

## Viewpoints

# A trait-based framework linking the soil metabolome to plant–soil feedbacks

### Summary

By modifying the biotic and abiotic properties of the soil, plants create soil legacies that can affect vegetation dynamics through plant–soil feedbacks (PSF). PSF are generally attributed to reciprocal effects of plants and soil biota, but these interactions can also drive changes in the identity, diversity and abundance of soil metabolites, leading to more or less persistent soil chemical legacies whose role in mediating PSF has rarely been considered. These chemical legacies may interact with microbial or nutrient legacies to affect species coexistence. Given the ecological importance of chemical interactions between plants and other organisms, a better understanding of soil chemical legacies is needed in community ecology. In this Viewpoint, we aim to: highlight the importance of belowground chemical interactions for PSF; define and integrate soil chemical legacies into PSF research by clarifying how the soil metabolome can contribute to PSF; discuss how functional traits can help predict these plant–soil interactions; propose an experimental approach to quantify plant responses to the soil solution metabolome; and describe a testable framework relying on root economics and seed dispersal traits to predict how plant species affect the soil metabolome and how they could respond to soil chemical legacies.

### Belowground chemistry: an overlooked component of plant–soil feedbacks?

Plant–soil feedbacks (PSF) occur when plants create belowground legacies by modifying the biotic and abiotic properties of the soil, which in turn affect the growth and performance of succeeding conspecifics and other species (Bever, 1994; Hendriks *et al.*, 2013; van der Putten *et al.*, 2013; Pineda *et al.*, 2020; Hannula *et al.*, 2021). These modifications of the biotic and abiotic components of the soil can persist after an individual's death and have important implications for coexistence among plant species (Klironomos, 2002; Callaway *et al.*, 2004; Kulmatiski *et al.*, 2008; Maron *et al.*, 2016; Lekberg *et al.*, 2018; Crawford *et al.*, 2019). For instance, microbial legacies caused by the accumulation of host-specific pathogens in the rhizosphere of plants can generate negative density-dependence and reduce mono-dominance, thereby acting as a mechanism to maintain plant species diversity (Yang

*et al.*, 2015; Maron *et al.*, 2016; Mommer *et al.*, 2018; Thakur *et al.*, 2021). Soil legacies can also lead to strong priority effects (Kardol *et al.*, 2007; Grman & Suding, 2010), in which the order and timing of species immigration influence further assembly by determining the way species affect one another (Fukami, 2015). Although soil legacies are often caused by a variety of mechanisms operating simultaneously (Bennett & Klironomos, 2019), changes in resource availability and the accumulation of pathogenic fungi or symbiotic mutualists in the plants' rhizosphere have been thought to be the major drivers of PSF (Kardol *et al.*, 2007; Semchenko *et al.*, 2018; Heinen *et al.*, 2020b). Recent evidence suggests that this picture is incomplete, as belowground chemical interactions can also be a source of soil legacies that modify coexistence among plant species (Semchenko *et al.*, 2019; Delory *et al.*, 2021).

Plants shape their local environment by releasing chemicals into the soil via root exudation and litter decomposition. This process, a component of niche modification (*sensu* Fukami, 2015) or niche construction (*sensu* Müller & Junker, 2022), can affect intra- and interspecific interactions within and across trophic levels (Bilas *et al.*, 2021; Ninkovic *et al.*, 2021; Majumdar *et al.*, 2023). Below the soil surface, biotic interactions partly rely on chemical compounds synthesised and released into the soil by plant roots (i.e. root exudates) and soil microorganisms (Mommer *et al.*, 2016; Tsunoda & van Dam, 2017; Oburger & Jones, 2018; Ehlers *et al.*, 2020). In addition to playing a central role in structuring the rhizosphere microbiome (Hu *et al.*, 2018; Sasse *et al.*, 2018; Zhou *et al.*, 2023), root exudates can mediate belowground positive and negative plant–plant interactions (Li *et al.*, 2007; Delory *et al.*, 2016; Kong *et al.*, 2018; Wang *et al.*, 2021), a phenomenon known as allelopathy (Hierro & Callaway, 2021). Evidence for this comes from studies showing that root-secreted chemicals can enhance or suppress the growth of neighbours (Zhang *et al.*, 2021), are involved in neighbour detection and recognition (Renne *et al.*, 2014; Semchenko *et al.*, 2014; Kong *et al.*, 2018; Wang *et al.*, 2021), and affect root placement and distribution (Wang *et al.*, 2023). In addition to root exudates, litter decomposition products have also been shown to mediate conspecific feedbacks and interact in complex ways with other feedback components (Mazzoleni *et al.*, 2015; De Long *et al.*, 2023a; Majumdar *et al.*, 2023).

