbial communities, leading to sudden declines in microbial biomass and activity, and a flush in microbial activity and rates of C and N mineralisation upon rewetting. Traditionally, most climate change research has focussed on elevated CO_2 and warming, but it is likely that extreme events, such as drought and freezing, might become more frequent and impact more severely on ecosystems and their functioning (Reichstein et al. 2013). As a result, a growing number of studies have looked at drought responses of soil microbial communities and a few clear trends emerge. For example, fungal abundance is promoted by drought over the abundance of bacteria, which is reduced, and there is some evidence that the diversity of bacteria is also reduced (Table 1, Table A3). These responses are consistent with the assumption that fungi are more resistant to drought than bacteria, because of their thick cell walls and more conservative growth strategies (Schimel et al. 2007, De Vries and Shade 2013). Despite this, studies show that Gram positive bacteria, which are considered to be relatively slow growing and have strong cell walls, are reduced, whilst Gram negative bacteria are increased with drought (De Vries and Shade 2013) (Table 1, Table A3).

Few studies have explored the effects of flooding and increased precipitation on soil microbial communities. Although opposite effects to those resulting from drought might be

expected, wetter soil conditions also appear to promote fungal abundance, presumably because fungi are better at coping with anaerobic conditions. The diversity and abundance of Archaea also seems to benefit from wetter conditions, as well as methanogens and methanotrophs, which thrive under anaerobic conditions (Table 1, Table A4).

<u>Impacts of climate change on soil faunal abundance and community composition</u>

Climate change effects on soil fauna have been comprehensively analysed in the metaanalysis by Blankinship et al. (2011). This metaanalysis focussed on the effects of warming, elevated CO_2, and altered precipitation (from drought to increased precipitation). The findings of this analysis are summarised in Table 2, which, on inspection, reveals that responses of different faunal groups to these drivers are highly variable. Only nematodes, collembolans, and enchytraieds show a significant response to climate change drivers; nematodes increase in abundance with warming, while both Collembola and enchytraieds increase with increased precipitation (Table 2). When organisms are grouped by feeding group, only fungal-feeding fauna increase in abundance with increased precipitation, and when grouped by body size, microbes and microfauna (nematodes) respond positively to elevated CO_2, while mesofauna (mites and Collembola) respond positively to increased rainfall (Table 2). Here, we will expand on what is known on the basis of this metaanalysis and other, more recent work.

Table 2. Summary of climate change effects on soil fauna from the metaanalysis by Blankinship et al. (2011). Mean standardised effect sizes and their confidence intervals are reported; mean responses of which the confidence interval (CI) is significantly different from zero are in bold.

	Elevated CO_2		Warming		Altered rainfall	
	Mean	CI	Mean	CI	Mean	CI
Taxon						
Protozoa	0.10	-0.07 to 0.22				
Nematodes	0.01	-0.14 to 0.15	**0.08**	0.02 to 0.26	0.37	-0.16 to 0.91
Collembola	-0.15	-0.66 to 0.43	-0.16	-0.42 to 0.04	**0.57**	0.24 to 0.93
Mites	-0.20	-0.52 to 0.03	0.02	-0.49 to 0.48	0.22	-0.14 to 0.71
Enchytraieds	-0.14	-1.30 to 0.41	0.36	-0.40 to 1.15	**0.90**	0.06 to 1.74
Body width class						
Microflora/ fauna	**0.05**	0.0008 to 0.11	-0.02	-0.15 to 0.12	0.17	-0.02 to 0.41
Mesofauna	-0.14	-0.46 to 0.14	-0.02	-0.25 to 0.25	**0.45**	0.16 to 0.78
Macrofauna					0.38	-0.24 to 1.51
Trophic group						
Herbivore	0.18	-0.13 to 0.40				
Bacterivore	0.06	-0.09 to 0.16			-0.07	-0.43 to 0.20
Fungivore	-0.10	-0.33 to 0.14			**0.43**	0.15 to 0.77
Predator	0.27	-0.36 to 0.52			0.36	-0.09 to 0.97

As already mentioned, effects of elevated CO_2 on soil organisms are primarily indirect, being driven by changes in plant growth and the supply of carbon, mainly in the form of root exudates. These belowground C inputs are first used by microorganisms such as fungi and

bacteria, which tend to increase in abundance and activity as a result. These changes in turn have bottom-up effects on the abundance of bacterial and fungal-feeding fauna, such as nematodes and Collembola, due to increased resource supply (Blankinship et al. (2011). Consistent with this, several long-term, free-air CO_2 enrichment experiments (FACE) detect increases the abundance of soil fauna under elevated CO_2 (Yeates et al. 1997, Sticht et al. 2009, Yeates and Newton 2009, Milcu et al. 2011, Eisenhauer et al. 2012a). However, responses are not always that straightforward, in that Xu et al. (2013) found that while numbers of Collembola decreased under elevated CO_2, their body size increased, resulting in no net effect on their biomass. Also, Meehan et al. (2010) found that the growth of both earthworms and collembolans was reduced under elevated CO_2 because of higher amounts of condensed-tannin in leaf litter. Several studies have also found a decrease in richness of faunal groups in response to elevated CO_2 (Kardol et al. 2011, Eisenhauer et al. 2013, Neher and Weicht 2013), which is likely due to shifts in competitive interactions as a result of increased resource availability. However, caution is needed in drawing conclusions from studies focussing on one vegetation type, since responses of soil fauna to elevated CO_2 appear to be strongly driven by plant species identity and community composition (Drigo et al. 2007, Sticht et al. 2009, Kardol et al. 2010, Eisenhauer et al. 2013, Neher and Weicht 2013, Xiao et al. 2013).

