

SPECIAL FEATURE – FORUM

PLANT–SOIL FEEDBACKS IN A CHANGING WORLD

Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle

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Summary

1. Interactions between plant and soil communities play a major role in determining the impact of climate change on ecosystem functioning and the carbon cycle, and the mechanisms involved operate over a wide range of spatial and temporal scales.

2. We present a framework for understanding the consequences of climate-induced changes in plant–soil feedback for the carbon cycle. The framework describes a hierarchy of mechanisms by which changes in climate impact on ecosystem carbon dynamics at three levels of response, namely individual and community reordering and species immigration and loss.

3. For each level, we identify the mechanisms by which climate change impacts on plant–soil interactions with consequences for the carbon cycle. We also demonstrate that the potential for decoupling of plant–soil interactions increases across the three levels of response, being greatest with species immigration and/or loss, for example, if plants were to undergo a biome shift, but their associated soil communities did not. Such decoupling is a largely unrecognized, but potentially important regulator of the future global carbon cycle.

4. *Synthesis.* The framework presented here highlights a need for a new approach to the study of climate change impacts on plant–soil interactions and carbon cycling that integrates this hierarchy of responses, and incorporates the decoupling of above-ground and below-ground networks, across a range of temporal and spatial scales, and ecosystems.

Key-words: carbon cycling, climate change, decomposition, decoupling plant–soil interactions, nutrient cycling, plant–soil (below-ground) interactions, range expansion, soil organisms

Introduction

Climate change impacts on biogeochemical cycles via a variety of mechanisms that involve interactions between plant and below-ground communities (Bardgett, Freeman & Ostle 2008; Kardol *et al.* 2010). These mechanisms operate across several spatial and temporal scales: in the short term, over intra- and interannual time-scales, climate change impacts on the physiology and activity of above-ground and below-ground biota; in the long term, over tens to hundreds of years, climate change can cause species range expansions and contractions. All of these have local- and, potentially, global-scale implications for biogeochemical cycles. Of these cycles, one that has

attracted much recent attention is the terrestrial carbon cycle, due largely to concerns about the potential for climate change to destabilize ecosystem carbon fluxes and thus amplify climate change (Cox *et al.* 2000; Friedlingstein *et al.* 2006). While climate change can impact directly on soil carbon, for instance by stimulating rates of decomposition under warming (Yuste *et al.* 2007), there is also potential for indirect impacts via changes in vegetation. Indeed, there is accumulating evidence that climate-induced changes in the growth and structure of plant communities will alter the amount and quality of plant-derived carbon entering soil via root exudates and plant litter (shoot and root), and that this in turn can have cascading effects on soil organisms and the processes of carbon cycling that they drive (Bardgett 2011). Given that the mechanisms underlying these changes operate at different temporal and spatial scales, their impact upon carbon cycling will likewise

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operate at multiple scales, varying from local, and relatively rapid changes at the community and ecosystem scale, to longer-term effects with consequences at the global scale.

In this article, we present a framework for understanding the consequences of climate-induced changes in plant–soil feedbacks for the carbon cycle. This framework describes a temporal and spatial hierarchy of plant–soil feedback responses to climate change and is intended as an aid in understanding the consequences of these responses for the carbon cycle at local and global scales. It is based on the hierarchical response framework of Smith, Knapp & Collins (2009), which was proposed for assessing ecosystem responses to chronic resource alterations resulting from global change. This framework identifies a hierarchy of mechanisms by which changes in climate indirectly impact on ecosystem carbon dynamics at three levels of response, namely individual and community reordering and species immigration and loss. Here, we modify this framework to consider the range of potential mechanisms by which plant–soil feedbacks can regulate carbon cycle responses to climate change at different spatial and temporal scales. We also illustrate how this framework can be used to identify important mechanisms and

inform future research about the way that climate-mediated changes in plant–soil interactions might impact on carbon cycling at multiple scales.