Clearly, soil chemical compounds, including root exudates and litter decomposition products, play important roles in mediating belowground biotic interactions. However, a crucial piece of information missing from our current understanding of the mechanisms governing plant–soil interactions is the role of the soil metabolome in generating PSF.

### Definition and mechanisms of soil chemical legacies

In a patch of soil in which individuals of one or more plant species coexist, soil chemical legacies arise from local and dynamic

variation in the identity, diversity (including richness and evenness) and abundance of volatile and nonvolatile chemical compounds in the soil, including the rhizosphere of plants. Chemical legacies can comprise hundreds of inorganic (e.g. macro- and micronutrients, and metals) and organic (primary and specialised metabolites) compounds, and vary depending on the environmental context (e.g. soil type, local microclimate, plant community composition and diversity). Here, we focus primarily on organic chemical compounds found in the soil solution (i.e. the aqueous liquid phase of the soil), which together constitute the soil solution metabolome, as a driver of PSF that has received least attention. In the following paragraphs, we will use the expression ‘soil chemical legacy’ to refer to the short- and long-term effects of plants and soil organisms on the abundance and composition of soil metabolites.

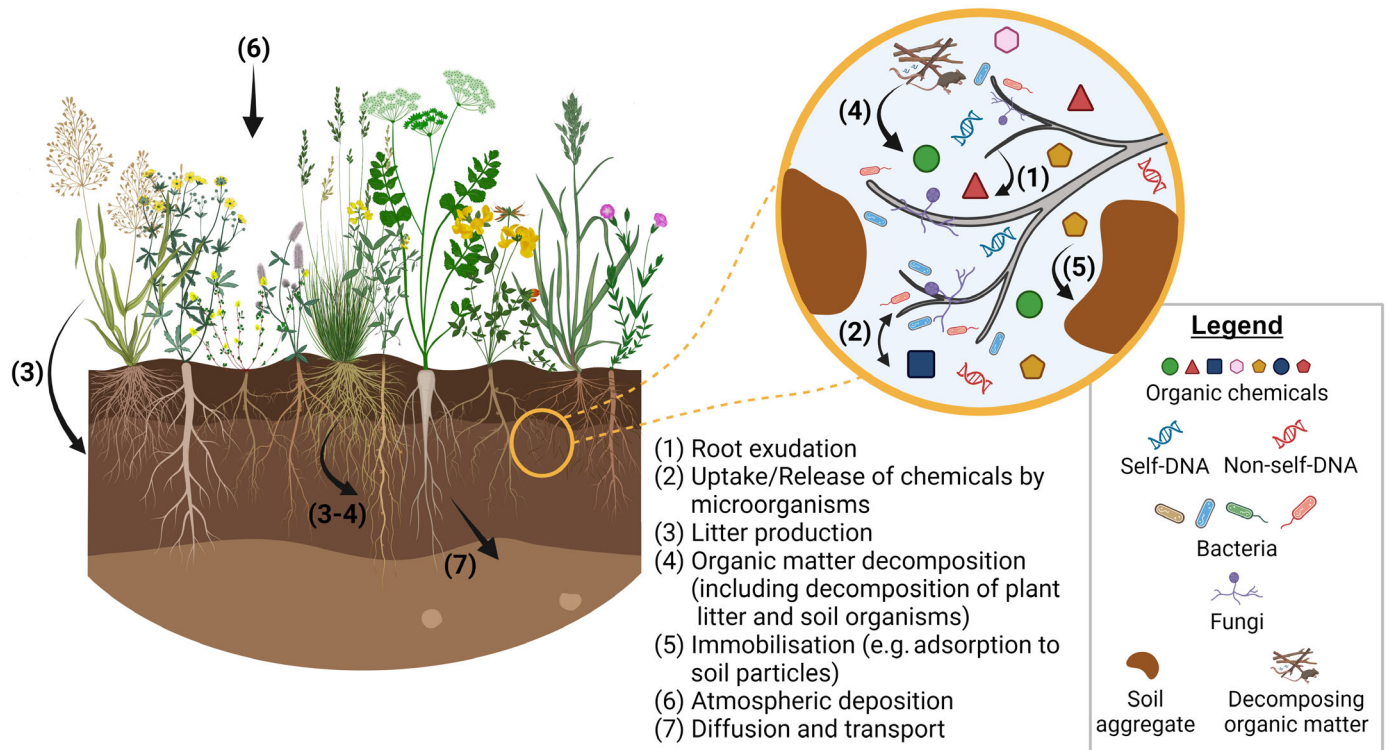
Local changes in soil solution metabolome result from a diversity of mechanisms operating simultaneously (Fig. 1), making them highly variable both spatially (e.g. location in the soil) and temporally (e.g. diurnal and seasonal variations in plant and microbial activities). Beyond a few specific examples of allelopathic soil chemical legacies on plant growth (Hierro & Callaway, 2021; Zhang *et al.*, 2021), our knowledge of the persistence and role of nontoxic legacies in regulating plant growth, foraging and life history traits is limited (Renne *et al.*, 2014;