Warming has also been shown to increase soil microbial biomass (Table 1) and activity, resulting in an increased availability of resources for root and microbial feeding fauna. Increases in abundance as a result in warming have been found for enchytraieds (Carrera et al. 2009, Briones et al. 2010) and Collembola (A'Bear et al. 2013a), although Collembola, mites, nematodes, and enchytraieds and epigeic (surface-dwelling) earthworms have also been shown to be reduced by warming (Briones et al. 2009, Bokhorst et al. 2012, Stevnbak et al. 2012, Krab et al. 2013, Van Dooremalen et al. 2013). Warming can also increase the species richness of soil faunal groups (Briones et al. 2009, Tsyganov et al. 2011, Lindo et al. 2012), and induce shifts in the functional traits, or life history characteristics, of soil fauna. For example, Bokhorst et al. (2012) found a shift from smaller to larges mites under warming, and Krab et al. (2013) found that soil-dwelling Collembola were increased relative to surface-dwelling ones, although Van Dooremalen et al. (2013) found that surface-dwelling Collembola were better able to tolerate heat than soil-dwelling ones. Also, Stevnbak et al. (2012) found that warming increased generation times of root feeding nematodes, and Briones et al. (2009) found an increase in fungivorous mites and Collembola under warming, which could be indicative of a shift from a bacterial-based to a fungal-based soil food web.

Impacts of drought on soil animals are especially strong for species that depend on a water film in soil, such as protozoa and nematodes, and other hydrophilic organisms such as enchytraieds (Bardgett 2005). Indeed, drought has been shown to reduce the abundance of most faunal groups, including protozoa (Larsen et al. 2011, Stevnbak et al. 2012, Tsyganov et al. 2013), nematodes (Kardol et al. 2010, Landesman et al. 2011, Eisenhauer et al. 2012a), Collembola (Makkonen et al. 2011, Petersen 2011, Lindo et al. 2012, Xu et al. 2012, A'Bear et al. 2013a), mites (Lindo et al. 2012, Xu et al. 2012), enchytraieds (Plum and Filser 2005, Larsen et al. 2011), and earthworms (Holmstrup 2001, Plum and Filser 2005). Studies have also found that species richness of Collembola and mites is reduced by drought (Lindberg and Bengtsson 2006, Kardol et al. 2011, Makkonen et al. 2011, Petersen 2011, Xu et al. 2012). Some studies looked into the response of different feeding groups or trait groups to drought; for example, Xu et al. (2012) found that the abundance of large mites

decreased under drought, while small mites increased, whereas Makkonen et al. (2011) found that large Collembola did better than small ones. Finally, Landesman et al. (2011) found bacterial-feeding nematodes were especially susceptible to drought, and Eggleton et al. (2009) found, in a UK based study, that epigeic earthworms were reduced more by drought than endogeic earthworms.

Very few studies have looked at the effects of flooding, or water addition, on soil faunal communities. Those that have were typically located in arid areas, which are not very representative of UK climatic conditions. For example, studies on the response of nematodes to water addition have been done in the McMurdo Dry Valley, Antarctica, which is one of the harshest and species poor places on Earth (Nielsen et al. 2012). Also, Sun et al. (2013) found that water addition to soil in an arid ecosystem reduced the abundance of fungivorous nematodes, plant parasitic nematodes, and omnivores/ predators, particularly when in combination with N addition. In a northern peatland, however, the abundance and richness of testate amoebae was reduced by extreme rainfall (Tsyganov et al. 2013). In a study done in a mediterranean old field, lower rainfall variability increased the abundance of earthworms (Moron-Rios et al. 2010), while in a field study in South Africa, flooding reduced the survival of worms (Owojori and Reinecke 2010).

<u>Indirect effects of climate change on soil organisms through changes in plant community composition</u>

An increasing number of studies show that the effects of climate change on soil organisms occur indirectly in response to changes in plant physiology and plant community composition, which alter the quantity and quality of organic matter supply to soil, and the physical environment of soil. For example, and as illustrated above, the effects of elevated atmospheric CO_2 and warming on soil microbes and soil fauna mostly operate through changes in plant growth and root exudation, and vary widely depending on the type of plant under study and the composition of the plant community. However, most climate change studies are not long enough in duration for changes in plant communities to appear, and where they do, it is hard to disentangle direct and indirect effects on soil communities (Kardol et al. 2010). Therefore, changes in plant communities are often incorporated as a separate treatment, and these plant community manipulations have often been found to be more important in driving belowground community composition and activity than climate change (Hagvar and Klanderud 2009, Eisenhauer et al. 2012a, Eisenhauer et al. 2013, Ward et al. 2013). However, since studies have been done in different ecosystems, and differ in the way plant communities were manipulated, it is hard to extract general patterns of the indirect effects of climate change on soil organisms via changes in plant communities.