A hierarchy of mechanisms

INDIVIDUAL RESPONSES

Individual responses involve changes in the activity, metabolism, behaviour and phenology of organisms, without alteration of community structure, at least in the short term. At this scale, plant and soil communities are tightly coupled via mutual responses to environmental cues such as temperature and moisture, which are themselves driven by short-term variability in weather and climate. Such coupling is effectively instantaneous (Fig. 1) and driven by plant inputs (litter and root exudates) of carbon and nutrients to soil, which act as a substrate for micro-organisms, and by microbial processes that regulate nutrient availability to plants (Fig. 2b). In most cases, climate change will affect plant–soil interactions by altering the magnitude of such coupling, for instance by increasing root exudation and stimulating microbial activity, albeit with

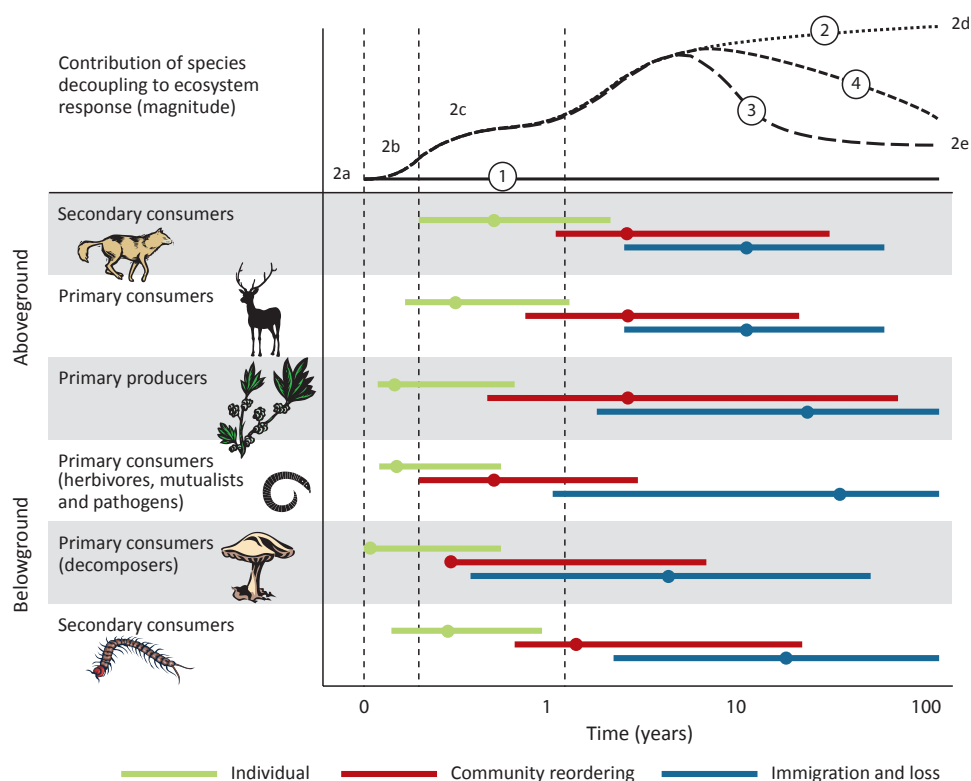


Fig. 1. The hierarchical response model of ecosystem response to climate change. The estimated time-scale of response to climate change for each class of mechanism is shown. The top panel shows the hypothetical contribution of species decoupling to ecosystem response under four scenarios: (1) Species remain coupled, or there is no decoupling because species are functionally equivalent; (2) Increasing decoupling across time, as outlined in the text; (3) Dispersal recouples species interactions system after a period of temporary disequilibrium (fairly rapid dampening); and (4) Evolution recouples species interactions after a period of temporary disequilibrium (slower dampening). Note that overall ecosystem response could still be strong in each of these scenarios. The lower panels show the approximate timings of the initial response to a chronic global change driver (as opposed to an extreme event) at the levels of the individual and community reordering and species immigration and loss. Each bar shows the range over which initial response is likely to occur, with the circle representing the median of the responses, that is, the point in time where most of the organisms from a functional group will respond. Long bars therefore reflect both uncertainty and within-group variation (e.g. in generation times or dispersal capacity). Vertical dashed lines refer to the scenarios presented in Fig. 2.