Semchenko *et al.*, 2014; Delory *et al.*, 2021; Gfeller *et al.*, 2023b). Soil metabolites can also have indirect effects on plants by affecting the structure and functioning of soil microbial communities, as well as soil nutrient availability (Inderjit & Weiner, 2001; Hu *et al.*, 2018). For instance, a recent analysis of trait relationships in 20 subtropical tree species found that fast-growing species have a higher activity of microbial extracellular enzymes involved in C-, P- and N-cycling in their rhizosphere (Han *et al.*, 2023), which could benefit other species by increasing organic matter mineralisation and nutrient availability.

Considering that plants rely strongly on chemicals to interact with other organisms (Metlen *et al.*, 2009; Delory *et al.*, 2016; Ninkovic *et al.*, 2021; Wang *et al.*, 2021; Müller & Junker, 2022), a better understanding of the chemical mechanisms underlying plant–soil interactions is key for predicting the impact of the soil metabolome on species coexistence and vegetation dynamics and advance the field of community ecology.

### Integrating the soil metabolome into PSF research

The effects of soil biota and soil chemical compounds on plants, and vice versa, are inherently interconnected, but are usually interpreted as independent processes. Roots release many chemical



**Fig. 1** Aboveground and belowground processes contributing to local changes in soil solution metabolome. This figure highlights seven dynamic, spatially variable and interconnected processes that contribute to soil chemical legacies by inducing variations in the quantity and composition of primary and specialised metabolites in the soil solution: (1) exudation of organic chemicals by living plant roots (root exudation); (2) uptake and release of organic chemicals by soil microbes; (3) litter production above- and belowground; (4) decomposition of soil organic matter, which includes decomposition from plants, animals and microorganisms; (5) adsorption of organic chemicals to soil particles; (6) atmospheric deposition of organic compounds at the soil surface; and (7) diffusion and transport of organic chemicals into the soil. All these processes are dependent on biotic (i.e. species identity, plant traits, etc.) and/or abiotic (i.e. temperature, precipitation, soil water content, soil texture) conditions, which contribute to the spatial and temporal variability of soil chemical legacies at a local scale. The figure was created with [BioRender.com](https://www.biorender.com).

compounds into the soil, including sugars, amino acids, organic acids and other specialised metabolites such as phenolic compounds (e.g. flavonoids) and terpenoids, that can repel or attract microbial antagonists and mutualists, which in turn have powerful effects on plants (Philippot *et al.*, 2013; Haichar *et al.*, 2014). The activity of soil microorganisms can also have a direct impact on the composition and persistence of soil chemicals from root exudation or litter decomposition, which can result in inhibition or stimulation of allelopathic effects (Bonanomi *et al.*, 2021) as well as in shifts in the direction of PSF effects (Majumdar *et al.*, 2023). These inherently interconnected processes are almost always studied as ‘net effects’ in the context of PSF (Van der Putten *et al.*, 1993; Bever, 1994). Since their discovery, PSF have been formally presented in the context of effects and responses to the ‘soil community’ (Bever, 1994) and ‘specific growth-depressing microorganisms’ (Van der Putten *et al.*, 1993). This microbe-centric perspective is important, and still predominant, but the role of plant and soil chemistry is gaining attention (Mazzoleni *et al.*, 2015; Nettan *et al.*, 2019; Veen *et al.*, 2019; Ehlers *et al.*, 2020; Gundale & Kardol, 2021; De Long *et al.*, 2023b; Nannipieri *et al.*, 2023; Steinauer *et al.*, 2023). For example, Semchenko *et al.* (2019) experimentally manipulated soil chemical interactions and microbial legacies and found that belowground chemistry and soil biota interacted to promote seedling survival and species coexistence in grassland mesocosms. More recently, Gfeller *et al.* (2023b) showed that wheat plants grown in the field on soil conditioned by a maize genotype capable of releasing root benzoxazinoids had more reproductive tillers, leading to higher grain yield. Root-emitted benzoxazinoids have also been shown to increase maize resistance to negative PSF (Gfeller *et al.*, 2023a). These studies demonstrate the important role of the soil biota and belowground chemical interactions in mediating PSF.

Explicitly accounting for the interactive effects of soil microbes and soil metabolites in mediating plant–soil interactions may allow us to address some of the unexplained variation in PSF effects, which may improve our ability to predict their strength and direction, as well as the possible implications for species coexistence and community dynamics. This is particularly important for invasion of plant communities by non-native species, which can be promoted by weaker negative feedbacks due to escape from pathogens in their native ranges (enemy release hypothesis), stronger positive feedback from newly encountered soil mutualists (enhanced mutualisms hypothesis), as well as by the synthesis and release of organic chemicals that negatively affect native species (novel weapons hypothesis; Callaway & Ridenour, 2004; Reinhart & Callaway, 2006; Maron *et al.*, 2014). Better understanding of the independent roles of soil microbes and soil metabolites, as well as their interactive effects, in mediating plant–soil interactions would help us shed light on the mechanisms behind successful plant invasions as well as range expansion by native species (Engelkes *et al.*, 2008; van der Putten *et al.*, 2016; Majumdar *et al.*, 2023).