In recent years, trait-based approaches have increasingly been used, both for predicting changes in plant communities as a result of climate change (e.g. Schroter et al. 2004, Klumpp and Soussana 2009, Soudzilovskaia et al. 2013), and for quantifying links between plant and soil communities and ecosystem processes (De Deyn et al. 2008, De Vries et al. 2012d, Grigulis et al. 2013). Studies are beginning to reveal how plants with similar sets of functional traits respond to climate change. For example, studies suggest that conservative plant traits that are linked to efficient water use and investment in belowground reserves increase under warming and drought (Weltzin et al. 2003, Debinski et al. 2010, Hoeppner and Dukes 2012). Elevated CO_2 has also been shown to favour C4 grasses over C3 grasses, and increase woody species and legumes (Hanley et al. 2004, Souza et al. 2010,

Pendall et al. 2011). Moreover, these changes in plant communities associated with the conservative-exploitative trait spectrum are likely to have consequences for soil food webs, as a growing number of studies show that slow growing, conservative plants are associated with fungal-dominated soil food webs, whereas fast growing, resource exploitative plants are associated with bacterial based soil food webs (Orwin et al. 2010, De Vries et al. 2012d, Grigulis et al. 2013).

Another way by which plant communities can interact with climate change in affecting soil communities is through the introduction of invasive plant species, which have been shown to affect soil communities. The success of invasive species correlates with the novelty of their traits compared to native organisms (Wardle et al. 2011). Because invasive plants generally have more exploitative traits, such as high leaf N and phosphorus (P) concentrations, growth rate, and specific leaf area, than natives (Wardle et al. 2011), they select for more bacterial-based soil food webs (Wardle et al. 2011, De Vries et al. 2012d), and thus potentially change the composition of native soil food webs. Moreover, bacterial-based soil food webs could potentially form a positive feedback to the performance of invasive plants with exploitative strategies (Wardle et al. 2004).

Invasive soil organisms

In recent years, the attention for invasive soil organisms has increased, with a strong focus on invasive earthworms. Exotic earthworm invasions are primarily the consequence of growing global trade, and can have devastating consequences on ecosystems via predation and competition, and through changing the soil environment , particularly in ecosystems that were previously earthworm-free (Hendrix and Bohlen 2002). Well-known examples are invasive European earthworms in North America (Eisenhauer et al. 2012b), and the invasion of the New Zealand flatworm in the UK (Murchie and Gordon 2013). However, northward range expansions of exotic earthworms into the UK have also been reported, most likely because of changed climatic conditions (Melody and Schmidt 2012). Other soil organisms are also likely to expand their range because of changed climatic conditions, and it has been suggested that the spread of fungal diseases is encouraged by global climate change (Fisher et al. 2012) with potential impacts on plant growth, including crops and native trees. However, aside earthworms, records of range expanding soil organisms are rare, and therefore the true extent of range expanding soil organisms is not known (Terauds et al. 2011, Treasure and Chown 2013).

Indirect effects through soil erosion

Climate change also has the potential to impact soil biota indirectly by increasing rates of soil erosion, which leads to reductions, or complete removal, of the soil habitat of biota and roots. Although a natural process, the magnitude of soil erosion can be affected by climate change via a variety of routes, the most direct being through increased frequency and intensity of erosive rainfall events (Pruski and Nearing 2002). However, it has also been proposed that climate change might indirectly impact the magnitude of soil erosion by increasing rates of organic matter decomposition in soil, thereby reducing soil carbon content, and by changing plant cover on the soil surface, and hence its susceptibility to erosive rainfall events (Nearing et al. 2005). In addition, it is likely that shifting land use as a result of climate change, including the use of new crops and complete changes in land use, will alter considerably rates or soil erosion in many parts of the world (Nearing et al. 2005).

Given the complexities of land use decisions under future climate change, coupled with uncertainties over changes in weather patterns, it is very difficult to predict how climate will impact soil erosion and the consequences of this for soil biota. Consistent with this, model predictions indicate a mix of increases and decreases in soil erosion under climate change, depending on the scenarios are considered, and suggest that indirect impacts of climate change on soil erosion (i.e. changes in land use and management) will be more influential in affecting future soil erosion rates than direct changes in climate alone (Mullan 2013).

Potential impacts of UK climate change on soil biodiversity and function

From the above, it is clear that climate change significantly impacts the composition of soil communities and soil food webs, although responses are highly variable, and depend greatly on factors like such as plant community composition, soil physical conditions, and interactions with other global change drivers. Despite this, it is likely that changes in soil communities and soil food webs resulting from climate change will have consequences for ecosystem functioning, especially given that soil organisms are the key performers of organic matter decomposition and nutrient mineralisation, and also impact on the physical structure of soil. Here, we briefly identify some of the potential implications of climate change impacts on soil biota for soil functioning in the UK

Links between soil biodiversity and ecosystem functioning

Although climate change effects on soil microbial diversity are inconsistent (Table 1), there is much evidence to suggest that climate change will impact the abundance of different functional groups, trophic groups and feeding groups of soil organisms (see sections above). Changes in the abundance of these groups have the potential to have both bottom-up (Blankinship et al. 2011, De Vries et al. 2012b, De Vries et al. 2012c, A'Bear et al. 2013a) or top-down (Wardle et al. 1998, A'Bear et al. 2012) effects on the abundance of other functional groups, especially soil microbes, thereby affecting the composition of soil food webs. Many studies now show that changes in both the number of functional groups present in soil and the diversity of these functional groups can have significant impacts on ecosystem functioning (Nielsen et al. 2011).

