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PLANT TRAIT-BASED APPROACHES FOR INTERROGATING BELOWGROUND FUNCTION

Richard D. Bardgett

ABSTRACT

Trait-based approaches, which focus on the functional characteristics of organisms rather than their taxonomic identity, offer a means to explain how plant communities and ecosystem functions respond to environmental change. Here I review recent developments in the use of plant trait-based approaches for interrogating the functioning of soils and their response to global change. Plant traits impact soil functioning via multiple routes with feedback consequences for biogeochemical cycles and plant community dynamics. They also display a high degree of plasticity in response to global change; as such, there is much potential for global change-induced shifts in trait spectra, both aboveground and belowground, to impact soil functions with feedbacks to biogeochemical cycling across multiple scales. Recent research reveals that root traits play a particularly important role in influencing the soil environment, with strong impacts on a host of physical, chemical and biological soil properties. Although a fast-moving topic, many challenges regarding the use of trait-based approaches to interrogate soil functioning remain. I identify three. First, there is a need for improved understanding of genotypic- and species-level variation in plant traits, especially of root traits that have the strongest potential to influence soil function. Second, there is a need to incorporate new understanding of links between plant traits and soil processes into terrestrial biogeochemical and dynamic vegetation models, in order to enhance their predictive power. Finally, there is a need to harness new understanding of plant traits and their impact on soil functions in sustainable food production systems, in particular to enhance resource acquisition by crop plants. This last point is especially important given the extent that soils are degraded worldwide, and the need to develop sustainable ways of managing soil to prevent further degradation whilst also increasing the production of food.

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INTRODUCTION

Understanding the factors that regulate the functioning of terrestrial ecosystems has long been a dominant theme in ecology, but it has risen in prominence in recent years due to its fundamental importance for managing Earth's natural resources. Many abiotic factors determine the functioning of terrestrial ecosystems, such as climate, geology and resource availability. However, a growing body of evidence points to biotic factors, including shifts in vegetation diversity and composition, also playing a prominent role. Much of this research has focussed on the importance of plant diversity and composition for aboveground ecosystem processes, especially plant productivity (Hooper *et al.* 2005; Cardinale *et al.* 2012; Tilman *et al.* 2014). However, an increasing focus of research is devoted to the belowground, exploring how changes in vegetation diversity and composition influence soil functions and their response to global change (Bardgett and Wardle 2010; Bardgett *et al.* 2013).

Trait-based approaches, which focus on the functional characteristics of organisms rather than their taxonomic identity, are increasingly being used to explain how plant communities and ecosystem functions respond to environmental change (Díaz *et al.* 2007; de Bello *et al.* 2010; Lavorel *et al.* 2013). Further, these approaches are being used to interrogate the belowground, in order to predict how changes in vegetation composition influence soil properties and processes (De Deyn *et al.* 2008; Bardgett *et al.* 2014; Laliberté 2017), and how shifts in the structure of complex belowground communities impact the functioning of soil (Allison 2012; Krause *et al.* 2014; Aguilar-Trigueros *et al.* 2015). The goal of this article is to provide a synthesis of recent developments in the use of plant trait-based approaches for interrogating soil functioning and the response of soil functions to global change.

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First, I consider recent advances in our understanding of how plant traits, both aboveground and belowground, influence soil functioning at different scales, ranging from individual plants to regional scales. Second, I consider how this new knowledge could be used to better predict how soils and their functions respond to global change, and to inform decisions on how best to manage soils sustainably for ecosystem services. This latter point is especially timely given the urgent need for improved understanding of soil functioning to inform sustainable soil management and efforts to restore degraded soils (Amundson *et al.* 2015; Bardgett 2016).

LEAF TRAITS AND BELOWGROUND PROPERTIES

It has long been known that vegetation can exert a powerful influence on soil properties. As long ago as the late 1800s the Danish forester P.E. Müller published his theory of contrasting mull and mor soils, which he observed were associated with distinctive vegetation types and soil animal communities (Müller 1884). Also, around the same time, the Russian soil scientist Vasily Dokuchaev, widely considered to be the father of soil science, identified vegetation to be one of the main soil-forming factors, along with geology, climate, topography and time (Dokuchaev 1883). Evidence of the importance of plant functional traits as drivers of belowground properties, however, only began to emerge during the late twentieth century. This was largely fuelled by two developments: first, the recognition that plant species differ greatly in their traits due to a fundamental trade-off between rapid resource acquisition and efficient resource conservation (Grime 1977; Coley *et al.* 1985; Reich 2014); and, second, mounting evidence that ecosystem properties depend more on the functional traits of vegetation, especially locally dominant species, than diversity *per se* (Grime 1998; Lavorel and Garnier 2002).