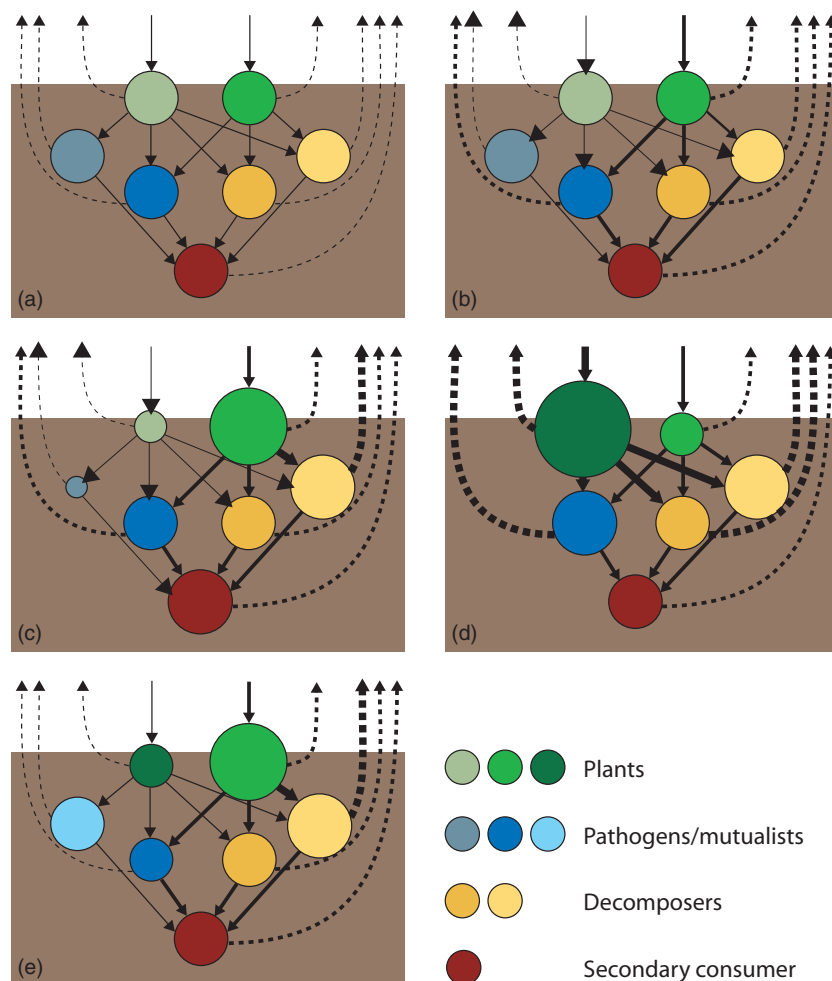


Fig. 2. Alteration of trophic relationships according to a hierarchy of responses to climate change and their effects upon carbon cycling. Arrows represent the flow of carbon; solid arrows represent net input, and dashed arrows represent net output, with arrow size proportional to flow. Circle size shows relative abundance of species in a simplified soil food web, with colours representing species identity. (a) The unperturbed system prior to the onset of a chronic global change driver. (b) The system after the onset of individual effects but before community reordering with one species less able to perform under the new conditions. (c) The system after community reordering has occurred with the poorly performing plant species becoming less abundant in competition with responding species. The abundance of its specialist symbiont or pathogen is proportionately reduced, whereas the abundance of one decomposer increases with increasing production of the responding plant species. (d) A long-term response in which the poorly performing plant species, and its pathogen or symbiont, is lost from the system, and in which a new competitively superior plant species is added that has escaped its natural enemies. As a result of the introduction of this highly successful species, the biomass of the non-specialist mutualist or pathogen increases, and the biomass of one decomposer remains high. (e) A long-term response in which an invasive microbe reduces the abundance of the invasive plant species, thus increasing the competitive ability of the native plant species and dampening the contribution of decoupling of ecosystem carbon cycling. The biomass of the native, non-specialist, mutualist or pathogen is reduced as a result of competition with the newcomer. See Fig. 1 for the time-scales of these changes.

