

# Going underground: root traits as drivers of ecosystem processes

Richard D. Bardgett<sup>1</sup>, Liesje Mommer<sup>2</sup>, and Franciska T. De Vries<sup>1</sup>

<sup>1</sup> Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford Road, Manchester M13 9PT, UK

<sup>2</sup> Nature Conservation and Plant Ecology Group, Wageningen University, PO Box 47, 6700 AA, Wageningen, The Netherlands

**Ecologists are increasingly adopting trait-based approaches to understand how community change influences ecosystem processes. However, most of this research has focussed on aboveground plant traits, whereas it is becoming clear that root traits are important drivers of many ecosystem processes, such as carbon (C) and nutrient cycling, and the formation and structural stability of soil. Here, we synthesise emerging evidence that illustrates how root traits impact ecosystem processes, and propose a pathway to unravel the complex roles of root traits in driving ecosystem processes and their response to global change. Finally, we identify research challenges and novel technologies to address them.**

## Plant functional traits and ecosystem processes

A growing number of ecologists are adopting trait-based approaches to better understand how community changes influence ecosystem processes [1,2]. This approach has been applied to understanding how changes in plant community composition resulting from global change influence ecosystem functions, such as aboveground primary productivity [2–4], but also to belowground processes such as decomposition, and C and nutrient cycling [5–7]. However, to date the bulk of this research has focussed on aboveground plant traits, whereas new evidence is pointing to root traits having a significant role, which is especially significant given that, for many biomes, most plant biomass is underground [8].

In addition to providing anchorage, the primary function of roots is to take up plant growth limiting nutrients, especially nitrogen (N) and phosphorus (P), and water from soil. As a result, plants have evolved a wide range of belowground strategies to capture these resources, and to respond to changes in their availability in space and time [9] (Figure 1). **These include architectural root traits, such as rooting depth and root length density, which determine the spatial configuration of the root system as a whole; morphological traits of individual roots or root size classes, such as root diameter and specific root length; physiological root traits, such as root respiration, nutrient uptake kinetics and root tissue nutrient**

content, as well as the release of root exudates; and, finally, biotic root traits that involve the ability of roots to interact directly with soil biota, including (mycorrhizal) fungi (see Glossary) and rhizobia, which play a major role in nutrient capture from soil (Figure 1). Not only is there considerable variation in these root traits among species and genotypes, but they are also highly plastic, enabling plants to cope with changing environmental conditions, especially soil nutrient and water supply [10,11].

Here, we synthesise emerging evidence that illustrates the mechanisms by which the aforementioned categories of root traits impact on ecosystem processes related to C and nutrient cycling, and the formation and structural stability of soils. We then use this information to explore how variation in root traits resulting from global change, both at an individual plant and community scale, will impact ecosystem processes. Finally, we propose future research priorities to unravel the complex roles of root traits in driving ecosystem processes in a changing world.

## Glossary

**Mycorrhizal fungi:** mutualistic association between most higher plant species and symbiotic soil fungi. The fungus gains from the relation by accessing carbohydrates from the plant, whereas the plant gains through improved nutrient acquisition and resistance to disease and drought.

**Nitrogen immobilisation:** the uptake of inorganic forms of N by microbes, which renders this N unavailable to plants.

**Nitrogen mineralisation:** the conversion of organic forms of N in soil, such as peptides and amino acids, into inorganic forms, especially nitrate and ammonium, which are available for plant uptake.

**Plant functional trait:** morphological, physiological and phenological characteristics of plants that represent ecological life history strategies and are hypothesised to determine the response of a plant to environmental factors.

**Priming:** a short-term change in the mineralisation of native soil organic matter caused by the addition of easily degraded organic C to soil. Priming effects are mostly positive, in that they accelerate organic matter breakdown and C loss from soil. But they can also be negative or neutral, if the added substrate inhibits soil microbial activity or if soil microbes use the added substrate as their energy source.

**Rhizosphere:** the zone of soil (~1 mm) immediately adjacent to plant roots.

**Root exudation:** the release from roots of exudates, comprising low-molecular-weight organic compounds, including sugars, carbohydrates, and organic and amino acids, into soil.

**Soil aggregate stability:** the ability of soil aggregates to resist stresses, such as wet-dry cycles, without breaking.

**Soil aggregates:** groups of soil particles that bind together more strongly than adjacent particles, and the spaces between aggregates provide pore space for roots to explore and for the movement of water and air.