Most early work on plant leaf traits and ecosystem properties focused on net primary productivity and biomass production (Lavorel and Garnier 2002; Garnier *et al.* 2004; Vile *et al.* 2006; Cadotte *et al.* 2009), although studies also explored effects of plant traits on belowground properties, notably decomposition, which is of central importance to soil carbon and nutrient cycling. For example, early studies performed across a wide range of plant species indicated that rates of litter decomposition are related to leaf traits such as growth rate (Cornelissen and Thompson 1997; Wardle *et al.* 1998), specific leaf area (Santiago 2007; Kurokawa and Nakashizuka 2008) and tissue strength (Cornelissen and Thompson 1997). Furthermore, studies revealed a general pattern of litter from plant species adapted to nutrient-poor conditions—typically low nutrient content with high concentrations of structural carbohydrates (e.g. cellulose and lignin) and defense compounds (e.g. polyphenols)—decomposing more slowly than that from plant species adapted to high resource conditions. As such, rates of litter decomposition generally increase along a sequence from coniferous species to woody angiosperm species, to herbaceous species (Cornelissen 1996), and leaf litter of plant species at the conservative end of the leaf economics spectrum decompose more slowly than litter from exploitative plant species (Wardle 2002). More recent studies have also demonstrated that community-weighted values of leaf traits, such as specific leaf area, leaf dry matter content and leaf nitrogen concentration, can explain a reasonable portion of variation in rates of litter decomposition across sites (Garnier *et al.* 2004; Quested *et al.* 2007; Fortunel *et al.* 2009; Eichenberg *et al.* 2015), pointing to the tractability of scaling from leaf traits to process rates at the landscape scale.

An area of focus for more recent research activity is the use of trait-based approaches to explain variation in soil microbial communities and the processes that they drive. It is well established that plant species vary considerably in their impact on the structure and functioning of soil microbial communities (e.g. Bardgett *et al.* 1999; Wardle *et al.* 1999; Turner *et al.* 2013); as such, ecologists have sought to identify the mechanisms involved, including the role of plant functional traits. Many factors regulate the structure and functioning of soil microbial communities, both abiotic and biotic, and these factors operate differently at different temporal and spatial scales (Bardgett and Van der Putten 2014). But it has been proposed that the leaf economics spectrum—a strikingly universal spectrum of leaf economics that runs from quick to slow return on investments of nutrients and dry mass in leaves (Wright *et al.* 2004)—could provide a framework for understanding how vegetation composition influences variation in soil microbial communities and their functioning across multiple scales (Bardgett and Wardle 2003; Wardle *et al.* 2004; De Deyn *et al.* 2008). The general idea, which is broadly analogous to ideas developed from detritus food webs with fungal- and bacterial-based energy channels (Hendrix *et al.* 1986; Wardle *et al.* 2004), is that plant species at the conservative end of the leaf economics spectrum, with low relative growth rate and low specific leaf area, produce litter of low resource quality and promote the growth of fungi relative to bacteria, which slows rates of nutrient cycling and enhances nutrient retention. In contrast, fast-growing exploitative plant species, with high relative growth rate and specific leaf area, produce high quality resource inputs in the form of litter and root exudates that promote the bacterial component of the microbial community, which is associated with rapid rates of nutrient cycling and nutrient loss from the soil system (Fig. 1).