potentially significant local-scale consequences for carbon cycling. For example, plants typically respond to warming and increased precipitation by increasing photosynthesis and respiration rates (Wu *et al.* 2011), and plants can respond rapidly to warmer temperatures by down-regulating respiration to maintain a positive carbon balance (Atkin & Tjoelker 2003). Atmospheric CO₂ enrichment also stimulates plant growth and the availability of photosynthate within the plant (Körner *et al.* 2005), which can increase carbon flux to roots, mycorrhizal fungi and free-living soil microbes via root exudation of easily degradable sugars, organic acids and amino acids. Such enhanced rhizodeposition can in turn stimulate root respiration (Pritchard *et al.* 2008; Jackson *et al.* 2009) and soil

organic matter mineralization (Drake *et al.* 2011; Phillips, Finzi & Bernhardt 2011), leading to soil carbon losses (Cheng *et al.* 2012; Phillips *et al.* 2012). It can also stimulate rates of nitrogen mineralization, thereby sustaining long-term increases in tree growth (Drake *et al.* 2011; Phillips, Finzi & Bernhardt 2011). However, in certain situations, enhanced root carbon supply (Diaz *et al.* 1993; De Graaff, Six & Van Kessel 2007), combined with increased carbon-to-nitrogen ratio of plant litter (Cotrufo *et al.* 1994; Körner & Miglietta 1994), under elevated CO₂ can lead to nitrogen immobilization, which limits nitrogen availability to plants, thereby creating a negative feedback on plant growth and carbon transfer to soil.

Climate change can also directly change the activity of below-ground organisms. For example, warming can directly increase soil microbial activity and differentially stimulate a host of functional genes involved in soil carbon degradation, leading to increased soil respiration (Yuste *et al.* 2007; Dorrepaal *et al.* 2009; Wu *et al.* 2011; Zhou *et al.* 2012). Although a topic of much debate, it has been argued that this increase is temporary and that, in the longer-term, microbial respiration acclimates to increased temperatures (Bradford *et al.* 2008; Hartley *et al.* 2008). In tandem, warming can also enhance microbial processes involved in nitrogen cycling, including nitrogen mineralization, nitrification and nitrogen fixation (Turner & Henry 2010), leading to increased plant nitrogen use and stimulated growth (Zhou *et al.* 2012). In fact, these indirect effects of warming are thought to be the strongest driver for greater plant production under increased temperatures (Lin, Xia & Wan 2010). However, it is not known whether these processes are down-regulated under prolonged warming.

Climate change can also decouple interactions between plant and soil communities. We define decoupling here as the disruption of a previously existing ecological interaction, due to altered activity or absence of one or both partners, as the result of differences in phenology, abundance, dispersal or extinction. In the short term, phenological differences will be the main cause of this decoupling. For example, changes in climate can affect plant phenology and alter both growing season length (Menzel & Fabian 1999; Piao *et al.* 2007) and flowering patterns (Fitter & Fitter 2002). Virtually nothing, however, is known about the impact of climate change on the phenology of below-ground organisms, although Gange *et al.* (2007) showed that recent climate change has extended the fruiting period of many British fungi. There is some evidence that such phenological changes in fruiting are mediated by plants, as many fungal species are ectomycorrhizal (Gange *et al.* 2007), and phenological changes above-ground and below-ground are closely linked (Kausserud *et al.* 2008). However, fungi display species-specific phenology and time-lags in their phenological response, with fruiting responses being influenced by the previous year's weather conditions (Kausserud *et al.* 2010). These complex patterns point to the potential for phenological decoupling between above-ground and below-ground organisms, particularly if weather becomes more variable in the future (IPCC 2007).

Decoupling of temporal dynamics between plants and soil microbes related to nutrient supply may also occur over intra-annual scales, with the potential to alter carbon cycling. This can be seen in alpine ecosystems where nitrogen, the main growth-limiting resource, is partitioned between plant and distinct microbial communities over the growing season (Jaeger *et al.* 1999; Bardgett *et al.* 2002), with fungal-rich microbial communities immobilizing nitrogen in winter when plant nitrogen demand falls, and bacterial communities, which mineralize nutrients for plant use, thriving in the summer (Schadt *et al.* 2003; Lipson & Schmidt 2004). Climate change could disrupt this intimate partitioning of nutrients between plant and microbial communities via increased soil freezing, as a

result of reduced snow cover, thereby impacting on winter microbial communities and the dynamics of carbon and nitrogen cycling (Monson *et al.* 2006). In general, below-ground organisms are highly susceptible to extreme weather events, perhaps even more so than to changes in temperature and precipitation regimes (Bardgett & Wardle 2010). However, the relative response of below-ground and above-ground organisms to extreme weather events is not known, making it difficult to assess whether or not they respond in synchrony to such environmental change. If mortality in response to extreme events of drought, heat and freezing differs between below-ground and above-ground organisms, then decoupling will occur, with likely impacts on the carbon cycle.