To make PSF effects more predictable, the soil metabolome should be integrated into existing frameworks linking PSF responses to plant functional traits. In the context of plant–

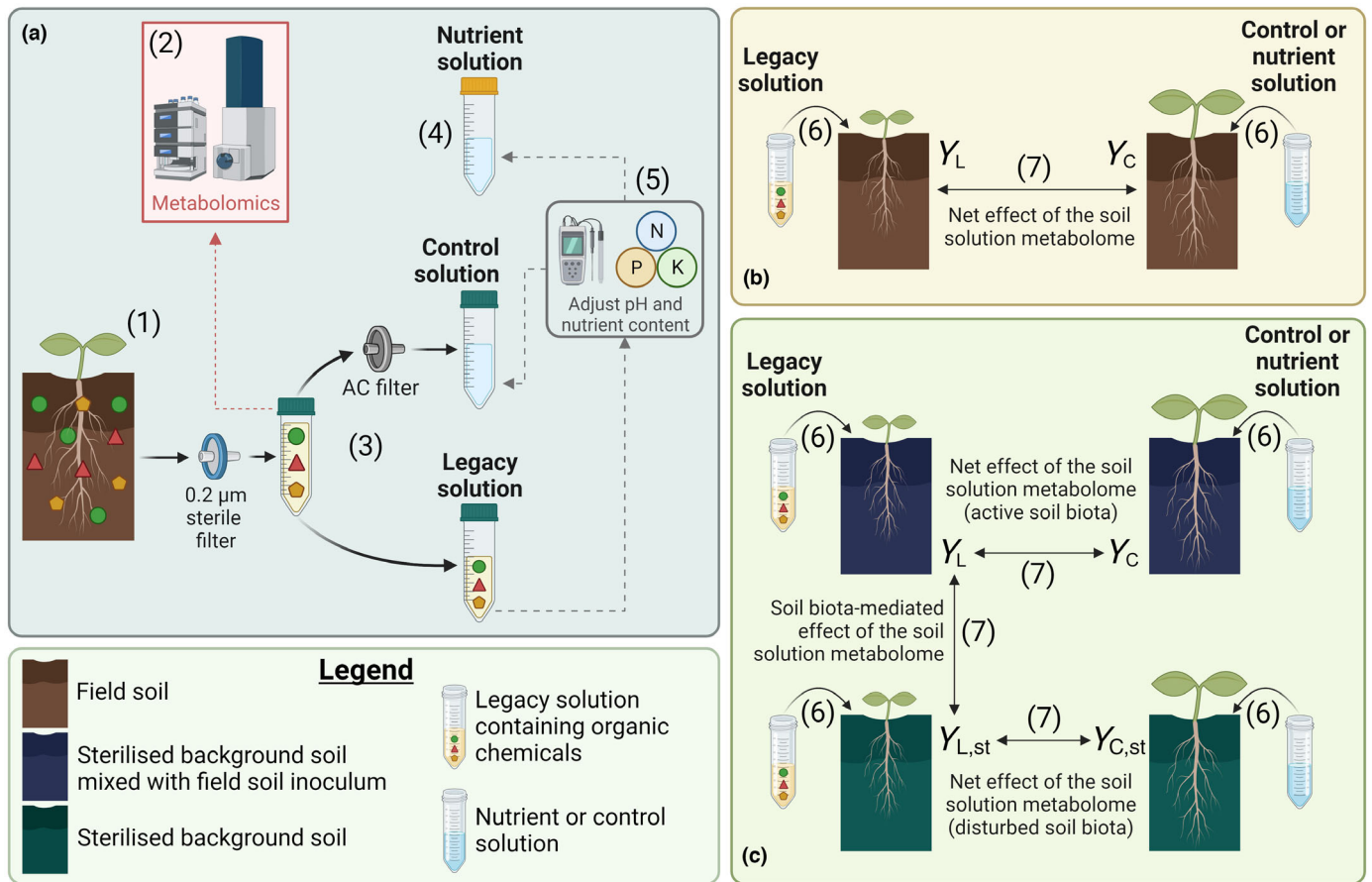
microbe interactions, such a trait-based framework was recently synthesised by Semchenko *et al.* (2022), and one key objective of this paper is to propose an extension of this framework to use functional traits related to root economics and seed dispersal for predicting the importance of chemical legacies in mediating plant–soil interactions. Specifically, we expect that traits describing plant strategies for soil resource acquisition and tissue construction can be used to predict how plants alter and respond to the soil metabolome.