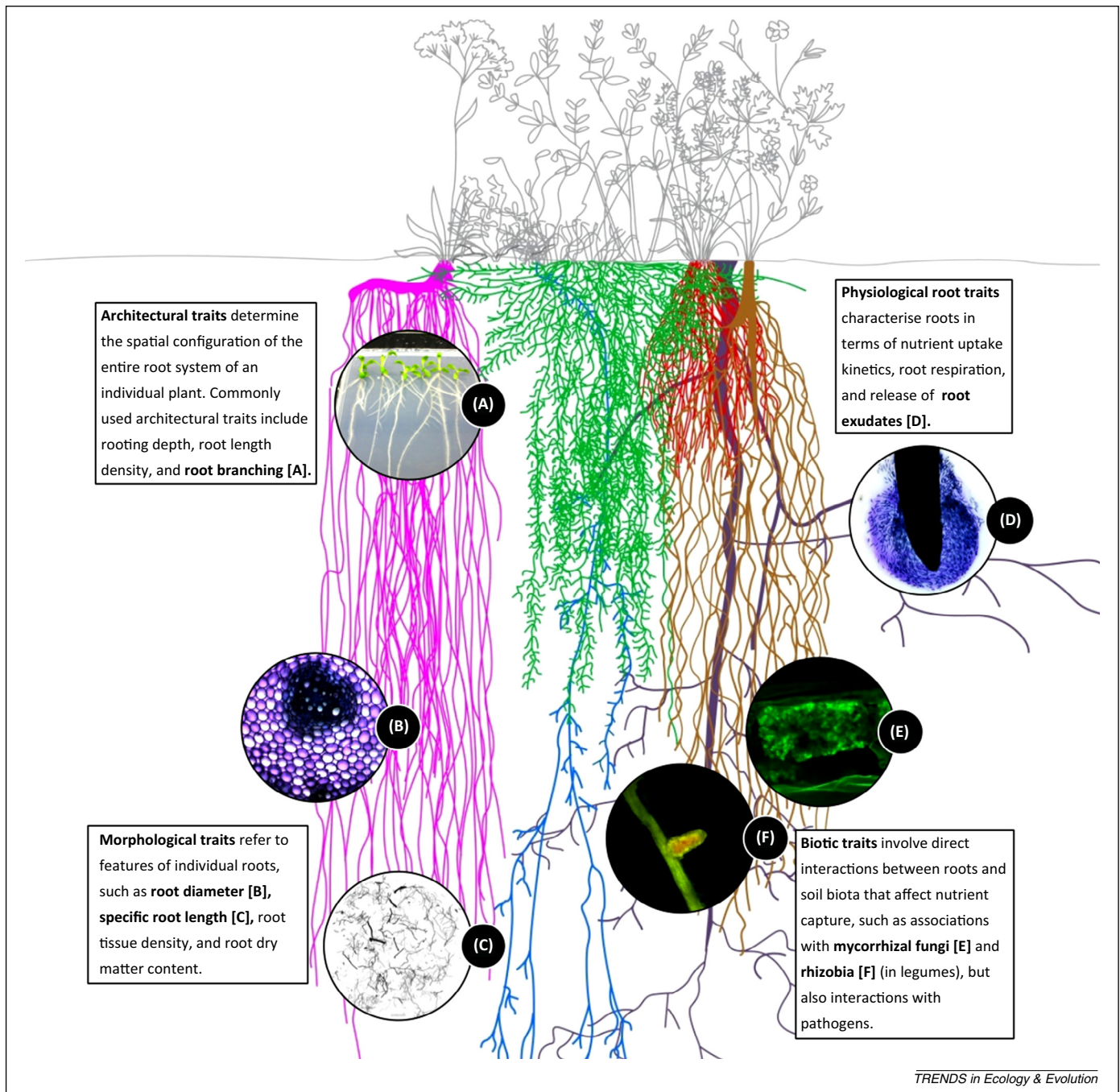
**Soil C sequestration:** The transfer of CO<sub>2</sub> from the atmosphere into the soil through plant and other organic matter inputs to soil, and in a form that is not immediately reemitted.

Corresponding author: Bardgett, R.D. ([richard.bardgett@manchester.ac.uk](mailto:richard.bardgett@manchester.ac.uk)).

Keywords: plant functional traits; roots; soil; carbon cycling; nutrient cycling; soil structure; global change.

0169-5347/

© 2014 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2014.10.006>



**Figure 1.** Categories of root traits that have potential to impact ecosystem processes, including architectural, morphological, physiological, and biotic traits. The general idea behind a trait-based framework is that variation in root traits across individual plant species, communities, and ecosystems captures variation in a range of ecosystem processes, including carbon and nutrient cycling, and the structural stability of soil. Images represent the different root trait categories with potential to impact ecosystem processes: (A) root systems of *Leucanthemum vulgare* growing on agar plates by Liesje Mommer, Wageningen University (WU), representing architectural traits; (B) cross section of root of *L. vulgare* stained toluidine blue by Eric Visser, Radboud University, Nijmegen; (C) root length scan of washed roots from diverse grassland community by Natalie Oram (WU), both representing morphological traits; (D) root nodule in *Medicago truncatula* by Erik Limpens (WU); (E) arbuscules of AM fungi in *M. truncatula* root by Rik Huiskes (WU), both representing biotic traits; and, finally (F) rhizodeposition around *Zea mays* root by Davey Jones, Bangor University, representing physiological traits. Image of root system adapted from Scientific American, May 1973.

### Root traits and the resource economic spectrum

The evolution of roots and the diversion of root traits occurred in response to major geological events, and because of their ancient history, root trait variation among species is extremely high (Box 1) [12,13]. To understand this variation, root traits are beginning to be viewed in the context of the resource economic spectrum [14], classifying traits along a spectrum from a more resource acquisitive

strategy that facilitates fast growing species, to a strategy aimed at the conservation of resources typical for slow-growing species. Plant species from the resource-acquisitive part of the trait spectrum are hypothesised to exhibit high specific root length (SRL), low root tissue density, high root N uptake and N content, low C content, high root respiration and low root life span, and *vice versa* for the resource-conservative spectrum [15]. However,

**Box 1. The evolution of root traits**

It has been proposed that the first fossil records of root-like structures originate from the Lower Devonian, and true roots evolved during the Mid Devonian [85]. The arrival of true roots caused a major global decrease in atmospheric CO<sub>2</sub> concentrations: increased weathering of silicate rock by penetrating roots and their exudates released huge quantities of calcium (Ca) and magnesium (Mg), which in turn precipitated into carbonate oceanic sediments [85]. Simultaneously, this increased weathering created a positive feedback that further decreased atmospheric CO<sub>2</sub> concentrations by releasing nutrients from parent material. The increase in larger and more structurally complex aboveground structures for absorbing photons and CO<sub>2</sub> resulted in an investment in deeper and more complex belowground structures, accelerating soil formation and promoting heterotrophic activity.