Within-trophic group diversity effects on ecosystem functioning, such as those that result from changes in the diversity of specific groups such as bacteria or microarthopods, generally occur at the lower end of species richness, which is suggestive of high levels of redundancy in soil communities (Nielsen et al. 2011). However, recent evidence suggests that changes in the composition of soil food webs are more important for ecosystem functioning than are within-trophic group changes. For example, in a UK-based study, De Vries et al. showed that the composition of soil food webs determined the extent of C and N loss from soil after a drought (De Vries et al. 2012b), and in another, European-wide study, they showed that changes in the ratio of fungi-to-bacteria were strongly linked to processes of C and N cycling (De Vries et al. 2013). Changes in the fungal-to-bacterial biomass ratio, or in the fungal-to-bacterial energy channel ratio, have been shown to be important determinants for processes of C and N cycling previously; fungal based soil food webs generally have more efficient C and N cycling and are less 'leaky' than bacterial-based ones (De Vries et al. 2006, Holtkamp et al. 2011, De Vries et al. 2012a). In addition, Handa et al. (2014) found that a reduction in functional diversity reduced litter decomposition across ecosystem types, and that a more complete decomposer community increased litter

decomposition rates, and Wagg et al. (2014) found in a mesocosm experiment, that a reduction in functional groups and a simplification of soil communities resulted in a reduction of ecosystem multifunctionality.

The abundance of individual trophic groups of the soil food web has also been linked to specific soil processes (De Vries et al. 2013). For example, the presence of higher trophic levels stimulates N mineralisation by grazing on microbes, which in turn results in greater plant growth (Setälä and Huhta 1991), and might increase plant community diversity (Wagg et al. 2014). Moreover, it is well known that earthworms play a key role in C and N cycling and also modify soil structure. However, it was recently shown that while earthworms are beneficial for soil fertility, they also increase emissions of both CO_2 and N_2O from soil, thus increasing the global warming potential of soil (Lubbers et al. 2013). Similarly, enchytraieds have also been linked to higher rates of N_2O emission from soil (Kuiper et al. 2013), although they are generally recognised as being a keystone species for the functioning of terrestrial ecosystems (Cole et al. 2002, Briones et al. 2007).

Although poorly explored, climate change driven changes in the diversity and structure of soil communities will also impact soil physical properties of soil, with consequences for the movement of water and gases, and also the microhabitat of the organisms themselves. This is especially the case for ecosystem engineers, such as earthworms and termites, which create macropores and channels as a consequence of their feeding and burrowing activities, thereby improving soil porosity and drainage (Bardgett 2005). However, given that different microbial groups differentially affect soil aggregate formation, there is also potential for changes in microbial community composition and diversity to also impact physical properties of soil. For instance, fungi promote soil aggregate stability through the physical enmeshment of soil particles by their extensive networks of mycelia, whereas bacteria produce metabolic products, mainly polysaccharides, which bind soil particles together (Hallett et al. 2009).

Finally, molecular methods have made it possible to quantify functional gene presence or the abundance of taxonomic microbial groups with known functions. Although shifts in the abundance of functional genes of well-defined functional groups do not necessarily translate into a change in functioning, these methods have greatly advanced our understanding of functional consequences of changes in soil microbial communities (Zak et al. 2006). For example, shifts in C and N cycling genes have been linked to changes in process rates of C and N cycling (Cantarel et al. 2012, Zhou et al. 2012).

Consequences of climate change impacts on soil biodiversity for ecosystem functioning in the UK

Elevated CO_2, through increasing the activity and abundance of many trophic groups in the soil food web, increases rates of soil organic matter decomposition, resulting in a net loss of soil C (van Groenigen et al. 2014). However, elevated CO_2 can also result in increased rates of N mineralisation, which can sustain long-term increases in plant growth (Drake et al. 2011, Phillips et al. 2011). In contrast, elevated CO_2 can also result in increased locking up, or immobilisation, of N by soil microbes, especially when resource quality is low, due to changes in litter chemistry and root exudates, and when N is limiting (de Graaff et al. 2006, Cotrufo et al. 2013); however, plants might bypass this reduced nutrient availability by greater investment in mycorrhizal fungi (Table 1). In addition, increased rates of root exudation, greater microbial biomass, greater investment in mycorrhizal fungi, and greater

earthworm abundance might all result in greater soil structural stability and soil aggregation (Young et al. 1998, Rillig et al. 1999, Bossuyt et al. 2005, Rillig and Mummey 2006). But, increased root biomass and root exudates might also result in a greater supply of labile C to methanogens and denitrifiers, resulting in an increase in the production of N_2O and CH_4 (Weier et al. 1993, Le Mer and Roger 2001). Indeed, in a recent metaanalysis, Van Groenigen et al. (2011) found that increased levels of atmospheric CO_2 stimulate emissions of N_2O and CH_4 from soil, offsetting any predicted increase in the terrestrial C sink under elevated CO_2.

Increases in the biomass and activity of soil microbes and the abundance of both C and N cycling genes as a result of warming(Table 1) results in greater respiration and N mineralisation rates (Dorrepaal et al. 2009, Wu et al. 2011b, Zhou et al. 2012). Microbial soil respiration rates are highly sensitive to warming and can thus form a considerable feedback to climate warming (Bardgett et al. 2008). Moreover, it is thought that the temperature sensitivity of soil organic matter decomposition increases with increasing molecular complexity of the substrate (Davidson and Janssens 2006), and thus important C stores such as the UK's northern peat soils might lose C faster than other UK soils. However, it has been argued that the temperature sensitivity of soil microbial respiration is only a temporary response and that, in the longer term, microbial respiration acclimates to increased temperatures (Bradford et al. 2008, Hartley et al. 2008, Bradford 2013). To date, however, it is not clear whether this acclimation is a consequence of substrate depletion, physiological acclimation of microbes, genetic adaptation, or microbial community change (Wei et al. 2014). Increased abundance of enchytraieds in peat soils has also been linked to increased C losses (Briones et al. 1998, Cole et al. 2002ab), but conversely, a shift to more fungal-based soil food webs under warming (see section above) could result in increased soil C storage and lower C and N loss from soil.