## Predicting plant–soil interactions using functional traits

Similar to leaf chemistry (Moore *et al.*, 2014), root exudate chemistry is likely taxon-specific, and may be organised into chemical classes based on their chemical structure and biological functions (Bennett & Wallsgrove, 1994; Bais *et al.*, 2006), which can be related to plant functional traits (Williams *et al.*, 2022). Considering the latter, analyses of trait relationships have shown that interspecific variation in fine root construction strategies can be described by two major gradients constituting the root economics space: a root–fungi *collaboration* gradient and a tissue *conservation* gradient (McCormack & Iversen, 2019; Bergmann *et al.*, 2020; Carmona *et al.*, 2021; Weigelt *et al.*, 2021). Along the collaboration gradient, species display resource uptake strategies ranging from ‘do-it-yourself’ to ‘outsourcing’ (Bergmann *et al.*, 2020). Do-it-yourself species produce long but fine roots allowing efficient exploration of the soil environment. Outsourcing plant species instead build shorter but thicker roots that are better suited for hosting arbuscular mycorrhizal fungi and enable outsourcing resource uptake to the fungi (Ma *et al.*, 2018; Bergmann *et al.*, 2020). The conservation gradient represents the trade-off between tissue longevity and fast return on investment into tissue construction. Species on the fast side of the gradient construct roots with a high metabolic activity and a high nitrogen content but low longevity, while species on the slow side of the gradient build roots with lower metabolic activity but higher tissue density, which enhances root lifespan (Bergmann *et al.*, 2020). Whether the root conservation gradient and the leaf economics spectrum, ranging from acquisitive to conservative leaves (Wright *et al.*, 2004), are aligned with each other is still debated (Carmona *et al.*, 2021; Weigelt *et al.*, 2021, 2023; Bueno *et al.*, 2023).

Leaf and root traits have been used successfully to predict interspecific differences in soil microbial community composition (de Vries *et al.*, 2012; Semchenko *et al.*, 2018; Spitzer *et al.*, 2021), as well as litter decomposability and rhizodeposition and their effects on soil carbon and nitrogen cycling (Freschet *et al.*, 2012, 2013; Henneron *et al.*, 2020a,b; Williams *et al.*, 2022). With regard to PSF, the focus has been on developing functional trait-based frameworks to predict plant responses to soil microbial communities, including specialist and generalist pathogens, mutualists and decomposers (Baxendale *et al.*, 2014; Kardol *et al.*, 2015; Cortois *et al.*, 2016; De Long *et al.*, 2019; Heinen *et al.*, 2020a; Semchenko *et al.*, 2022; Spitzer *et al.*, 2022). Phylogenetic relatedness has also been proposed as a