Plant-fungal associations existed even before the appearance of true roots. These arbuscular mycorrhiza-like associations are thought to have evolved from endophytic fungi, which were probably attracted to the large quantities of plant exudates under the carbon-rich atmosphere in the Ordovician [86]. Thus, AM fungi already occurred in association with bryophytes and early vascular plants, while the first records of ECM fungi are found in members of the

Pinaceae (gymnosperms) [86]. Early angiosperms had thick roots that supported colonisation by AM fungi [86,87]. The evolution of longer, thinner roots has been proposed to either result from the decline in atmospheric CO<sub>2</sub> concentrations during the Cretaceous or by the decline in soil nutrient availability and a cooling climate [88]. Thinner roots reduced the dependency on mycorrhizas, and the first non-mycorrhizal plants appeared [86]. They also had a higher frequency of root tips to support ECM fungi, which independently evolved in several lineages of the angiosperms [86,87], and allowed plants to access organic pools of N and P. Differences between AM and ECM root systems have been phylogenetically conserved, with AM roots being coarser, with higher root diameter and lower branching intensity than ECM roots [87]. In addition, roots of non-mycorrhizal plants in extant species are still thinner, with higher specific root length, than those of mycorrhizal plants [87,89, but see 90].

The evolution of legumes occurred in the late Cretaceous [91]. An abrupt increase in temperature caused a massive release of carbon from sea-floor methane reserves [92]. These high atmospheric CO<sub>2</sub> levels increased N limitation for plant growth, which in turn might have favoured the evolution of N fixation [91].

experimental data testing for such correlations is scarce, and evidence is not always consistent with the theory, suggesting deviations in root traits from the resource economic spectrum of leaves [16].

Root traits also vary considerably within species because roots are highly plastic in response to environmental gradients and species-species interactions [10,17,18]. The most studied example of belowground trait plasticity is selective root placement (i.e., locally increased root branching and proliferation) and adjusted nutrient uptake (i.e., physiological plasticity) [11] in response to heterogeneous distribution of nutrients in soil. Also, there is a rich literature showing plants to grow roots according to the distribution of available water in soil, with the production of thinner and deeper roots being important traits enabling acquisition of water under drought [19,20]. It has been suggested, based on meta analysis of available data in grassland species, that the degree of selective root placement forms part of a suite of traits related to fast growth rate and thus, potentially, the resource economic spectrum [21]. Future studies using a larger number of plant species from different ecosystems are clearly needed to confirm this pattern and to place foraging precision and plasticity in resource acquisition in the context of resource economy strategies.

**Root traits as drivers of ecosystem processes****Carbon cycling**

A process of central importance to ecosystem C cycling is the input of C to soil [1]. Although aboveground plant litter contributes significantly to this process, the input of C from dead roots also plays a major role. As a result, architectural roots traits that determine the spatial configuration of root systems, such as root length density and rooting depth, contribute significantly to the input of C to soil [1]. However, the amount of C that enters the soil as dead roots is also strongly determined by root life span, which is related to a range of physiological and morphological root traits [22]. Studies show, for example, that root lifespan is negatively related to SRL, root N:C ratio and soluble compound concentrations [23,24], and positively to high lignin or

cellulose concentrations [23]. Biotic root traits also affect root turnover, with root infection by pathogenic fungi reducing root life span and accelerating root decay [25], and mycorrhizal fungi acting as a recalcitrant soil C pool themselves [26]. Recent evidence also points to arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi having contrasting roles in soil C cycling: the former promote decomposition by providing a labile C source [27], whereas the latter retard decomposer activity by outcompeting them for N [28].

Another process of major importance for ecosystem C cycling is soil CO<sub>2</sub> efflux, which is the largest annual flux of C from the terrestrial biosphere to the atmosphere [29]. This efflux of CO<sub>2</sub> is strongly regulated by two key metabolic traits: root respiration and exudation. Plants can allocate significant amounts of photoassimilate C to their roots and symbionts, and a large portion of this C is respired by roots or released into soil via root exudation [30]. The contribution of root respiration to total soil CO<sub>2</sub> flux is on average 40–50% [31,32], although it varies considerably across plant species, and with factors such as root N and soil N availability [33,34] and the presence and identity of mycorrhizal fungi colonising roots [35,36]. Less is known about how root exudation impacts soil respiration, although research shows that the release of exudates can stimulate microbial activity and the breakdown of organic matter, thereby increasing soil C loss at an ecosystem scale [37].

Root traits also impact soil C cycling indirectly through influencing the composition of the soil microbial community. For instance, it has been proposed that root traits that stimulate the growth of fungi over bacteria, such as high lignin and low root N content, promote soil C sequestration [1,38]. This view is consistent with the knowledge that these microbial groups have inherent differences in metabolism: not only do fungi respire less C per unit fungal biomass C gained, resulting in higher C use efficiency in fungi than in bacteria [39], but also fungal metabolites reside longer in soil than those from bacteria. This is because fungal mycelia comprise complex, nutrient poor C forms, such as chitin and melanin, whereas bacterial membranes mainly comprise phospholipids that are quickly mineralised on death ([40], but see [41]).



### Nutrient cycling

New research points to metabolic root traits, especially root exudation, having a major role in influencing soil nutrient availability. Plants can increase the availability of P for example by exuding root exudates rich in organic acids [9,42], which increase desorption and solubilisation from mineral surfaces [43]. Another strategy is the release of root exudates to enhance microbial mineralisation of organic matter resulting in a higher availability of nutrients into the soil. This process of priming, which is especially prevalent in N poor soil, involves the stimulation of microbial extracellular enzymes involved in the breakdown of organic N, thereby accelerating rates of N cycling and the supply of N to plants [44,45]. However, stimulation of microbial growth via exudation can also cause microbial immobilisation of N, thereby reducing nutrient availability to plants [44]. Such contrasting responses suggest that there is a fine balance between how root exudation impacts on microbial mineralisation-immobilisation dynamics, which is probably controlled by variations in the quality of exudates released from roots, the extent that microbes are nutrient limited [45,46], and the response of specific groups of microbes involved in nutrient transformations [47].