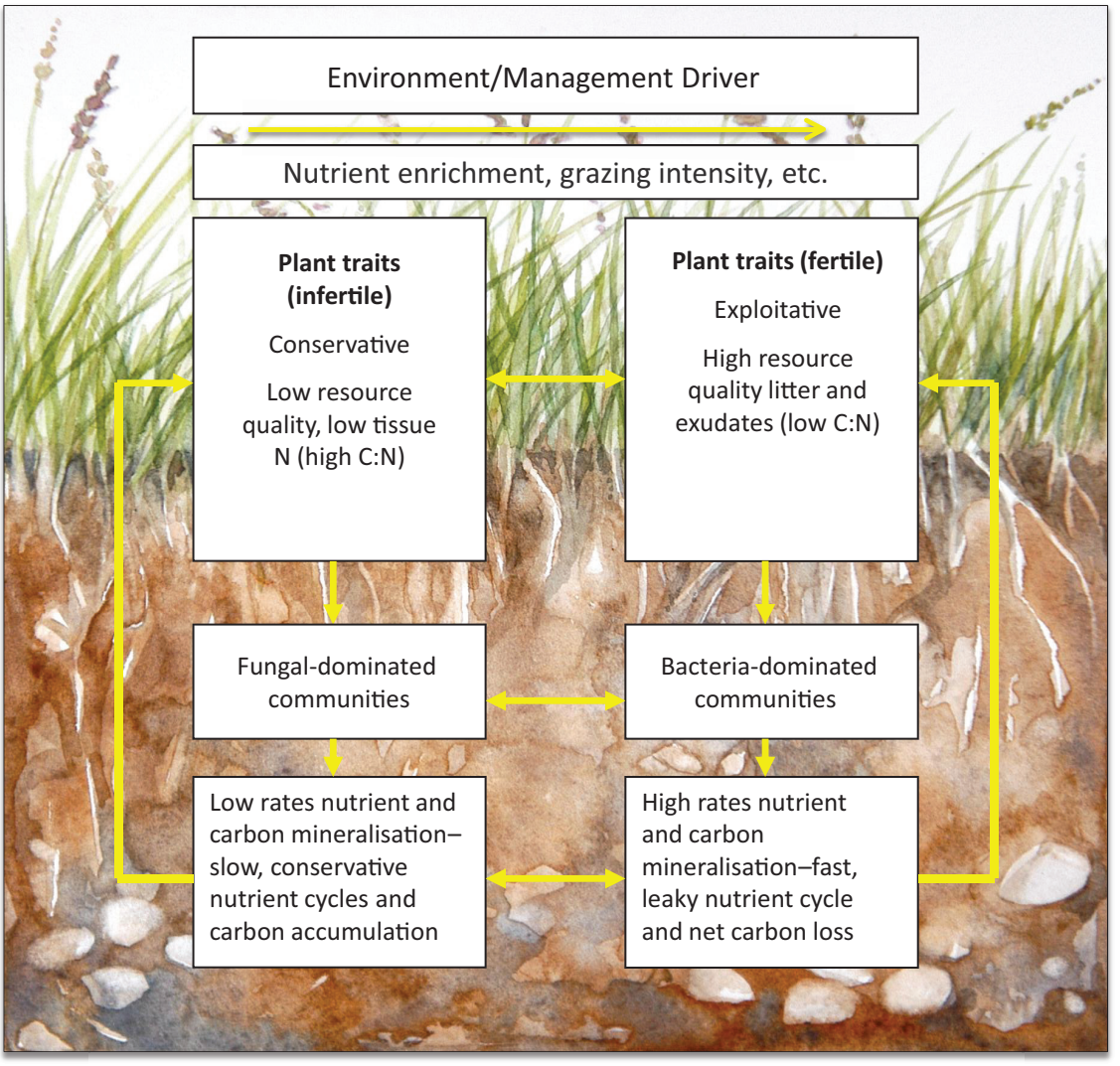


Fig. 1—Hypothetical influence of plant traits on soil fungal and bacterial energy channels in soil food webs and their relation to soil carbon and nitrogen cycles (adapted from Wardle *et al*. 2004). Image by Jill Bardgett.

A number of studies have demonstrated that plant resource strategies influence soil microbial communities in a way that is broadly consistent with the above framework based on the leaf economics spectrum. A comparative study of grassland plant species, for example, showed that exploitative grassland species with high leaf and litter quality promote the bacterial component of the soil microbial community and high rates of nutrient mineralization (Orwin *et al*. 2010). Similarly, the abundance of archaeal ammonia oxidisers (AOA), but not bacterial ammonia oxidisers (AOB), has been shown to respond to plant traits, being greater in soil modified by exploitative plant species of high nitrogen demand than conservative grasslands species (Thion *et al*. 2016). It has also been shown that effects of plant traits on soil microbial communities are indirectly mediated by changes in soil nitrogen availability caused by differences in plant nitrogen use and altered plant-microbial competition for nitrogen (Moreau *et al*. 2015). Similar patterns have also been found at the ecosystem and landscape scale. In a study of forest understory vegetation, for example, communities dominated by fast-growing species of high leaf nitrogen and specific leaf area were found to be associated with soils that have high nitrification potential (Laughlin 2011). Furthermore, studies conducted across multiple grassland sites show that grasslands dominated by exploitative species have bacterial-dominated microbial communities, rapid rates of microbial activity and low soil carbon stocks and nitrogen retention; whereas dominance by conservative species is associated with fungal dominated microbial communities, reduced bacterial activity and greater soil carbon storage and nitrogen retention (De Vries *et al*. 2012; Grigulis *et al*. 2013).

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It should be noted that most of the aforementioned studies were done in temperate grassland systems, whereas the connection between leaf traits and microbial community composition in other ecosystems, such as tropical forests, appears to be less strong. In a study of a large number of samples taken from a single 50ha tropical forest plot in Panama, that has been intensively characterized for its vegetation, leaf functional traits were not found to be useful predictors of microbial community composition (Barberán *et al.* 2015). Rather, the best predictor of soil microbial community composition, after accounting for topography and soil abiotic properties, was the taxonomic and phylogenetic structure of the plant assemblages, and this was especially strong for fungi. As noted by the authors, the most likely explanation is that the plant functional traits not included in their analyses, such as litter chemistry and root traits, are more important drivers of microbial communities of hyper diverse tropical forest soils than are leaf traits. This is likely to be the case given the important role of litter traits for microbial-driven processes of decomposition and nutrient cycling in tropical and other forested ecosystems (Cornwell *et al.* 2008; Dale *et al.* 2015), and vegetation effects on forest soil microbial communities are likely to be strongly driven by root traits. Another possible reason for the lack of coupling between leaf traits and microbial communities is a mismatch in spatial scales, given that soil microbial diversity is strongly driven by spatial heterogeneity, and the diversity of microhabitats found within a single, three-dimensional soil profile could be equivalent to that found aboveground within an entire forest ecosystem (Bardgett and Van der Putten 2014).