Drought negatively affects the abundance of many soil organisms (see previous section), and results in a flush of C and N mineralisation upon rewetting (the Birch effect), in part because it disrupts soil structure, but also because of the remineralisation of dead microbes and soil animals (Gordon et al. 2008, Borken and Matzner 2009, De Vries et al. 2012b). Thus, drought results in a significant loss of C and N from soil. The effects of drought on soil food webs can have long lasting legacy effects on the functioning of soil, and fungal-based soil food webs have been shown to lose less C and N under drought. Although drought forms a significant threat for aboveground primary productivity (Reichstein et al. 2013), the increased availability of N in soil after the drought has ended can also promote plant growth (De Vries et al. 2012c). It has been found that drought can reduce the positive effect earthworms have on plant growth (Blouin et al. 2007), but depending on the plant species, earthworms can also ameliorate the negative effect of drought on plant growth (Johnson et al. 2011).

Finally, although the effects of flooding on soil communities are far from clear (see previous section), the increased soil anaerobicity, the greater abundance of both methanogens and methanotrophs, and the apparent increase in soil fungi, might result in altered C and N cycling. Moreover, since flooding can reduce the abundance of earthworms, soil structure might deteriorate and soils might become compacted.

Implications for ecosystem services

Crop production

While elevated CO_2 and warming might increase plant production and the abundance and activity of soil organisms, thereby positively affecting crop yield, extreme events like drought, flooding, and heat waves will reduce yields (Reichstein et al. 2013) and potentially cause increased C and nutrient losses from soil, resulting in reduced primary productivity. Moreover, repeated episodes of drought and warming will likely result in reduced soil C stocks due to the repeated losses of C and N, both as gases and in the form of leachates, following rewetting events (De Vries et al. 2012b), and due to the stimulation of respiration by warming. As outlined above, increased frequency of erosive rainfall events is predicted to increase soil erosion, and flooding might result in soil compaction, increased runoff of soil nutrients, and soil anaerobicity, thereby resulting in a loss of soil structural stability and nutrients from soil. So, overall, climate change is likely to result in a reduction of soil quality and fertility, and crop yield.

Climate change mitigation

Although in some cases elevated CO_2 has been shown to promote soil C storage, in general, it leads to a loss of soil C through the input of more labile C sources to soil, which promote microbial breakdown of soil organic matter, a process called priming (van Groenigen et al. 2014). Moreover, it can also result in a disproportionate increase in the emission from soil of other potent greenhouse gases, such as N_2O and CH_4, thereby accelerating global climate change (van Groenigen et al. 2011). Warming can also increase soil C loss through increasing respiration and decomposition rates, especially where organic matter quality is low and under wet and cold climatic conditions, such as in peatlands. Successive drought also has the potential to promote loss of soil C and N after rewetting, primarily as CO_2 and N_2O, which are both potent greenhouse gases. The emission of methane, another potent greenhouse gas, might be increased by flooding, although also methane consumption might be stimulated, making the net effect on the efflux of this greenhouse gas hard to predict. Thus, elevated CO_2, warming, drought, and flooding all
have the potential to exacerbate climate change (Bardgett et al. 2008).

Disease suppression

A relatively unexplored topic is how climate change will affect the disease suppresiveness of soils, and the spread of plant and animal diseases, but also soil-borne human pathogens. Warming can accelerate egg development and hatching rate of parasites, and thus increase the seasonal window for parasite growth and infection (Hernandez et al. 2013). Consistent with this, the cumulative relative devilment rate of potato blight and brown spot has been shown to be increased with wetter, warmer winters (Van der Waals et al. 2013), and an oilseed rape infecting nematode has been shown to complete its life cycle faster under increased temperatures (Kakaire et al. 2012). However, the effects of climate change on the performance and spread of soil-borne human pathogens is unknown, although it has been suggested that they might increase with warming (Lee et al. 2013). Soil communities are important determinants for the success of invasive plant species (Callaway et al. 2004) and soil microbes (Van Elsas et al. (2012); thus, changes in soil communities as a result of climate change might alter the success of invasive organisms (Meisner et al. 2013).

Conclusions

The impacts of climate change on soil communities and their functioning vary widely, but it is clear that the different climatic drivers considered here significantly impact on soil communities. In general, soil functioning and the delivery of soil-based ecosystem services will be negatively affected, although there are still many unknowns. Other global change drivers, and their interactions with climate change drivers, form a significant threat for soil communities and the delivery of soil-based ecosystem services. Particularly N addition, land use change, and plant species diversity and identity have been shown to be major drivers of soil organisms responses to climate change, and have often been found to be more important in driving belowground community composition than climate change (Hagvar and Klanderud 2009, De Vries et al. 2012b, Eisenhauer et al. 2012a, Eisenhauer et al. 2013). Moreover, plant communities themselves might change in response to climate change, and the effects on the composition and functioning of soil food webs under these new conditions are relatively unexplored, but recent evidence suggests that changes in plant communities might be more important than direct effects of climate change for ecosystem functioning (Ward et al. 2013).