Few studies have tested for relationships between root traits and nutrient cycling in the field; those that have give mixed results. For instance, across a broad range of grassland plant species covering a spectrum of functional traits, Orwin et al. [48] found that soil properties related to N and P cycling were more strongly related to shoot traits, especially those reflecting high leaf litter quality (e.g., N content), than to root traits such as root N and P. In contrast, Hobbie et al. [49] found that soil N dynamics across a broad range of tree species were largely explained by interspecific variation in root chemistry and biomass, with root N in particular being positively related to rates of N mineralisation. Recent studies reveal other mechanisms by which root traits impact nutrient transformations, with, for example, dense root systems with higher SRL reducing nitrous oxide emissions and N leaching from soil [50], and hydraulic lift of water from sub-surface soil by roots enhancing selective root foraging [51] and N cycling in surface soil [52].

Despite much uncertainty about how root traits impact nutrient cycles, conceptual frameworks have been proposed that incorporate their influence on biogeochemical processes. It was recently proposed, for example, that the nutrient economy of forest ecosystems can be predicted on the basis of dominance of trees with either AM or ECM fungi, with the former having an inorganic nutrient economy, with rapid rates of decomposition and nutrient mineralisation, and the latter having an organic nutrient economy with slower rates of nutrient cycling [53]. This framework is based on two pieces of knowledge: first, that tree species predominately associate with a single type of mycorrhizal fungi, namely AM or ECM fungi, and second, that these two types of fungi differ in their modes of nutrient acquisition, with the former relying more on uptake of inorganic N and the latter on complex organic N forms. This framework is not dissimilar to that proposed to link microbial communities and their function to the

resource economics spectrum, namely that dominance of plant species with exploitative traits is associated with bacterial-dominated soil microbial communities, high rates of N mineralisation and N loss, whereas dominance of plants with conservative traits is associated fungal dominated microbial communities and slow rates of N cycling [54]. Recent studies using community weighted aboveground traits confirm this pattern in grasslands [7,55], but also that root traits better capture variation in microbial parameters related to N cycling than do shoot traits [56].

### Soil formation and structural stability

Root traits had a major role in soil formation over geological time (Box 1), but also play a major role in shaping the physical environment of contemporary soils. For instance, morphological root traits, such as root length density and root diameter, strongly influence soil stability (the ability to resist breakdown when subject to disruptive forces) because denser, finer root systems bind soil more effectively than do coarse root systems [57]. Root diameter also affects the density of soil, because roots push soil particles aside as they grow; hence, larger roots increase soil bulk density adjacent to the root, whereas finer roots can decrease bulk density by increasing soil porosity [58]. Rooting depth is also a key trait for reinforcement of soil, with deeper roots acting to stabilise soil at depth, especially on slopes where deep-rooting plants can increase slope stability [59]. Other architectural root traits such as branching also act to anchor roots and fix soil, thereby increasing soil stability and the resistance of soil to erosion.

The root trait that has the strongest impact on soil structure is root exudation, which increases soil aggregate stability [60,61]. This is because root exudates contain polysaccharides (mucilages) and proteins, which act like glue, bonding mineral particles together [61]. These compounds also form hydrophobic coatings on soil particles, which act as a water repellent, thereby reducing wetting rates and slaking of soil [62]. Plants that release more exudates will probably enhance their impact on the stability of soil. Also, given that plant species vary in the composition of their exudates [63], species that exude relatively larger molecules, such as polysaccharides and proteins that act as effective binding agents [60], will have a greater impact on aggregate stability of soil. In general, our understanding of how variations in root exudation profiles in soil influence soil structure is limited; we argue that this represents a major gap in knowledge.

Biotic root traits, especially the degree and type of mycorrhizal infection, impact soil aggregate stability mainly through physical enmeshment of soil particles by their extensive networks of mycelium [62], and the binding of soil via the production of extracellular polysaccharides and proteins, including the protein glomalin [64]. Glomalin is deposited in soil through the degradation of AM hyphae, and, as well as binding soil, it is a hydrophobin and hence it alters the wetting behaviour of soil; by impeding soil wetting, aggregate stability is enhanced because of reduced slaking [65]. Mycorrhizal fungi also impact soil formation by acting as biological agents of mineral weathering, with studies showing ECM fungi to be especially

effective at enhancing mineral dissolution through acidification and release of organic acids and chelating compounds [66,67].

### Root trait frameworks and global change

The potential for trait-based frameworks to inform on ecosystem responses to global change has been demonstrated for aboveground plant traits [2,7,68]. Given the high variation in root traits both between and within species, and their enormous plasticity in relation to changing resource supply, global change phenomena have considerable potential to modify root traits and their impact on ecosystem processes across a range of scales, from the individual plant to the Earth system scale (Figure 2). Frameworks have already been proposed for understanding biogeochemical responses of forests to global change, based on tree species associations with mycorrhizal fungi [53], and recent research is beginning to reveal the power of root traits to capture variation in soil microbial parameters related to N cycling in grasslands [7,48,55]. However, the true potential of frameworks based on root traits to improve understanding of ecosystem responses to global change is yet to be explored.