DIGGING DEEPER: THE ROLE OF ROOT TRAITS

Roots have many functions, including plant anchorage and the uptake of water and nutrients from soil, and they have evolved a variety of strategies to capture these resources from soil. As such, between species variation in root traits is very high and, moreover, they are extremely plastic, which enables them to capture changing resource supplies in heterogeneous soil (Hodge 2004; Chapman *et al.* 2012). Given this, and the fact that plant biomass is greater belowground than aboveground in many biomes, it is no surprise that root traits have enormous potential to impact on the functioning of soil. Recent observational and experimental studies that have attempted to disentangle the mechanisms by which plant traits influence ecosystem processes, suggest that root traits play a dominant role. For example, Legay *et al.* (2014) showed that root traits explained more variation in soil microbial properties than did leaf traits across different grassland sites; similarly, Legay *et al.* (2016) manipulated grassland plant functional composition in a multisite experiment and discovered that root traits, along with various soil microbial traits, best explained ecosystem processes that underpin nutrient cycling, especially in nitrogen-rich soils. Likewise, studies testing how different plant populations and plant community attributes, including variations in the dominance, diversity and range of plant functional traits, influence nitrogen cycling processes, show that root traits play a key role, both directly and indirectly by influencing plant nitrogen capture and retention in soil (Cantarel *et al.* 2015; De Vries and Bardgett 2016).

The jury is still out on whether leaf and root traits related to resource acquisition are correlated with each other; not only are data on correlations between leaf and root traits scarce, but also the evidence that is available is not always consistent with the theory. For instance, studies of grasses have found little relationship between leaf and root traits, expect for leaf and root nitrogen (Craine *et al.* 2005), whereas studies of tree species showed that while some root traits align with the leaf spectrum, others do not, which is indicative of the multidimensional nature of roots (Kramer-Walter *et al.* 2016). Moreover, the mechanisms by which different root traits, or combinations of root traits, impact soil processes remains poorly understood (Bardgett *et al.* 2014). Nevertheless, it is clear is that root traits have the potential to have profound impacts on the functioning of soil. With regard to soil carbon cycling, for example, architectural root traits that determine the spatial configuration of root systems—such as root length density and rooting depth—contribute significantly to the input of carbon to soil, as do physiological traits that influence root life span, such as root nitrogen and lignin concentrations (Silver and Miya 2001; McCormack *et al.* 2012). Physiological root traits, especially root respiration and exudation, also regulate carbon dioxide efflux from soil, thereby contributing to soil carbon loss. The contribution of root respiration to total soil carbon dioxide flux can be upward of 50% (Bond-Lamberty *et al.* 2004), but this varies considerably depending on root nitrogen and biotic root traits, such as the presence and identity of mycorrhizal fungi (Martin and Stutz 2004; Trocha *et al.* 2010). Less is known about how root exudation influences soil respiration, although exudates, comprising low-molecular-weight compounds (e.g. sugars, carbohydrates and amino acids), can stimulate organic matter mineralisation and hence soil carbon loss via altering the composition of the microbial community and/or stimulating heterotrophic microbial activity (Fontaine *et al.* 2004; De Deyn *et al.* 2008).

There is also plentiful evidence to suggest that root traits have an important influence on soil nutrient cycling. For example, Wardle *et al.* (1998)

found effects of herbaceous plant species on the soil microbial biomass to be related to certain root traits, such as specific root length, and Hobbie *et al.* (2006) discovered that soil nitrogen dynamics across a broad range of tree species was explained by variation in root traits, with rates of nitrogen mineralisation being positively related to root nitrogen. Also, in a study of several sites across the world, including natural forests and croplands, a combination of root chemical traits—including lignin, carbon and nitrogen concentrations—best explained root decomposition rates at the community level (Prieto *et al.* 2016). And the aforementioned study by Thion *et al.* (2016) found that the abundance of AOA in the rhizosphere, a key group of microbes involved in the nitrogen cycle, was strongly and positively related to root nitrogen content, indicating a strong influence of plant nitrogen strategy on nitrogen cycling in soil.

Studies have also shown that root exudates can stimulate microbial extracellular enzymes involved in organic nitrogen mineralisation, thereby increasing nitrogen availability and supply to plants (i.e., the process of priming) (Dijkstra *et al.* 2013). However, root exudates are also known to have differential effects on key groups of soil microbes involved in the nitrogen cycle (Moreau *et al.* 2015; Thion *et al.* 2016), and in some situations they can stimulate microbial growth and immobilisation of nitrogen, thereby reducing nutrient availability to plants (Bengtson *et al.* 2012). New research has also shown that root traits impact soil nitrogen cycling via other mechanisms, for instance via hydraulic lift of sub-soil water that promotes nitrogen cycling in surface soil (Cardon *et al.* 2013), and via dense root systems with high specific root length that reduce nitrous oxide emissions and nitrogen leaching from soil (Abalos *et al.* 2014).

Biotic root traits, especially mycorrhizal associations, also influence nutrient cycling. It has been proposed that the nutrient economy of forest ecosystems can be predicted on the basis of dominance of trees with either AM or ECM fungi: the former has an inorganic nutrient economy, with rapid rates of decomposition and nutrient mineralisation, whereas the latter has an organic nutrient economy with slower rates of nutrient cycling (Phillips *et al.* 2013). The rationale for this is that tree species predominately associate with either arbuscular (AM) or ectomcorrhizal (ECM) fungi and that the former rely more on uptake of inorganic nitrogen and the latter on complex organic N forms (Phillips *et al.* 2013). This framework is broadly consistent with the global pattern of elevated soil carbon storage observed in ECM-dominated ecosystems (Averill *et al.* 2014) and experimental evidence that ECM reduce rates of both soil nitrogen and carbon cycling by effectively competing for nitrogen with free living decomposers (Averill and Hawkes 2016). This framework is similar to that proposed to link soil microbial processes and nutrient cycling to the resource economics spectrum, namely that dominance of plant species with exploitative traits is associated with high rates of microbial nitrogen mineralisation, whereas dominance of plants with conservative traits is associated low rates of nitrogen cycling and plant nitrogen supply (Bardgett *et al.* 2014).