An understudied topic is the recovery of organisms and communities, as well as mechanisms of acclimation and adaptation, and the role of evolutionary changes in response to climate change. It has been shown that functional traits are important determinants of the recovery of organisms and communities after disturbance (Lindberg and Bengtsson 2006) (De Vries and Shade 2013), and that the recovery of processes of C and N cycling is linked to changes in communities (De Vries et al. 2012). Moreover, warming reduces generation times and can result in genetic adaptation, but also in greater horizontal gene transfer (Pritchard et al. 2011). These mechanisms might play an important role in the response of soil communities and their functioning to climate change (Orsini et al. 2013).

Finally, to predict and prevent the consequences of climate change for the functioning of terrestrial ecosystems, we need to quantify the relative role of the above mechanisms, and their interactions at different temporal and spatial scales, including fine scale responses within the soil microhabitat. This can be addressed by a variety of experimental approaches, including long-term, observational studies to gain knowledge on base line fluctuations, long-term field-based experiments manipulating interacting climate change and global change drivers, and plant community composition, and fine scale mechanistic experiments to address the response of soil biota at the phenotypic, genotypic, and functional level, and linking these responses to ecosystem functioning at different spatial and temporal scales.

Appendix

Table A1. Summary of the number of experimental studies reporting a decrease, increase, or no effect, for different microbial properties and groups, as a result of elevated CO_2. The summary column summarizes the effects found in the literature: + means the majority of studies found a positive effect, - indicates the majority of studies found a negative effect, 0 means that the majority of studies found no effect, or that the number of studies finding a positive and a negative effects was balanced.

	Up	Down	No effect	Summary
Microbial diversity	1 (Hayden *et al.* 2012)	1 (He et al. 2012)		0
Bacterial diversity	1 (Hayden *et al.* 2012)		4 (Ebersberger et al. 2004, Lipson et al. 2006, Austin et al. 2009, Ge et al. 2010)	0
Fungal diversity	0	0	2 (Klamer et al. 2002, Anderson et al. 2013)	0
Microbial abundance	6 (Klironomos et al. 1996, de Graaff et al. 2006, Chung et al. 2007, He et al. 2010, Eisenhauer et al. 2012a, Eisenhauer et al. 2013)	0	3 (Zak et al. 2000, Niklaus et al. 2007, Haugwitz et al. 2014)	+
Fungi	7 (Klironomos et al. 1996, Klamer et al. 2002, Lipson et al. 2006, Chung et al. 2007, Kandeler et al. 2008, Cheng et al. 2011, Guenet et al. 2012)	0	7 (Zak et al. 2000, Ebersberger et al. 2004, Niklaus et al. 2007, Van Groenigen et al. 2007, He et al. 2010, Anderson et al. 2013, Haugwitz et al. 2014)	+
Endophytes	1 (Brosi et al. 2011)	0	0	+
AMF*	3 (Klironomos et al. 1996, Drigo et al. 2007, Drigo et al. 2013)	0	0	+
Bacteria	3 (Klironomos et al. 1996, He et al. 2010, Drigo et al. 2013)	1 (Hayden *et al.* 2012)	6 (Zak et al. 2000, Ebersberger et al. 2004, Niklaus et al. 2007, Austin et al. 2009, He et al. 2010, Haugwitz	0

			et al. 2014)	
Gram negative bacteria	0	1 (Guenet et al. 2012)	0	-
Actinobacteria	0	1 (He et al. 2012)	0	-
Acidobacteria	1 (Lipson et al. 2006)	2 (Deng et al. 2012, He et al. 2012)	0	-?
Alpha-proteobacteria	1 (Lipson et al. 2006)	0	0	+
Beta-proteobacteria	1 (Lipson et al. 2006)	0	0	+
Proteobacteria	0	1 (He et al. 2012)	0	-
Cyanobacteria	0	1 (Deng et al. 2012)	0	-
Firmicutes	1 (Hayden *et al.* 2012)	1 (He et al. 2012)	0	0
Bacteroidetes	1 (Hayden *et al.* 2012)	0	0	+
Verrucomicrobia	0	1 (He et al. 2012)	0	-
Gemmatimonadaceae	0	1	0	-
AOB*	1 (Cantarel et al. 2012)	2 (Horz et al. 2004, Kelly et al. 2013)	0	-?
Archaea	0	0	0	?
Crenarcheota	0	1 (He et al. 2012)	0	-
Methanogens	0	0	1 (Liu et al. 2012)	0
N-cycling genes	2 (He et al. 2010, Kelly et al. 2013)	0	0	+
C-cycling genes	1 (He et al. 2010)	0		+

* AMF: arbuscular mycorrhizal fungi, AOB: ammonia oxidinsing bacteria

Table A2. Summary of the number of experimental studies reporting a decrease, increase, or no effect, for different microbial properties and groups, as a result of warming. The summary column summarizes the effects found in the literature: + means the majority of studies found a positive effect, - indicates the majority of studies found a negative effect, 0 means that the majority of studies found no effect, or that the number of studies finding a positive and a negative effects was balanced.