At the individual plant level, there is much evidence that several root traits respond rapidly to global change and that these responses are of a scale that is likely to impact ecosystem processes. It is known, for example, that root traits, such as root branching and mycorrhizal infection, respond to N enrichment [8,69], although responses are species and genotype specific [8], and vary with soil conditions, such as the availability of P [70]. Likewise, many architectural and morphological root traits are able to respond rapidly to changes in soil water availability

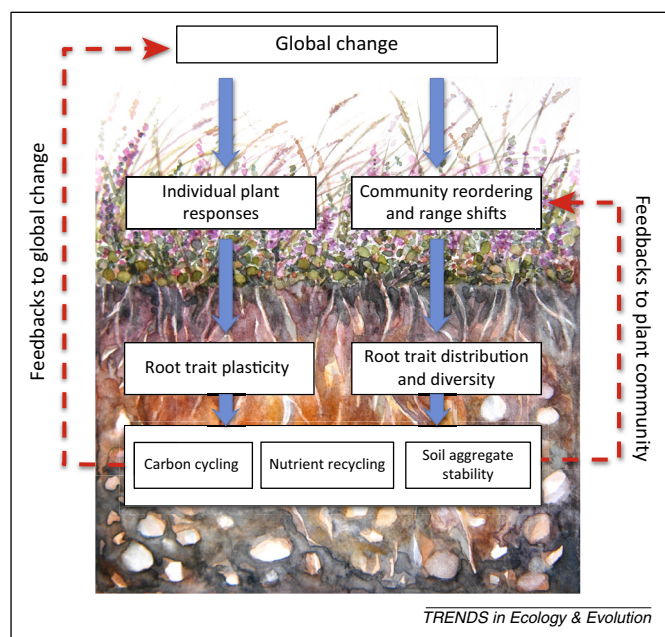
caused by drought, although some plant species and genotypes are more plastic than others [71,72]. Also, a recent meta-analysis of field studies across a broad range of ecosystems revealed significant responses of a spectrum of root traits to elevated atmospheric CO<sub>2</sub>, including increases in root length (+26.0%), diameter (+8.4%), and total root biomass (+28.8%), pointing to an expansion of root systems, and stimulation of root respiration (+58.9%), exudation (+37.9%), and mycorrhizal colonisation (+3.35%) [73]. The scale of these responses across a wide spectrum of root traits, coupled with their potential to impact soil microbial communities and biogeochemical cycles, suggests an urgent need to incorporate such knowledge into ecosystem models to improve prediction of biogeochemical responses to climate change [73].

Reorganisation of root trait spectra can also result from global change induced shifts in vegetation composition, which occurs at both local and regional scales. **At the community level**, for example, reduced precipitation [19,20] and warming [20,74] have been shown to increase the dominance of deeper rooting plant species, whereas elevated CO<sub>2</sub> has been shown to increase the relative abundance of C<sub>4</sub> grasses [75], woody species [76], and legumes [77], which all have distinct root trait syndromes and the potential to cause shifts in belowground communities and ecosystem processes. At regional scales, there is also much evidence that climate warming is causing expansion of species ranges, including upward movement of alpine plant species [78,79], northward expansion of boreal forest [80], shrub expansion in arid and semi-arid ecosystems [81], and shrub encroachment in arctic tundra [82]; such range shifts introduce new sets of root traits into ecosystems which have consequences for soil biogeochemical processes and feedbacks to climate change.

### Concluding remarks and future challenges

**Our synthesis reveals multiple routes by which root traits impact a range of soil-based ecosystem processes, which emphasizes the need to extend the trait-based approach underground. We also demonstrate the potential for global change to modify relations between root traits and their soil environment, with potentially far reaching implications for biogeochemical cycles and the formation and stability of soil.** It is also evident that multiple suites of root traits operate simultaneously to impact these ecosystem processes, often with opposing and uncertain effects (Figure 3). Therefore, understanding how suites of traits, and trade-offs among them, respond to environment change and their impact on multiple ecosystem processes will be crucial for future prediction of impacts of global change.

**The study of root traits in ecological settings is still in its infancy, at least compared with how much is known about aboveground plant traits and their ecosystem impacts.** As a result, major research challenges still face ecologists working at the interface between root traits and ecosystem processes. Perhaps one of the largest challenges is the need for improved knowledge of variation in root traits within and among species across a broad range of communities, ecosystems and biomes. Databases such as the TRY Plant Trait Database [83] are now available for mostly



**Figure 2.** Root trait responses and feedbacks triggered by global change. Global change phenomena, such as climate and land use change, impact root traits and ecosystem processes via individual plant responses (root trait plasticity) and community level responses (root trait distribution). 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<sub>2</sub> flux. Image by Jill Colquhoun Bardgett.

		Carbon cycling		Nutrient cycling			Structural stability		
		Inputs	Decomposition	Inputs	Mineralisation	Plant uptake	Erosion resistance	Porosity	Aggregate formation
Architectural	Root length density	↑	→	↑	↑	↑	↑	↑	↑
	Rooting depth	↑	→	↗	?	↑	↑	↑	→
Morphological	Specific root length	↑	↗	?	↗	↑	↑	↑	↑
Physiological	Root N content	↑	↑	↑	↑	?	?	?	?
	Root exudates	↑	?	↑	?	?	↑	?	↑
Biotic	Rhizobia	↑	↑	↑	↑	↑	↘	↑	↑
	Mycorrhizae	↑	→	?	→	↑	↑	?	↑
	Pathogens	?	↑	↑	↑	↓	?	?	?

TRENDS in Ecology &amp; Evolution

**Figure 3.** Root traits and their potential impact on processes of carbon cycling, nutrient cycling, and measures of soil structural stability, based on the literature reported in the main text. Upward pointing arrows designate a predominantly positive effect, downward pointing arrows designate a negative effect, horizontal arrows designate no effect, and question marks indicate that not enough is known to draw conclusions. Shade of colouring indicates the amount of evidence available and/or the degree of uncertainty surrounding the direction of response. Abbreviation: N, nitrogen.

aboveground plant traits, which are successfully being used to predict how changes in trait diversity impact belowground processes at different scales [7,55]. But given the tremendous functional role of roots traits, similar resources with comprehensive information on belowground traits, which are often challenging to measure (Box 2), are urgently required. Such information, along with improved knowledge of relationships between easily measured aboveground and belowground traits, will pave the way for improved prediction of the consequences of vegetation change for ecosystem functioning.