COMMUNITY REORDERING

Short-term physiological and phenological changes to individual organisms in response to changing precipitation patterns, temperature increases and elevated CO₂ will, on time-scales of years to decades, lead to community reordering, both above-ground and below-ground (Fig. 1). This second class of mechanism involves changes to species abundance, but not to the extinction or invasion of species (Fig. 2c). Changes in plant community structure alter the amount and quality of organic carbon entering soil and modify the soil physical and chemical environments. Therefore, climate-induced vegetation shifts can have substantial impacts on soil communities and carbon cycling. For example, Zhang *et al.* (2011a) showed in tallgrass prairie that warming increased the above-ground biomass of C₄, but not C₃ plants, resulting in a lower-quality carbon inputs to soil, thereby increasing fungal abundance and lowering soil respiration (Zhang *et al.* 2011b). Also, studies have shown that reduced precipitation (Debinski *et al.* 2010; Hoepfner & Dukes 2012) and warming (Weltzin *et al.* 2003; Hoepfner & Dukes 2012) select for deeper rooting, woody plant species, which in turn increase below-ground carbon inputs and mycorrhizal colonization (Rillig 2004), thereby increasing soil carbon stabilization through aggregate formation (Wilson *et al.* 2009). Finally, elevated CO₂ has been shown to favour C₄ grasses (Pendall *et al.* 2011), woody species (Souza *et al.* 2010) and legumes (Hanley, Trofimov & Taylor 2004), which all have distinct litter chemistries, thereby impacting microbial communities and carbon dynamics.

Climate-induced changes in soil communities typically occur over shorter time-scales than those in plant communities, potentially causing decoupling of the above-ground and below-ground subsystems (Fig. 1). There is evidence that some plant communities are highly resistant to simulated climate change (Grime *et al.* 2008; Hudson & Henry 2010), and several studies reveal that below-ground communities are affected by climate manipulations, while above-ground communities are not. For example, Yergeau *et al.* (2012) found consistent changes in microbial communities after three years of warming across sub-Antarctic and Antarctic environments, but no change in plant communities. Similarly, Cantarel *et al.* (2012) found, in a factorial climate change

experiment on grassland, that the gene copy abundance of N₂O reducer and ammonia-oxidizing bacteria increased after four years of experimental warming, whereas plant communities were unchanged. Conversely, a study of climate change impacts in a Californian grassland showed that soil bacteria and archaea did not respond to rainfall manipulations, despite profound responses of plant and animal communities above-ground (Cruz-Martinez *et al.* 2009), indicating that, in some cases, soil microbial communities may be more resistant to alterations in climate than their associated above-ground communities.

The mechanisms for differential responses between above-ground and below-ground organisms to climate change are unclear, but it is likely to be due to differences in generation times and in the resistance and resilience of above-ground and below-ground communities. For example, it has been shown that drought results in rapid death of soil microbes and fauna, with long term, and potentially irreversible consequences for community composition and carbon and nutrient cycling (Lindberg & Bengtsson 2006; De Vries *et al.* 2012a). Moreover, these responses are related to the life history strategies of soil organisms: fast-growing organisms are generally more susceptible to drought, but their populations recover quicker than slow-growing organisms do (De Vries *et al.* 2012a). Higher trophic levels, which influence nutrient and carbon cycling through trophic cascades (Laakso, Setälä & Palojarvi 2000), also recover more slowly than lower trophic levels (Lindberg & Bengtsson 2006; De Vries *et al.* 2012b; Fig. 1). The consequences of such differential above-ground and below-ground responses to climate change for carbon cycling are not known. However, the decoupling of networks, both within below-ground food webs and between plant and below-ground communities, is likely to influence future ecosystem resistance and resilience to climate change-related disturbances (De Vries *et al.* 2012a,b).