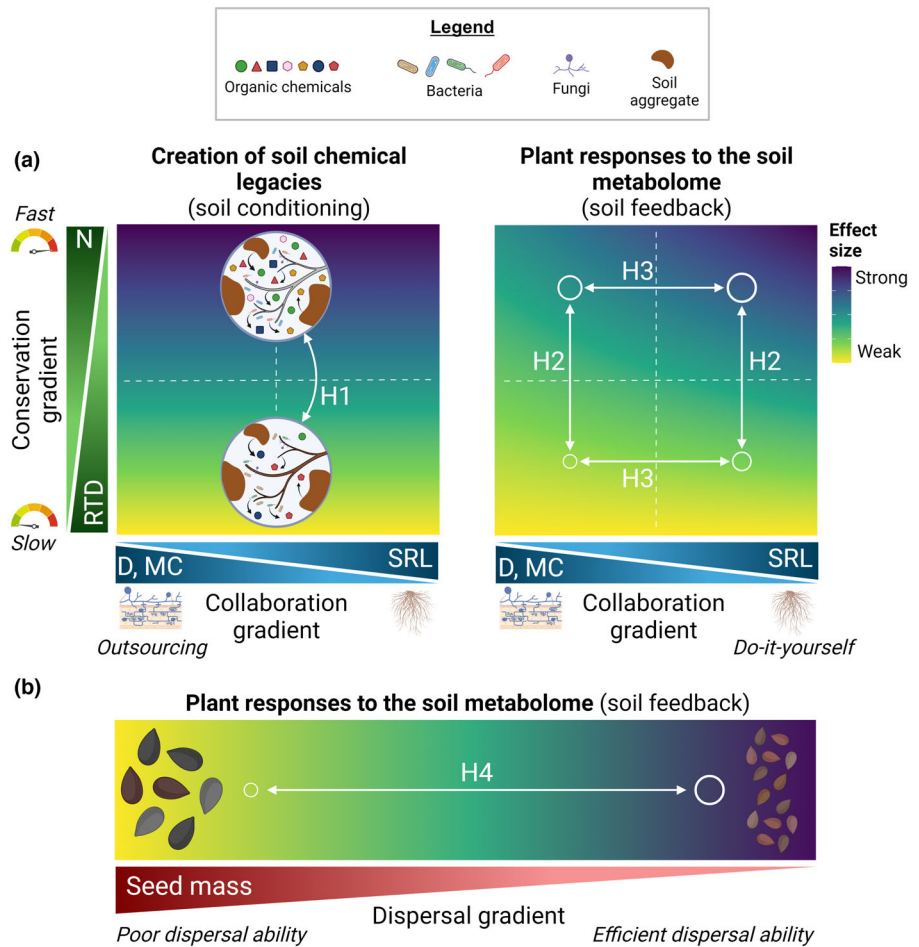




**Fig. 2** Experimental approach for the quantification of plant responses to the soil metabolome. This figure only illustrates how to estimate conspecific feedback effects due to water-soluble chemical compounds. Heterospecific feedback effects can be estimated using the same approach, except that the species used in the conditioning (a) and feedback (b, c) phases of the experiment would be different. Panel (a): (1) the first step is to collect soil solution samples and removing microorganisms using sterile syringe filters (0.2 μm) if needed. (2) Dissolved organic carbon (DOC) concentration could be measured as a proxy for chemical abundance, and differences in composition and chemical diversity between soil solution metabolomes can be characterised using a targeted or untargeted metabolomics approach (Uthe *et al.*, 2021). (3) After collection, the soil solution can be split into two fractions, and one fraction can be filtered using activated carbon to remove DOC and create a control solution with reduced DOC concentration; (4) a nutrient solution could also be used as a control solution. (5) The pH and nutrient concentrations can be adjusted in control and nutrient solutions so that they correspond as closely as possible to the values measured in the original soil solution. Panels (b, c) illustrate two complementary ways to quantify plant responses to the soil metabolome. (6) As shown in (b), the simplest way to quantify the net effect of the soil metabolome on a response variable of interest ( $Y$ ) is to apply each solution type to separate individuals of the focal species growing on field soil. (7) The net effect of the soil metabolome on  $Y$  can be estimated by calculating an absolute or relative effect size analogous to those used in plant–soil feedbacks (PSF) research, such as a log response ratio:  $\log_e(Y_L : Y_C)$ . The approach illustrated in (c) allows the separate quantification of the net and soil biota-mediated effects of the soil metabolome on  $Y$ . In this situation, each soil solution type described in (a) is applied to separate individuals of the focal species growing on sterilised soil or on sterilised soil in which the soil biota was reinoculated (6). Given that soil sterilisation is known to increase soil nutrient availability ('nutrient flush', Hendriks *et al.*, 2013), the use of sterilised background soil reinoculated with soil biota is preferable to the use of unsterilised field soil. If log response ratios are used as effect sizes, the net effect of the soil solution metabolome on each response variable of interest ( $Y$ ) can be calculated as  $\log_e(Y_L : Y_C)$ , while the soil biota-mediated effect would be calculated as  $\log_e(Y_L : Y_{L,st})$  (7). This figure was created with BioRender.com.

However, the relationship between root exudation rate and the root collaboration gradient is not clear because both positive and negative associations between relevant root traits and root exudation rates have been documented. For instance, de Vries *et al.* (2019) and Meier *et al.* (2020) found that plants with higher specific root length had higher exudation rates, whereas Williams *et al.* (2022) reported a positive relationship between root diameter and root exudation. Adding to the uncertainty, across 18 woody species no relationship between specific root length or root diameter and root exudation rates was found (Sun *et al.*, 2021).

Although these studies were conducted on different species and study systems, these contradictory findings can appear surprising considering that root chemical composition seems to be strongly linked to the root collaboration gradient (Xia *et al.*, 2021; Han *et al.*, 2022). For example, by analysing trait relationships between 34 temperate tree species, Xia *et al.* (2021) unravelled the existence of a trade-off between mycorrhizal colonisation and chemical protection. They found that species with a do-it-yourself strategy (fine roots with low mycorrhizal colonisation) had a greater concentration of structural and nonstructural chemical compounds



**Fig. 3** Trait-based framework linking the soil metabolome to plant–soil feedbacks (PSF). Panel (a) focuses on root economics traits, whereas (b) focuses on traits related to seed dispersal. The proposed framework relies on the following hypotheses, which are not mutually exclusive: (H1) species on the fast side of the root conservation gradient maintain a greater concentration of soil metabolites, but create less persistent chemical legacies than species on the slow side of the gradient; (H2) species on the fast side of the root conservation gradient are more likely to respond to the soil metabolome than species on the slow side of the gradient; (H3) do-it-yourself species respond to the soil metabolome more strongly than outsourcing species; and (H4) species with efficient dispersal ability respond more strongly to the soil metabolome than species with poor dispersal ability. This figure was created with [BioRender.com](https://www.biorender.com). D, average root diameter; MC, mycorrhizal colonisation; N, root N concentration; SRL, specific root length (i.e. root length per unit root mass); RTD, root tissue density (i.e. root mass per unit root volume).