Finally, evidence is emerging that root traits can also strongly modify the soil physical environment, which is of key importance to the functioning of soil and its resistance to erosion. Many factors influence soil physical structure, including the texture and mineralogy of soil. However, root traits can also impact the soil physical environment via a range of mechanisms (Bardgett *et al.* 2014). For instance, architectural root traits, such as root length, directly impact soil structure through binding and compressing soil particles (Miller and Jastrow 1990; Gyssels *et al.* 2005), and rooting depth and branching can increase soil stability and soil resistance to erosion, especially on slopes (Stokes *et al.* 2009). Physiological root traits, especially root exudation, impact soil structure by stimulating microbial activity (Oades and Waters 1991; Graf and Frei 2013), and mycorrhizal networks enmesh soil particles (Hallett *et al.* 2009) and bind soil via the production of extracellular polysaccharides and proteins (Rillig *et al.* 2015).

While it is clear that root traits have the capacity to influence the physical structure of soil, their role in explaining diversity effects on the soil environment remains poorly understood. A handful of studies have detected broad relationships between plant species richness and soil physical properties (Pohl *et al.* 2009; Pérès *et al.* 2013; Berendse *et al.* 2015), but whether or not these effects are related to plant functional traits, especially root traits, was not tested. This issue, however, was recently tackled by Gould *et al.* (2016) who combined a glasshouse and a long-term field study to show that high plant diversity in grassland systems increases soil aggregate stability—a vital structural property of soil—and that root traits play a major role in determining diversity effects. In particular, they discovered that higher species richness increased root length and reduced the average root diameter, which led to increased soil aggregate stabilisation. Added to this, strong effects of species identity on soil physical properties were detected; grass species with the greatest root length, specific root length and narrowest average diameter of species tested had the greatest positive effect on soil aggregate stability, reflecting their fine rooting behaviour and exploitative strategy to maximise resource uptake (Hodge 2004; Cahill and McNickle 2011). As suggested by the authors, these significant links between plant functional diversity and soil physical properties

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could provide the basis for combating soil physical degradation and restoring function to degraded soils.

PLANT TRAITS AND PLANT-SOIL FEEDBACK

The study of plant-soil feedbacks has become a dominant theme in plant ecology, largely because of their role in explaining plant population and community dynamics (Van der Putten *et al.* 2013). Put simply, plant–soil feedbacks occur when plant-induced changes in soil conditions influence the growth of future plants, either negatively, for example via the promotion of pathogens and/or reduced nutrient availability, or positively via the promotion of symbionts and/or nutrient availability (Bever *et al.* 1997; Kulmatiski *et al.*, 2008; Van der Putten *et al.*, 2013). Given the capacity of plant traits to modify soil function, it makes sense that traits will influence the outcome of plant-soil feedback by both determining how species modify the soil and how they respond to these changes (Kulmatiski *et al.*, 2008); this is also consistent with the distinction between 'effect' traits that affect ecosystem function, and 'response' traits that affect the response of organisms to a change in their environment (Díaz and Cabido 2001; Lavorel and Garnier 2002).

To date, only a handful of studies have tackled this idea. One such study was by Baxendale *et al.* (2014) who measured how monocultures and mixtures of a wide range of temperate grassland plant species covering a spectrum of growth strategies responded to soil that had been conditioned by model grassland plant communities dominated by either conservative or exploitative grassland species. Consistent with theory, it was found that soils conditioned by the exploitative community had higher nitrogen availability than those conditioned by the conservative community. However, the influence of plant traits on plant-soil feedbacks was detected only when plants were grown in mixtures rather than in monocultures: all species grew better in nutrient-rich soil conditioned by the exploitative community irrespective of their resource strategy, whereas in mixtures, conservative plant species produced more aboveground biomass, and exploitative species produced more belowground biomass, in soils conditioned by species with similar traits. These findings were taken to support the idea that plant traits influence plant-soil feedbacks, but that species perform better in soil conditioned by species with similar traits when grown in a competitive environment.

In another study, Cortois *et al.* (2016) tested whether plant traits could predict plant-soil feedbacks for coexisting grassland species. The authors tested the hypothesis that species with traits targeted at rapid resource acquisition, such as high relative growth rate, specific leaf area and specific root length, and low AM fungal colonization, will have more negative feedback with soil biota compared to species with traits indicative of a more conservative growth strategy. Consistent with this idea, the authors found that species with an exploitative resource strategy suffered most from negative feedback from soil biota, whereas conservative species benefitted from feedback with soil biota. They also found that plant-soil feedback correlated positively with AM fungal colonization of roots, which was negatively related to specific root length; this is consistent with the knowledge that the benefits to plants of AM fungi are greater when specific root length is lower (Smith and Read 2010).