Changes in the abundance of below-ground mutualists, pathogens and pests can also feedback to plant communities and alter their response to climate change. An example of this concerns below-ground pathogens that are likely to be affected by climate change phenomena, such as increased growing season length, increased temperature or CO₂ and changes in precipitation (Newton, Johnson & Gregory 2011). Increases in temperature can increase reproduction rates of below-ground pathogens, and warmer soil temperatures during winter might allow novel pathogens to overwinter (Pritchard 2011; Fitzpatrick 2012). Disease outbreaks as a result of these changes can affect plant communities and correspondingly ecosystem carbon cycling. Olofsson *et al.* (2011) provide a striking example of this; they found in a snow manipulation experiment that an outbreak of the host-specific fungal pathogen *Atyridia empetri* (which is favoured by extended humid periods) in plots with increased snow cover strongly reduced the abundance of the dwarf shrub *Empetrum hermaphroditum*, switching the ecosystem from a carbon sink to a source. Warming might also stimulate horizontal gene transfer between bacterial and fungal species, with implications for microbial pathogenicity or mycorrhizal relationships

(Pritchard 2011), thus generating functionally novel organisms with potential knock-on effects for carbon cycling. Finally, the picture is complicated further by impacts of climate change on multi-trophic interactions involving plants, grazers and their predators, which can have significant, but unpredictable, impacts on carbon and nutrient cycling (Stevnbak *et al.* 2012).

SPECIES IMMIGRATION AND LOSS

The long-term consequence of individual species responses and community reordering to climate change is the entry and loss of species from ecosystems, both above-ground and below-ground; this is the third mechanism through which climate change alters plant–soil interactions (Figs 1 and 2d,e). The consequence of these changes is that entirely new functional attributes may be added to the ecosystem or lost; new biotic interactions between species, both above-ground and below-ground, can emerge, while existing biotic interactions may cease (Wardle *et al.* 2011; van der Putten 2012). While invasion and extinction may occur rapidly at local scales, landscape-level change of this kind can take decades, and for long-lived, slowly dispersing species, the process may take hundreds of years (Figs 1 and 2d,e). Species gain and loss are extremely complex and involve a wide array of processes including physiological changes, dispersal and altered community interactions. As a result of this complexity and the variety of species responses to climate change, long-term changes in climate will decouple above-ground and below-ground communities, with potentially major consequences for ecosystem carbon cycling (Figs 1 and 2d,e).

There is much evidence of climate change causing major shifts in species ranges, with many species recently expanding their ranges towards the poles and higher elevations (Walther *et al.* 2002; Parmesan & Yohe 2003; Hickling *et al.* 2006). Also, species that cannot adapt or disperse quickly enough under changing climatic conditions may be pushed beyond their niche limits, leading to species losses (Thomas *et al.* 2004; Schweiger *et al.* 2008; Zhu, Woodall & Clark 2012). Such range shifts lead to species gains and losses in the new and old range, respectively, and, in the longer term, biome shifts, which will consequently impact on the global carbon cycle. This global reorganization of ecosystems is already taking place. For example, warming is responsible for the widespread upward movement of alpine plant species (Walther, Beissner & Burga 2005; Lenoir *et al.* 2008), northward expansion of boreal forest (Danby & Hik 2007), shrub expansion in arid and semi-arid ecosystems (Schlesinger *et al.* 1990) and shrub encroachment in arctic tundra (Wookey *et al.* 2009); such range shifts can impact on below-ground processes and the carbon cycle. For example, expanding shrubs in the arctic produce recalcitrant litter that decelerates decomposition, thereby potentially reducing ecosystem carbon losses (Cornelissen *et al.* 2007). Evidence for range-expanding below-ground organisms is limited, but the northward movement into Ireland of the earthworm *Proseolodrilus amplusetosus*, an endemic to southern France, has been docu-

mented (Melody & Schmidt 2012). This has implications for carbon cycling because it is known to feed upon soil carbon fractions that are inaccessible to resident species (Melody & Schmidt 2012).