involved in plant defence and mechanical resistance in their roots than outsourcing species. The activity of root phosphatases, a class of extracellular enzymes mobilising inorganic P from soil organic compounds, has also been shown to be related to the root collaboration gradient, as do-it-yourself species display greater phosphatase activity than outsourcing species (Han *et al.*, 2022; Yaffar *et al.*, 2022).

The composition of root exudates has been linked to root functional traits. Metabolically active roots with a high nitrogen content, such as those of legumes, exude more amino acids, organic acids, hydrocarbons and sugars than roots that are less metabolically active (Williams *et al.*, 2022). Interestingly, Williams *et al.* (2022) did not find a strong relationship between phylogeny and root exudate composition – comparing 17 perennial grassland species from three plant functional groups (grasses, forbs and legumes). This suggests that several metabolites are shared between species growing under similar environmental conditions, even among distantly related species, as they probably originate from the same metabolic pathways (e.g. primary metabolites; Weng *et al.*, 2012; Defosse *et al.*, 2021). It is therefore likely that specialised metabolites better explain interspecific differences in soil metabolome.

In addition to root exudation, litter is a major contributor to the soil metabolome and PSF (Veen *et al.*, 2019). Acquisitive

fast-growing plant species produce the greatest biomass (Wardle *et al.*, 2004), but litter decomposability is strongly related to organ-specific traits such as carbon, dry matter and lignin content, with roots decomposing slower than leaves (Freschet *et al.*, 2012, 2013). Therefore, tissues of species with a slow strategy are likely to decompose slower due to their higher dry matter content and tissue density, as well as greater investment in chemical defences (Endara & Coley, 2011). By contrast, species with high nitrogen content will decompose more quickly (Wardle *et al.*, 2004). It is therefore likely that the litter of species on the slow side of the conservation gradient will affect the soil metabolome more slowly, but over a longer time (i.e. greater persistence) than species on the fast side of the gradient. While root conservation traits clearly affect the rate of litter decomposition, the feedback effects of litter on plant growth are less predictable and the underlying mechanisms poorly understood (Zhang *et al.*, 2016; Gabinet *et al.*, 2018; Bueno de Mesquita *et al.*, 2019; Veen *et al.*, 2019; De Long *et al.*, 2023a,b).

The importance of litter production and decomposition to the soil metabolome is probably also dependent on the position of a species along the root collaboration gradient. However, the extent to which the litter of do-it-yourself and outsourcing species contribute to changes in the soil solution metabolome remains poorly understood. In comparison with roots of outsourcing

species, do-it-yourself roots have a higher concentration of chemicals involved in tissue construction and protection than outsourcing species (Spitzer *et al.*, 2021, 2022; Xia *et al.*, 2021). The greater mechanical resistance of do-it-yourself roots (Mao *et al.*, 2023), combined with their higher concentration in specialised protective compounds, will likely reduce the decomposability of their litter, which may retard the development of soil chemical legacies. However, the greater concentration of chemical compounds in do-it-yourself roots may lead to stronger and more persistent chemical legacies.

Considering that species on the fast side of the root conservation gradient are likely to exude more C into the soil and produce more higher-quality litter, we predict that these species will affect the soil metabolome more strongly than species on the slow side of the gradient, in the sense that the abundance of organic chemical compounds will be greater in soils conditioned by species with a fast strategy. Given the abundance-dependence of chemical diversity (Wetzel & Whitehead, 2020), this greater abundance of soil organic chemicals should be paralleled by a greater number of detectable metabolites in soils conditioned by species on the fast side of the root conservation gradient. Whether or not a greater abundance of metabolites in soils conditioned by fast-growing species would be associated with a greater soil metabolite richness per unit mass of dissolved organic carbon (i.e. standardised metabolite richness) is not clear. Alternatively, standardised metabolite richness may be greater in soils conditioning by species located on the slow side of the conservation gradient, because these species invest proportionally less in growth and could invest more resources in producing a more diverse range of specialised metabolites (Fine *et al.*, 2004; Panda *et al.*, 2021). Although species with a slow and do-it-yourself strategy may generate soil chemical legacies more slowly, their effect may be more persistent due to slow decomposition, as well as antimicrobial properties and greater chemical richness of their rhizodeposits and litter.