The importance of nutrient-acquisition strategy as a trait for explaining plant-soil feedback was also recently shown by Teste *et al.* (2017). In a study of hyperdiverse Australian shrublands, these authors found that ECM plants displayed positive feedback, whereas nitrogen-fixing and non-mycorrhizal plants displayed negative feedback; further, these feedbacks contributed to the maintenance of high diversity in these shrublands. In another study of an extensive range of North American tree populations and species, Bennett *et al.* (2017) also discovered that plant-soil feedbacks were consistently dependent on mycorrhizal type: AM trees experienced negative feedback, whereas ECM trees displayed positive feedback, which contributed to forest vegetation dynamics. Collectively, these studies indicate that plant traits offer potential to improve prediction of plant-soil feedbacks and their role in plant population and community dynamics. However, further studies are clearly needed spanning a wider range of species and ecosystems to test the importance of plant traits for predicting plant-soil feedback relative to other factors known to influence vegetation dynamics.

PLANT TRAITS, SOILS AND GLOBAL CHANGE

Trait-based approaches offer a potential framework for understanding how global change induced shifts in vegetation influence soil functioning, and informing decisions on sustainable soil management, for instance via mapping of soil-based ecosystem services. The capacity of trait-based approaches to predict how soil and ecosystem processes respond to environmental change draws on the aforementioned 'response–effect' framework, which considers both how plant traits respond to environmental change and their effect on ecosystem properties (Díaz and Cabido 2001; Lavorel and Garnier 2002) (Fig. 2). Such frameworks have already been adapted to predict how plant community dynamics impact ecosystem functions, including soil nutrient cycling (Suding *et al.* 2008) and how environmental change influences ecosystem service delivery by multitrophic systems, for example to identify the mechanisms by which vegetation change effects soil

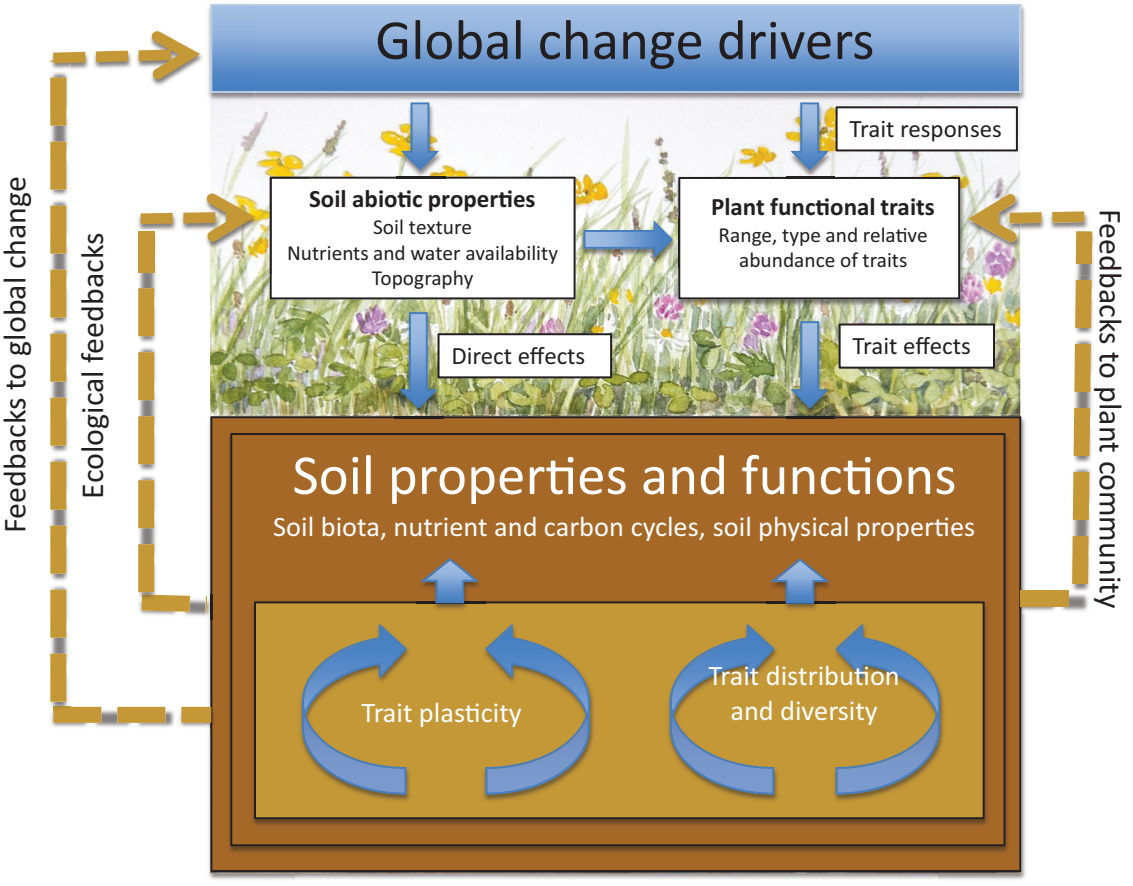


Fig. 2—Plant trait responses and feedbacks triggered by global change. Global change drivers, such as climate and land use change, impact soil properties and functions indirectly via plant traits at the individual plant (trait plasticity) and community level (trait distribution), and directly via modifying soil abiotic properties. In turn, these belowground responses feedback to the plant community, for example via altered nutrient and water availability in soil, and to the Earth system, via changes in soil CO_2 flux. Image by Jill Bardgett.

nitrogen cycling via feedbacks involving plants traits and soil microorganisms (Lavorel *et al.* 2013).