	Up	Down	No effect	Summary
Microbial diversity	1 (Hayden *et al.* 2012)	1 (Sheik et al. 2011)	3 (Kuffner et al. 2012, Weedon et al. 2012, Zhang et al. 2013)	0
Bacterial diversity	1 (Hayden *et al.* 2012)	2 (Sheik et al. 2011, Deslippe et al. 2012)	1 (Yergeau et al. 2012)	-
Fungal diversity	1 (Deslippe et al. 2012)	1 (A'Bear et al. 2013b)	1 (Anderson et al. 2013)	?
Methanogen diversity		1 (Kim et al. 2012)		-
Microbial abundance	5 (Kandeler et al. 1998, van Meeteren et al. 2008, Sheik et al. 2011, Djukic et al. 2013, Haugwitz et al. 2014)	1 (Andresen et al. 2014)	5 (Schindlbacher et al. 2011, Weedon et al. 2012, Zhou et al. 2012, Rousk et al. 2013, Zhang et al. 2013)	+
Fungi	7 (Clemmensen et al. 2006, Fujimura et al. 2008, Rinnan et al. 2009, Castro et al. 2010, Ma et al. 2011, Schmitt and Glaser 2011, Yergeau et al. 2012, Haugwitz et al. 2014)	4 (Rinnan et al. 2007, Gray et al. 2011, Jung et al. 2011, Li et al. 2013, Luo et al. 2014)	6 (Zogg et al. 1997, Schindlbacher et al. 2011, Gutknecht et al. 2012, Anderson et al. 2013, Rousk et al. 2013, Zhang et al. 2013)	+
Endophytes	0	0	1 (Brosi et al. 2011)	0
AMF	0	1 (Gray et al. 2011)	0	-
EMF*	2 (Clemmensen et	0	0	+

	al. 2006, Deslippe et al. 2012)			
Bacteria	6 (Kandeler et al. 1998, Rinnan et al. 2009, Sheik et al. 2011, Rousk et al. 2012, Yergeau et al. 2012, Haugwitz et al. 2014)	2 (Castro et al. 2010, Hayden et al. 2012)	4 (Schindlbacher et al. 2011, Gutknecht et al. 2012, Rousk et al. 2013, Zhang et al. 2013)	+
Gram negative bacteria	1 (Zhang et al. 2013)	1 (Gray et al. 2011)	0	0
Actinobacteria	4 (Sheik et al. 2011, Deslippe et al. 2012, Hayden et al. 2012, Kuffner et al. 2012, Luo et al. 2014)	0	0	+
Acidobacteria	1 (Sheik et al. 2011)	1 (Yergeau et al. 2012, Luo et al. 2014)	0	+
Alpha-proteobacteria	3 (Sheik et al. 2011, Hayden et al. 2012, Yergeau et al. 2012)	0	0	+
Proteobacteria	0	1 (Deslippe et al. 2012, Luo et al. 2014)	0	-
Verrucomicrobia	1 (Sheik et al. 2011)	0	0	+
Planctomycetes	1(Sheik et al. 2011, Luo et al. 2014)	0	0	+
Gemmatimonadaceae	0	1 (Deslippe et al. 2012)	0	-
Firmicutes	1 (Gray et al. 2011)	0	0	+
Methanotrophs	1 (Zheng et al. 2012)	0	0	+
AOB	0	1	0	-

		(Long et al. 2012)		
Archaea	0	1 (Jung et al. 2011)	0	-
AOA*	0	1 (Jung et al. 2011)	0	-
Crenarcheota	1 (Sheik et al. 2011)	0	0	+
Methanogens	0	1 (Kim et al. 2012)	0	-
N-cycling genes	3 (Jung et al. 2011, Cantarel et al. 2012, Zhou et al. 2012)	1 (Yergeau et al. 2012)	1 (Lamb et al. 2011)	+
C-cycling genes	1 (Zhou et al. 2012, Luo et al. 2014)	1 (Yergeau et al. 2012)	0	+

* EMF: ectomycorrhizal fungi; AOA: ammonia oxidising bacteria

Table A3. Summary of the number of experimental studies reporting a decrease, increase, or no effect, for different microbial properties and groups, as a result of drought. The summary column summarizes the effects found in the literature: + means the majority of studies found a positive effect, - indicates the majority of studies found a negative effect, 0 means that the majority of studies found no effect, or that the number of studies finding a positive and a negative effects was balanced.

	Up	Down	No effect	Summary
Microbial diversity	2 (Sheik et al. 2011, De Vries et al. 2012b)	0	0	+
Bacterial diversity	0	3 (Landesman and Dighton 2011, Yuste et al. 2011, Bouskill et al. 2013)	0	-
Fungal diversity	1 (Hawkes et al. 2011)	1 (Toberman et al. 2008)	2 (Landesman and Dighton 2011, Yuste et al. 2011)	0
Microbial abundance	2 (van Meeteren et al. 2008, Gray et al. 2011)	3 (Sheik et al. 2011, Hueso et al. 2012, Stevnbak et al.	1 (Rousk et al. 2013)	0