Another major challenge is the need to improve understanding of the mechanisms by which root traits impact ecosystem process via their interactions with microbial communities in soil. We have highlighted that many ecosystem functions are determined by biotic root traits involving direct interactions with microorganisms, especially mycorrhizal fungi. But there is growing evidence that root traits have strong impacts on ecosystem processes via interactions with free-living microorganisms, largely via the release of root exudates that stimulate the activity of microbial communities in soil. Despite growing recognition

## Box 2. Methods for studying root traits

Several methods offer exciting opportunities to advance understanding of the role of root traits and root–root interactions in terrestrial ecosystems.

### Visualising root structural traits using X-ray tomography

Recent developments in X-ray computed tomography (CT) enable non-destructive measurement of architectural and morphological root traits in 3D in undisturbed soil cores. Until recently, the technique, which uses X-rays to acquire cross-sectional image slices of an object that are then reconstructed to produce a 3D image, lacked the spatial resolution required to discriminate roots from the soil matrix and took a long time to create images. State-of-art X-ray CT scanners can now gain spatial resolution of <500 nm, enabling the visualisation and quantification of fine roots and their effects on surrounding soil structure [93]. Also, ‘fast scan’ techniques can create images in a matter of minutes, and it is possible to visualise soil columns of up to 1 m in depth, enabling the study of root–soil interactions at realistic spatial and temporal scales [93].

### DNA-based techniques for quantifying root abundance

Our knowledge of species distributions belowground is limited, at least compared with what is known about aboveground distributions. This is because roots of different species are so intermingled and difficult to separate, and they cannot be easily traced back to an

individual plant of known identity. New DNA-based methods overcome this problem by enabling quantitative assessment of relative species abundances in mixed plant communities [94,95]. The first DNA-based approaches for identifying roots were qualitative [96,97]. Now, alternative approaches based on the use of quantitative real-time PCR of species-specific and generic plant barcode markers are being developed [98].

### Quantifying root exudates

Quantifying rates of root exudation is difficult because soil microbes capture them rapidly and break them down. Existing approaches for the collection of exudates include the growing plants in hydroponics under sterile conditions, the transfer of intact plants or roots from soil to liquid collection media, and *in situ* collection by suction cups or anion exchange membranes. All these methods have drawbacks: exudates collected under sterile conditions differ greatly from those in natural soil; the use of nutrient solutions to collect exudates interferes with the quantification of C compounds; and exudates collected *in situ* include organic compounds from soil organic matter and microbial origin. The development of stable isotope probing techniques overcome some of these problems by enabling *in situ* tracing of photosynthetic  $^{13}\text{C}$  flow to roots and soil microbes, via  $^{13}\text{C}$  enrichment of microbial biomarkers [99] or microbial DNA/RNA [100].



of the functional importance of such interactions, our knowledge of the specific traits that impact soil microbial communities, and how they relate to plant ecological strategies, is limited. Therefore, future studies need to explore how root traits influence the soil microbial community and its activities, and how these impacts cascade to the soil processes on which the functioning of terrestrial ecosystems depend.

Finally, it is evident that global change phenomena substantially impact a suite of root traits with cascading effects on soil-based ecosystem processes that underpin many of the services that ecosystems provide. There is now growing recognition that trait-based approaches offer potential for elucidating the complexity of ecological responses to global change and consequences for ecosystem services, and frameworks based on aboveground traits have been proposed for predicting ecosystem service responses to environmental change [68,84]. As we show here, there is an urgent need to extend these approaches belowground in order to improve prediction of ecosystem responses to global change.