Because species differ strongly in their capacity to tolerate and migrate in response to climate change (Fig. 1), novel communities of organisms are likely to become commonplace in the future (Keith *et al.* 2009; Lavergne *et al.* 2010). There have been numerous discussions of these changes in the context of species conservation (Abeli *et al.* 2012; Crossman, Bryan & Summers 2012), disease spread (Coakley, Scherm & Chakraborty 1999; Bradley, Gilbert & Martiny 2008) and pest management (Thomson, Macfadyen & Hoffmann 2010; Ziska *et al.* 2011). However, it is less widely recognized that such community restructuring will decouple existing functional interactions between, and within, above-ground and below-ground communities and that this could have consequences for carbon cycling (Figs 1 and 2d,e). An example of this concerns the close association that develops between plant species and the decomposer community, whereby plant litters decompose more rapidly in their home environment than in those dominated by other plant species (Vivanco & Austin 2008; Ayres *et al.* 2009). This phenomenon, called home field advantage, appears to be stronger for plants producing more complex litter and involves several groups of soil organisms (Milcu & Manning 2011), many of which may not disperse at the same rate as plants. Therefore, when plants migrate, but their associated decomposers do not, such home field advantages may be disrupted, with consequences for decomposition and hence ecosystem carbon cycling. However, most evidence points to plant litter quality and climate as the main determinants of decomposition (Cornwell *et al.* 2008), and the influence of soil food webs relative to these factors varies across biomes (Gonzalez & Seastedt 2001; Wall *et al.* 2008); hence, the consequence of plants encountering new decomposer communities is unclear and likely to be ecosystem or biome specific.

The decoupling of plants from their specialist pathogens and mutualists could also alter carbon cycling, as it is known that these organisms influence plant productivity and community structure (Maron *et al.* 2011; Schnitzer *et al.* 2011). Evidence that soil pathogens are less able to disperse than plants comes from studies of invasive species, which often escape specialist pathogens from their native range. Invasive species experiencing such enemy release display greater growth and dominance in their new range (Klironomos 2002), and range-expanding plants may similarly suffer less from pathogen-driven negative feedback and hence form new communities with greater above-ground and below-ground productivity (van Grunsven *et al.* 2007; Engelkes *et al.* 2008) and higher carbon input to the soil (Fig. 2d). This effect may be strongest in species-poor communities where the effects of specialist pathogen suppression are strongest (Maron *et al.* 2011; Schnitzer *et al.* 2011). The capacity of mutualistic micro-organisms to disperse and form relationships with invading plants may also have implications for the global carbon cycle. The growth of invasive legumes can be limited by

the suitability of local bacterial species (Parker, Malek & Parker 2006; Callaway *et al.* 2011), and there is evidence that tree invasion of new habitats can be limited by ectomycorrhizal availability (Terwilliger & Pastor 1999; Collier & Bidartondo 2009). Such limitations could potentially exert an influence over biome redistribution under climate change and would represent a major deviation from current estimates of future carbon cycling derived from dynamic global vegetation models (DGVM's) where effective dispersal is assumed (Sitch *et al.* 2003; Ostle *et al.* 2009). There is also the possibility that plant–mutualist interactions are less effective in the new range when compared with the original range; invasive plants can form mycorrhizal relationships, but these deliver less benefit to them than those formed in their native range (Klironomos 2003). The consequence of this would be reduced plant growth and below-ground carbon transfer.

Ultimately, the natural enemies of expanding plants, as well as their predators, might arrive in the expansion range of their host, and changes could be nullified (Figs 1 and 2e). However, species differences in phenological cues and the potential to form novel relationships with species encountered within the new range mean that there is uncertainty as to whether the original interactions will become reestablished (Richardson *et al.* 2000; Menendez *et al.* 2008; Fig. 1) and whether the decoupling of above-ground–below-ground interactions will destabilize ecosystem functions (Mougi & Kondoh 2012). Another possibility is that, in the long term, the co-evolution of species and their new associates may result in new ecosystems that function similarly to those found today (Fig. 1), although the capacity for this to occur remains highly uncertain.