While such frameworks provide a general guide for predicting how environmental change impacts soil functioning, uncertainties remain. One such uncertainty concerns the enormous plasticity of plant traits, especially root traits that respond rapidly to global change at a scale that likely matters for belowground functioning. Root branching, for example, can respond rapidly to changes in soil nitrogen supply (Hodge *et al.* 1999). Furthermore, many architectural and morphological root traits show high levels of plasticity in response to changing water supply, including drought, although this plasticity varies among species (Comas *et al.* 2013; De Vries *et al.* 2016). Root traits are also highly responsive to elevated atmospheric carbon dioxide, and studies reveal consistent increases in root length and diameter, and increased root exudation, respiration and mycorrhizal colonisation (Nie *et al.* 2013). The scale of such responses across a wide spectrum of root traits, and their capacity to impact soil functioning, suggests a need to incorporate such knowledge into ecosystem models to improve prediction of belowground responses to climate change (Bardgett *et al.* 2014).

Despite the above, it should be noted that there is considerable uncertainty about the role of plasticity in root traits in responding to changes in soil resource supply. Not only is it very difficult to measure root plasticity, but also a very large range of root traits are involved in nutrient acquisition from heterogeneous soil (Hodge 2004; Croft *et al.* 2015), making it very tricky to experimentally assess their importance for nutrient supply. Coupled with this complexity, the importance of plasticity in root traits for exploiting changing soil resource supply varies across plant species and also depends on factors such as the attributes of the resource (e.g. its size, concentration and duration) (Hodge 2004) and the presence of competitors (Cahill *et al.* 2010; Mommer *et al.* 2012). Recent studies also raise doubt over the importance of plasticity in root traits for plant resource acquisition. For example, a study

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of plant responses to resource supply (light and nutrients) showed that plasticity in root functional traits, at least in terms of root morphology (specific root length), was not as important for plant resource acquisition as plasticity in leaf functional traits (Freschet *et al.* 2015). However, as noted by the authors, it is possible that other root traits involved in soil nutrient acquisition not considered, such as root hair length and density, and mycorrhizal colonization, may show a higher degree of plasticity in response to changing resource supply than specific root length (Freschet *et al.* 2015). Together, these uncertainties present a major challenge to gaining a full understanding of the importance of plasticity in root traits for soil functioning, and make it tricky to incorporate them into predictive global change models.

Shifts in vegetation composition and species distributions resulting from global change also cause shifts in trait spectra, both aboveground and belowground, with impacts on soil functioning at both local and regional scales. Global change phenomena, such as climate change, are not only causing local changes in vegetation composition and reorganisation of trait spectra, but also expansion of species ranges, and the gain and loss of species and associated traits by invasion and extinction, which all have consequences for soil biogeochemical processes and feedbacks to climate change (Wardle *et al.* 2011; Bardgett *et al.* 2014). As an example, comparative studies of leaf trait data show that invasive plants have higher specific leaf area, leaf nitrogen and phosphorus concentrations than do natives (Leishman *et al* 2007); because of this, invasive plants can have significant impacts on soil nutrient stocks and rates of nutrient cycling (Liao *et al.* 2008). It was recently shown that broad patterns of fine root turnover and lifespan exist across temperate forests of the eastern United States of America, and that climate change induced changes in dominant tree species could cause major shifts in forest fine root turnover and lifespan with important implications for belowground carbon cycling (McCormack *et al.* 2013); the authors argued that such patterns and future changes in root turnover and lifespan should be incorporated into terrestrial biogeochemistry model descriptions of belowground carbon cycling.

The recognition that plant traits and soil functioning are strongly linked has also led scientists to test the utility of trait-based approaches for mapping the ecosystem services of relevance to global change, such as soil carbon storage, which plays a key role in climate change mitigation. In a study of pastoral landscapes in the French Alps, for example, leaf traits, along with data on land use and abiotic characteristics, were successfully used to identify 'hot' and 'cold' spots of ecosystem service delivery at a landscape scale, including soil carbon sequestration, and trade-offs among services (Lavorel *et al.* 2011). Also, in a study of UK grasslands, leaf traits, along with simple soil abiotic and climatic properties, were used to explain regional and national scale variation in surface soil carbon stocks; this again points to the utility of using plant traits, along with other simple climatic and soil abiotic measures, to map the distribution of soil-based ecosystem services at scales that actually matter for climate mitigation (Manning *et al.* 2015). Collectively, these studies not only suggest that trait-based approach could help to refine existing models of soil carbon stocks, but also that they contribute to a more mechanistic understanding of the distribution of soil carbon at larger scales. Moreover, given that several plant traits can be assessed using remote sensing, and that ecosystem service prediction using remote sensing and trait-based approaches are similar (Homolova *et al.* 2014), there is scope to employ emerging mechanistically based relationships between plant traits and soil properties and functions to refine their prediction at regional or even global scales.