## References

- De Deyn, G.B. *et al.* (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11, 516–531
- Diaz, S. *et al.* (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. U.S.A.* 104, 20684–20689
- Cadotte, M.W. *et al.* (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4, e5695
- Roscher, C. *et al.* (2012) Using plant functional traits to explain diversity-productivity relationships. *PLoS ONE* 7, e36760
- Craine, J.M. *et al.* (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.* 16, 563–574
- Fortunel, C. *et al.* (2009) Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* 90, 598–611
- Grigulis, K. *et al.* (2013) Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *J. Ecol.* 101, 47–57
- Poorter, H. *et al.* (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50
- Lambers, H. *et al.* (2008) Plant nutrient-acquisition strategies change with soil age. *Trends Ecol. Evol.* 23, 95–103
- Chapman, N. *et al.* (2012) Roots, water, and nutrient acquisition: let's get physical. *Trends Plant Sci.* 17, 701–710
- Hodge, A. (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol.* 162, 9–24
- Kemmel, S.W. and Cahill, J.F. (2011) Independent evolution of leaf and root traits within and among temperate grassland plant communities. *PLoS ONE* 6, e19992
- Comas, L.H. and Eissenstat, D.M. (2009) Patterns in root trait variation among 25 co-existing North American forest species. *New Phytol.* 182, 919–928
- Reich, P. (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
- Roumet, C. *et al.* (2006) Suites of root traits differ between annual and perennial species growing in the field. *New Phytol.* 170, 357–368
- Mommer, L. and Weemstra, M. (2012) The role of roots in the resource economics spectrum. *New Phytol.* 195, 725–727
- Chen, W.L. *et al.* (2013) Variation of first-order root traits across climatic gradients and evolutionary trends in geological time. *Glob. Ecol. Biogeogr.* 22, 846–856
- Valverde-Barrantes, O.J. *et al.* (2013) The distribution of below-ground traits is explained by intrinsic species differences and intraspecific plasticity in response to root neighbours. *J. Ecol.* 101, 933–942
- Debinski, D.M. *et al.* (2010) Montane meadow change during drought varies with background hydrologic regime and plant functional group. *Ecology* 91, 1672–1681
- Hoepfner, S.S. and Dukes, J.S. (2012) Interactive responses of old-field plant growth and composition to warming and precipitation. *Glob. Change Biol.* 18, 1754–1768
- Kemmel, S.W. *et al.* (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Ann. Bot. (Lond.)* 101, 1295–1301
- Chen, H.Y.H. and Brassard, B.W. (2013) Intrinsic and extrinsic controls of fine root life span. *Crit. Rev. Plant Sci.* 32, 151–161
- Silver, W.L. and Miya, R.K. (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129, 407–419
- McCormack, M.L. *et al.* (2012) Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol.* 195, 823–831
- Hodge, A. *et al.* (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* 413, 297–299
- Langley, J.A. *et al.* (2006) Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecol. Lett.* 9, 955–959
- Herman, D.J. *et al.* (2012) Interactions between an arbuscular mycorrhizal fungus and a soil microbial community mediating litter decomposition. *FEMS Microbiol. Ecol.* 80, 236–247
- Averill, C. *et al.* (2014) Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505, 543–545
- Raich, J.W. and Schlesinger, W.H. (1992) The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Ser. B: Chem. Phys. Meteorol.* 44, 81–99
- Jones, D.L. *et al.* (2004) Plant and mycorrhizal regulation of rhizodeposition. *New Phytol.* 163, 459–480
- Bond-Lamberty, B. *et al.* (2004) A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob. Change Biol.* 10, 1756–1766
- Hanson, P.J. *et al.* (2000) Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48, 115–146
- Phillips, R.P. and Fahey, T.J. (2007) Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. *New Phytol.* 176, 655–664
- Reich, P.B. *et al.* (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecol. Lett.* 11, 793–801
- Martin, C.A. and Stutz, J.C. (2004) Interactive effects of temperature and arbuscular mycorrhizal fungi on growth, P uptake and root respiration of *Capsicum annuum* L. *Mycorrhiza* 14, 241–244
- Trocha, L.K. *et al.* (2010) Ectomycorrhizal identity determines respiration and concentrations of nitrogen and non-structural carbohydrates in root tips: a test using *Pinus sylvestris* and *Quercus robur* saplings. *Tree Physiol.* 30, 648–654
- Fontaine, S. *et al.* (2004) Carbon input to soil may decrease soil carbon content. *Ecol. Lett.* 7, 314–320
- Bardgett, R.D. *et al.* (2013) Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle. *J. Ecol.* 101, 334–343
- Six, J. *et al.* (2006) Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.* 70, 555–569
- White, D.C. *et al.* (1979) Determination of the sedimentary microbial biomass by extractable lipid phosphate. *Oecologia* 40, 51–62
- De Vries, F.T. *et al.* (2009) High turnover of fungal hyphae in incubation experiments. *FEMS Microbiol. Ecol.* 67, 389–396
- Li, L. *et al.* (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proc. Natl. Acad. Sci. U.S.A.* 104, 11192–11196
- George, T.S. *et al.* (2011) Phosphorus nutrition: rhizosphere processes, plant response and adaptations. In *Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling* (Bunemann, E.K. *et al.*, eds), pp. 245–271, Springer-Verlag
- Bengtson, P. *et al.* (2012) Evidence of a strong coupling between root exudation, C and N availability, and stimulated SOM decomposition caused by rhizosphere priming effects. *Ecol. Evol.* 2, 1843–1852
- Dijkstra, F.A. *et al.* (2013) Rhizosphere priming: a nutrient perspective. *Front. Microbiol.* 4. Published online July 29, 2013. (<http://dx.doi.org/10.3389/fmicb.2013.00216>)