Synthesis and reflections

The hierarchical response framework used here (Smith, Knapp & Collins 2009) demonstrates that climate change alters plant–soil interactions across several scales, ranging from rapid individual and physiological responses that operate at a local scale to longer-term impacts caused by community reordering and immigration with possible consequences for the global carbon cycle. Distinguishing these scales and the mechanisms involved provides a means of structuring current knowledge and guiding the design of future studies. It also highlights that, despite significant gaps in knowledge, most quantitative information on climate change impacts on plant–soil interactions and the carbon cycle is at individual and community reordering scales. In contrast, very little is known about the potential for climate change to impact on plant–soil interactions at regional or continental scales, which involves processes of species immigration and loss that occurs over decades or hundreds of years.

Our synthesis reveals that there is significant potential for climate change to decouple plant–soil interactions across all three scales. We identify that there is enormous potential for climate change to disrupt the myriad of biotic interactions that have evolved over time between plant and soil communities, involving mutualists, pathogens, consumers and decomposers,

and that this will have unknown, but potentially highly significant consequences for ecosystem functioning and the carbon cycle. In particular, we highlight that differences in the dispersal, and hence immigration of above-ground and below-ground communities under climate change, could disrupt existing biotic interactions and create new ones (Berg *et al.* 2010; van der Putten 2012). The impact of these changes will be strongly dependent on the degree of redundancy in soil communities and the specificity of interactions between species; and decoupling will have the greatest impact if species are not functionally equivalent and differ strongly in their interaction strengths with other organisms. Documenting and understanding the consequences of such disruption to above-ground and below-ground interactions for the global carbon cycle represent a major research challenge.

To improve our understanding of the consequences of plant–soil interactions and species decoupling for the global carbon cycle (Fig. 1), we require a new, more integrated research approach. This should link all three scales of the hierarchical response framework, for example, by incorporating species range shift modelling that includes realistic assumptions about the dispersal of below-ground organisms, with experiments that examine short (intra- and interannual)- and long-term (decadal) effects of multiple climate change drivers on individual and community reordering and their consequences for the carbon cycle. For example, data detailing the current distribution of below-ground organisms could be fed into mechanistic climate envelope models, and modelled outputs could generate scenarios of species loss and gain. These could then be simulated using experimental addition and removal of species in selected ecosystems. Resulting information could ultimately inform larger-scale ecosystem models, such as DGVMs, which do not currently contain dispersal limitations or biotic interactions (Sitch *et al.* 2003; Ostle *et al.* 2009). Such a research programme would be demanding, but its findings could prove essential if we are to accurately predict the response of the global carbon cycle to climate change.

Future directions

Our article highlights a critical need for a hierarchical approach to the study of climate change impacts on plant–soil interactions and carbon cycling that incorporates mechanisms and responses that occur across different temporal and spatial scales. To achieve this, we identify a series of research challenges.

- 1 There is a need for improved understanding of the distribution patterns and dispersal capacity of different groups of below-ground organisms and the factors that control these; without such information, we cannot predict how below-ground community composition and species ranges will change in the face of climate change at local, regional or continental scales.
- 2 There is a need to understand the speed and magnitude of evolutionary responses to previously un-encountered organisms and networks. Key questions include the following: will co-evolutionary change lead to the reestablishment of specific interactions between plants and soil organisms like those seen before species immigration or loss, returning function to levels seen in equivalent climates today (Fig. 1; scenario of dampened response)? Or will species fail to evolve or form new biotic interactions and functional relationships with no current day equivalent (Fig. 1; scenario of heightened response), resulting in functionally novel ecosystems?
- 3 The extent to which plant–soil interactions are driven by climate versus soil fertility is not known, although the relative importance of these factors as drivers of above-ground and below-ground communities is likely to vary across ecosystems. Therefore, we require an improved understanding of how impacts of climate change on plant–soil interactions and carbon cycling vary across communities, ecosystems and biomes.
- 4 Better understanding of the role of multi-trophic interactions, involving plants and soil communities, and also grazers and their predators, in governing climate change impacts on carbon cycles at individual, community and regional scales (Fig. 1). Such information is needed to accommodate biotic factors in predictive models to accurately simulate ecosystem carbon dynamics.
- 5 Finally, there is a need for greater consideration of plant–soil interactions, and the hierarchy of mechanisms involved, in carbon cycling models. Current models explore controls on carbon cycling at different scales, ranging from global circulation models to soil carbon process models at the field scale. But they are very coarse and do not accurately represent the hierarchy of biological interactions highlighted here.

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