		2012)		
Fungi	13 (Gordon et al. 2008, Hawkes et al. 2011, Schmitt and Glaser 2011, Yuste et al. 2011, De Vries et al. 2012b, Evans and Wallenstein 2012, Guenet et al. 2012, Allison et al. 2013, De Vries and Shade 2013, Kaisermann et al. 2013, Zeglin et al. 2013, Fuchslueger et al. 2014, Haugwitz et al. 2014)	5 (Liiri et al. 2002, Williams 2007, Williams and Rice 2007, Toberman et al. 2008, Berard et al. 2012)	3 (Bapiri et al. 2010, Hueso et al. 2012, Rousk et al. 2013)	+
AMF	1 (Fuchslueger et al. 2014)	0	0	+
Bacteria	1 (Fuchslueger et al. 2014)	6 (Liiri et al. 2002, Bapiri et al. 2010, Berard et al. 2012, Hueso et al. 2012, Allison et al. 2013, Goransson et al. 2013)	2 (Williams 2007, Rousk et al. 2013)	-
Gram positive bacteria	2 (De Vries and Shade 2013, Fuchslueger et al. 2014)	3 (Schmitt and Glaser 2011, Guenet et al. 2012, Hueso et al. 2012)	1 (Berard et al. 2012)	-
Gram negative bacteria	2 (Schmitt and Glaser 2011, Fuchslueger et al. 2014)	0	0	+
Actinomycetes	0	1 (Schmitt and Glaser 2011)	0	-
Actinobacteria	1 (Bouskill et al. 2013)	1 (Evans and Wallenstein 2012)	0	0
Acidobacteria	1	1	0	0

	(Evans and Wallenstein 2012)	(Bouskill et al. 2013)		
Alpha-proteobacteria	1 (Bouskill et al. 2013)	0	0	+
Verrucomicrobia	1 (Evans and Wallenstein 2012)	0	0	+
Planctomycetes	1 (Bouskill et al. 2013)	0	0	+
AOB	0	0	1 (Peralta et al. 2013)	0
Archaea	0	0	0	
AOA	0	0	1 (Peralta et al. 2013)	0
N-cycling genes	1 (Liu et al. 2012)	0	1 (Peralta et al. 2013)	+

Table A4. Summary of the number of experimental studies reporting a decrease, increase, or no effect, for different microbial properties and groups, as a result of water addition and flooding. The summary column summarizes the effects found in the literature: + means the majority of studies found a positive effect, - indicates the majority of studies found a negative effect, 0 means that the majority of studies found no effect, or that the number of studies finding a positive and a negative effects was balanced.

	Up	Down	No effect	
Archaeal diversity	1 (Kemnitz et al. 2004)	0	0	+
Microbial abundance	1 (Zhou et al. 2012)	2 (Mentzer et al. 2006, Gray et al. 2011)	1 (Zhang et al. 2013)	-?
Fungi	2 (Williams 2007, Williams and Rice 2007)	0	1 (Bi et al. 2012)	+
AMF	0	1 (Mentzer et al. 2006)	0	-
Bacteria	0	0	1 (Bi et al. 2012)	0
Gram positive bacteria	2 (Mentzer et al. 2006, Guenet et al. 2012)	1 (Schutz et al. 2009)	1 (Bi et al. 2012)	+

Gram negative bacteria	1 (Mentzer et al. 2006)	0	1 (Bi et al. 2012)	+
Acidobacteria	1 (Castro et al. 2010)	0	0	+
Proteobacteria	0	1 (Castro et al. 2010)	0	-
Methanotrophs	1 (Bodelier et al. 2012)	0	0	+
AOB	0	0	1 (Peralta et al. 2013)	0
Archaea	0	0	0	
Methanogens	1 (Kemnitz et al. 2004)	0	0	+
AOA	0	0	1 (Peralta et al. 2013)	0
N cycling genes	0	0	1 (Lamb et al. 2011)	

Literature search

We reviewed the literature for effects of elevated CO_2, warming, drought, and flooding on soil microbial communities, and soil fauna in Web of Science. For soil microbial communities, we included all years, while for soil fauna, we focussed on studies published after the comprehensive metaanalysis of Blankinship et al. (Blankinship et al. 2011), from 2008 to present. We sorted all relevant papers manually, and we ignored systems, vegetation types, and climate change drivers that are irrelevant to the UK.

Search terms used:

"soil biodiversity" and "climate change"

Soil fauna* and "climate change"

"soil food web" and "climate change"

Soil fauna* and drought

Soil fauna* and warming

Soil fauna* and CO2

Soil nematode* and "climate change"

Soil protozoa* and "climate change"

Soil microarthropod* and "climate change"

Soil mite* and "climate change"

Soil collembola* and "climate change"

Earthworm* and "climate change"

Soil nematode* and drought

Soil protozoa* and drought

Soil microarthropod* and drought

Soil mite* and drought

Soil collembola* and drought

Earthworm* and drought

Soil nematode* and warming

Soil protozoa* and warming

Soil microarthropod* and warming

Soil mite* and warming

Soil collembola* and warming

Earthworm* and warming

Soil nematode* and CO2

Soil protozoa* and CO2

Soil microarthropod* and CO2

Soil mite* and CO2

Soil collembola* and CO2

Earthworm* and CO2

Soil nematode* and flooding

Soil protozoa* and flooding

Soil microarthropod* and flooding

Soil mite* and flooding

Soil collembola* and flooding

Earthworm* and flooding

Soil microb* communit* and "climate change"

Microbial diversity and warming

"Microbial community" and warming

"Fungal community" and warming

"Bacterial community" and warming

Microbial diversity and CO2

"Microbial community" and CO2

"Fungal community" and CO2

"Bacterial community" and CO2

Microbial diversity and drought

"Microbial community" and drought

"Fungal community" and drought

"Bacterial community" and drought

Microbial diversity and flooding

"Microbial community" and flooding

"Fungal community" and flooding

"Bacterial community" and flooding

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