- 46 Drake, J.E. *et al.* (2013) Stoichiometry constrains microbial response to root exudation—insights from a model and a field experiment in a temperate forest. *Biogeosciences* 10, 821–838
- 47 Bremer, C. *et al.* (2007) Impact of plant functional group, plant species, and sampling time on the composition of nirK-Type denitrifier communities in soil. *Appl. Environ. Microbiol.* 73, 6876–6884
- 48 Orwin, K.H. *et al.* (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *J. Ecol.* 98, 1074–1083
- 49 Hobbie, S.E. *et al.* (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87, 2288–2297
- 50 Abalos, D. *et al.* (2014) Plant species identity surpasses species richness as a key driver of N<sub>2</sub>O emissions from grassland. *Glob. Change Biol.* 20, 265–275
- 51 Prieto, I. *et al.* (2012) Hydraulic lift promotes selective root foraging in nutrient-rich soil patches. *Funct. Plant Biol.* 39, 804–812
- 52 Cardon, Z.G. *et al.* (2013) Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences. *Proc. Natl. Acad. Sci. U.S.A.* 110, 18988–18993
- 53 Phillips, R.P. *et al.* (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytol.* 199, 41–51
- 54 Wardle, D.A. *et al.* (2004) Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633
- 55 De Vries, F.T. *et al.* (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol. Lett.* 15, 1230–1239
- 56 Legay, N. *et al.* (2014) Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. *Ann. Bot. (Lond.)* 114, 1011–1021
- 57 Loades, K.W. *et al.* (2010) Planting density influence on fibrous root reinforcement of soils. *Ecol. Eng.* 36, 276–284
- 58 Gysels, G. *et al.* (2005) Impact of plant roots on the resistance of soils to erosion by water: a review. *Prog. Phys. Geogr.* 29, 189–217
- 59 Stokes, A. *et al.* (2009) Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant Soil* 324, 1–30
- 60 Whalley, W.R. *et al.* (2005) Structural differences between bulk and rhizosphere soil. *Eur. J. Soil Sci.* 56, 353–360
- 61 Czarnes, S. *et al.* (2000) Root- and microbial-derived mucilages affect soil structure and water transport. *Eur. J. Soil Sci.* 51, 435–443
- 62 Hallett, P.D. *et al.* (2009) Disentangling the impact of AM fungi versus roots on soil structure and water transport. *Plant Soil* 314, 183–196
- 63 Bais, H.P. *et al.* (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* 233–266
- 64 Rillig, M.C. and Mummey, D.L. (2006) Mycorrhizas and soil structure. *New Phytol.* 171, 41–53
- 65 Guggenberger, G. *et al.* (1999) Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. *Soil Sci. Soc. Am. J.* 63, 1188–1198
- 66 Quirk, J. *et al.* (2014) Ectomycorrhizal fungi and past high CO<sub>2</sub> atmospheres enhance mineral weathering through increased below-ground carbon-energy fluxes. *Biol. Lett.* 10. Published online July 2, 2014. (<http://dx.doi.org/10.1098/rsbl.2014.0375>)
- 67 Taylor, L.L. *et al.* (2009) Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. *Geobiology* 7, 171–191
- 68 Lamarque, P. *et al.* (2014) Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13751–13756
- 69 Nasholm, T. *et al.* (2013) Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytol.* 198, 214–221
- 70 Johnson, N.C. *et al.* (2003) Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. *Ecology* 84, 1895–1908
- 71 Nippert, J.B. and Knapp, A.K. (2007) Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos* 116, 1017–1029
- 72 Comas, L.H. *et al.* (2013) Root traits contributing to plant productivity under drought. *Front. Plant Sci.* 4. Published online November 5, 2013. (<http://dx.doi.org/10.3389/fpls.2013.00442>)
- 73 Nie, M. *et al.* (2013) Altered root traits due to elevated CO<sub>2</sub>: a meta-analysis. *Glob. Ecol. Biogeogr.* 22, 1095–1105
- 74 Weltzin, J.F. *et al.* (2003) Potential effects of warming and drying on peatland plant community composition. *Glob. Change Biol.* 9, 141–151
- 75 Pendall, E. *et al.* (2011) Soil carbon storage under simulated climate change is mediated by plant functional type. *Glob. Change Biol.* 17, 505–514
- 76 Souza, L. *et al.* (2010) CO<sub>2</sub> enrichment accelerates successional development of an understory plant community. *J. Plant Ecol.* 3, 33–39
- 77 Hanley, M.E. *et al.* (2004) Species-level effects more important than functional group-level responses to elevated CO<sub>2</sub>: evidence from simulated turves. *Funct. Ecol.* 18, 304–313
- 78 Lenoir, J. *et al.* (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768–1771
- 79 Walther, G.R. *et al.* (2005) Trends in the upward shift of alpine plants. *J. Veg. Sci.* 16, 541–548
- 80 Danby, R.K. and Hik, D.S. (2007) Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Glob. Change Biol.* 13, 437–451
- 81 Schlesinger, W.H. *et al.* (1990) Biological feedbacks in global desertification. *Science* 247, 1043–1048
- 82 Wookey, P.A. *et al.* (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Glob. Change Biol.* 15, 1153–1172
- 83 Kattge, J. *et al.* (2011) TRY - a global database of plant traits. *Glob. Change Biol.* 17, 2905–2935
- 84 Lavorel, S. *et al.* (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.* 24, 942–948
- 85 Raven, J.A. and Edwards, D. (2001) Roots: evolutionary origins and biogeochemical significance. *J. Exp. Bot.* 52, 381–401
- 86 Brundrett, M.C. (2002) Coevolution of roots and mycorrhizas of land plants. *New Phytol.* 154, 275–304
- 87 Comas, L.H. *et al.* (2014) Patterns in root traits of woody species hosting arbuscular and ectomycorrhizas: implications for the evolution of belowground strategies. *Ecol. Evol.* 4, 2979–2990
- 88 Comas, L.H. *et al.* (2012) Evolutionary patterns and biochemical significance of angiosperm root traits. *Int. J. Plant. Sci.* 173, 584–595
- 89 Kong, D. *et al.* (2014) Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytol.* 203, 863–872
- 90 Maherali, H. (2014) Is there an association between root architecture and mycorrhizal growth response? *New Phytol.* 204, 192–200
- 91 Sprent, J.I. (2007) Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. *New Phytol.* 174, 11–25
- 92 Bowen, G.J. *et al.* (2004) A humid climate state during the Palaeocene/Eocene thermal maximum. *Nature* 432, 495–499
- 93 Mooney, S.J. *et al.* (2012) Developing X-ray Computed Tomography to non-invasively image 3-D root systems architecture in soil. *Plant Soil* 352, 1–22
- 94 Mommer, L. *et al.* (2008) Unravelling below-ground plant distributions: a real-time polymerase chain reaction method for quantifying species proportions in mixed root samples. *Mol. Ecol. Resour.* 8, 947–953
- 95 Hiiesalu, I. *et al.* (2012) Plant species richness belowground: higher richness and new patterns revealed by next-generation sequencing. *Mol. Ecol.* 21, 2004–2016
- 96 Linder, C.R. *et al.* (2000) A universal molecular method for identifying underground plant parts to species. *Mol. Ecol.* 9, 1549–1559
- 97 Jackson, R.B. *et al.* (1999) Ecosystem rooting depth determined with caves and DNA. *Proc. Natl. Acad. Sci. U.S.A.* 96, 11387–11392
- 98 Mommer, L. *et al.* (2011) Belowground DNA-based techniques: untangling the network of plant root interactions. *Plant Soil* 348, 115–121
- 99 Paterson, E. *et al.* (2007) Rhizodeposition shapes rhizosphere microbial community structure in organic soil. *New Phytol.* 173, 600–610
- 100 Singh, B.K. *et al.* (2004) Unravelling rhizosphere–microbial interactions: opportunities and limitations. *Trends Microbiol.* 12, 386–393