CONCLUSIONS AND FUTURE CHALLENGES

It is clear that plant traits can impact soil functioning via multiple routes, and, further, they display a high degree of plasticity in response to global change. Given this, there is much potential for shifts in plant trait spectra, both aboveground and belowground, to impact soil functions with feedbacks to plant community dynamics and biogeochemical cycling across multiple scales. Research also reveals that both leaf and root traits operate to impact soil functions simultaneously, often in contrasting ways, but that root traits are the dominant driver of soil functioning, having major impacts on a host of soil physical, chemical and biological properties. Being a topic in its relative infancy, there are many challenges regarding the use of trait-based approaches to interrogate soil functioning, especially when considering root traits involved in nutrient acquisition, and much has been written about these challenges elsewhere (Lavorel *et al.* 2013; Bardgett *et al.* 2014; Laliberté 2017). As such, I focus on those related to the potential use of trait-based to inform soil functioning and sustainable soil management at scales that matter for ecosystem services, especially food production and climate mitigation.

First, in order to realise the potential of trait-based approaches for interrogating the soil environment, there is a need for improved understanding of genotypic and species level variation in plant traits, especially of root traits that have the strongest potential to influence soil processes. Extensive databases are available on aboveground traits, such as TRY (Kattge *et al.* 2011), and they have been effectively used to identify relationships between leaf traits, soil microbial communities and soil carbon stocks at national scales (De Vries *et al.* 2012;

Manning *et al.* 2015). However, similar resources with comprehensive information on root traits across species, ecosystems, and environmental gradients are also needed (Bardgett *et al.* 2014). Coupled with this is a need for improved understanding of genotypic and species variation in plant traits, and the influence of this variation on the functioning of complex soil microbial consortia and the chemical and physical properties on which soil fertility depends. Progress is being made here through the rapid development of high-throughput phenotyping facilities that enable comprehensive analyses of plant traits. This includes the development of non-destructive, image-analysis-based phenotyping of leaf traits in the field (Walter *et al.* 2015) and new automated platforms for assessment of root traits (Kuijken *et al.* 2015). However, as noted by Laliberté (2017), many root traits are difficult to measure, especially in field settings. Therefore, there is value in exploring potential proxy measurements of root traits, such as easily measurable leaf traits. To achieve this, however, requires improved understanding of linkages between leaf and roots traits related to resource acquisition.

Second, improved understanding of links between plant traits and soil processes is needed to enhance the predictive power of terrestrial biogeochemical and dynamic vegetation models (DGVMs), which are often limited by inadequate detail on key belowground processes (Ostle *et al.* 2009; Warren *et al.* 2015). Most DGVMs, for example, include trait data averaged across very broad plant functional groups, thereby obscuring regional and global variation in plant traits that are of critical for belowground processes (Ostle *et al.* 2009). For instance, studies indicate that broad patterns of fine root turnover and lifespan exists at regional scales, which are currently not represented in biogeochemical models (McCormack *et al.* 2013), and the inclusion of roots in models is usually static and discrete, and thus does not represent the plasticity of root traits nor their mechanistic link to the cycling of water, nutrient and carbon in soil (Warren *et al.* 2015). Future studies clearly need to assess the sensitivity of terrestrial biogeochemical models to critical plant traits, both aboveground and belowground, and integrate our fast developing knowledge of relationships between plant traits and belowground processes to provide an improved predictive capacity of biogeochemical processes at both regional and global scales.

Third, and finally, a major challenge for the future is to harness new understanding of plant traits and their impact on soil microbial processes in sustainable food production systems, in particular to enhance resource acquisition by crop plants. As highlighted in this article, there is mounting evidence that plant resource strategies are linked to the activity of specific components of the microbial community involved in nutrient transformations (Moreau *et al.* 2015; Thion *et al.* 2016). It is also becoming clear that certain root traits have profound impacts on soil microbial consortia involved in soil nutrient transformations that could potentially feedback to crop nutrient acquisition and yield as well as the retention of nutrients in soil, which is of fundamental importance for efficient nutrient cycling and minimising nutrient losses to the environment (Bardgett *et al.* 2014). Moreover, studies show that root traits have a profound impact on soil physical properties and processes of soil carbon sequestration and stabilisation in soil, indicating that they have the potential to bring wider benefits for soil health and ecosystem services in food production systems (Gould *et al.* 2016). This is especially important given the extent that soils are degraded worldwide, which threatens food security and has plunged millions into hunger and poverty (Bardgett 2016); as such, there is an urgent need to develop sustainable ways of managing soil to prevent further degradation whilst also increasing the production of food. To date, breeding efforts have been targeted largely at aboveground traits related to crop yield, but there is clearly much promise to modify root traits in crops to enhance nutrient and water acquisition, and enhance the health of soil.

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