Considering that allelopathic effects are dose-dependent, with greater chemical concentrations generally triggering stronger allelopathic effects (Zhang *et al.*, 2021), it is likely that PSF effects mediated by the soil metabolome are stronger when soil organic chemical compounds are more abundant. A greater concentration of soil metabolites also increases the probability that a chemical compound exhibits allelopathic properties that would positively or negatively affect the growth, development or reproduction of a species entering the community. If species located on the fast side of the root conservation gradient indeed create the strongest chemical legacies with a greater abundance of soil chemical compounds, it follows that plants should respond the strongest to the soil metabolome produced by species on the fast side of the conservation gradient.

**Hypothesis 2:** Species on the fast side of the root conservation gradient are more likely to respond to the soil metabolome than species on the slow side of the gradient (Fig. 3 – H2).

To date, we have insufficient empirical data to generalise the types of species which should be more responsive to the soil metabolome. However, if responses to soil legacies are a special case

of phenotypic plasticity or root foraging behaviour, some predictions can be made based on the findings from these related fields of research. Species with acquisitive trait values are often more plastic than resource-conservative species (Grime & Mackey, 2002; de Kroon & Mommer, 2006). Indeed, phenotypic plasticity has been found to be positively correlated with specific leaf area (Stotz *et al.*, 2022), with high values of plasticity for species located on the fast side of the leaf economics spectrum (Wright *et al.*, 2004). The precision of root foraging for soil nutrients is also variable among species (Kembel & Cahill, 2005; Stiblíková *et al.*, 2023), with dicotyledonous plants tending to forage more precisely than monocotyledons (Grime & Mackey, 2002; Kembel & Cahill, 2005). Species with high root foraging precision are generally short-lived and have high growth rates, N-rich tissues and respiration rates (Kembel *et al.*, 2008). This suggests that species on the fast side of the root conservation gradient may forage more precisely for nutrients than slow species. However, a recent meta-analysis across 123 herbaceous species found that root N content and root tissue density, which are traits associated with the fast–slow conservation gradient (see Fig. 3), were poor predictors of interspecific differences in root foraging precision (Stiblíková *et al.*, 2023).

Given our knowledge of factors affecting plant phenotypic plasticity and root foraging, we can predict that species located on the fast side of the root conservation gradient should express stronger plastic responses when exposed to the soil metabolome of conspecifics or heterospecifics. Fast-growing species should be more responsive to the soil metabolome because such species can effectively utilise chemical cues to locate and identify competitors and adjust their foraging with metabolically active but short-lived roots. On the other hand, the high cost of producing long-lived roots with high tissue density may prohibit slow-growing species from responding dynamically to changes in soil metabolome. In an experiment studying how two grassland species with contrasting trait values respond to soil chemical legacies, Delory *et al.* (2021) found that the forb *Dianthus deltooides* responded to the soil solution metabolome from forb and grass communities by decreasing soil foraging, while the grass *Festuca rubra* showed no significant response. Along the root conservation gradient, *D. deltooides* is closer to the fast side than *F. rubra* because of its greater root N concentration and lower root tissue density (Delory *et al.*, 2021). Despite this being consistent with our hypothesis, we need far more replication. There is therefore a need for experiments to measure plant responses to the soil metabolome using a wider range of species and in different environments.

In addition to plant functional traits, species and genotype identity also play an important role in determining if and how plants react to the soil metabolome. If an individual plant is exposed to the soil metabolome of conspecifics, negative PSF effects can be expected because of the inhibitory effects that chemical compounds from the home litter can have on the growth of conspecifics (Mazzoleni *et al.*, 2015). Nonspecific inhibitory effects of plant litter seem to be mainly due to short-lived phytotoxic compounds (e.g. phenolic and aromatic compounds of low molecular weight) that are rapidly released following the start of litter decomposition, while longer-term autotoxicity seems to be mainly due to self-DNA

fragments (Fig. 1), which are more slowly degraded, accumulate during litter decomposition and cause severe plasmolysis in epidermal and cortical root cells (Mazzoleni *et al.*, 2015; Bonanomi *et al.*, 2022). Plants integrate soil chemical cues to optimise the timing of germination (Renne *et al.*, 2014) and distinguish between self and nonself organs (self/non-self recognition), as well as between closely related and distantly related individuals (kin recognition; Mahall & Callaway, 1991; Biedrzycki *et al.*, 2010; Fang *et al.*, 2013; Wang *et al.*, 2021), which will likely affect the way they respond to the soil metabolome of conspecifics (including differential effects of closely vs distantly related genotypes) or heterospecifics (Cahill *et al.*, 2010; Cahill & McNickle, 2011; Semchenko *et al.*, 2014; Callaway & Li, 2020).

**Hypothesis 3:** Do-it-yourself species respond to the soil metabolome more strongly than outsourcing species (Fig. 3–H3).

This hypothesis is based on the assumption that do-it-yourself plants rely more on the physiology and activity of their roots than do mycorrhizal outsourcing plants (Cheng *et al.*, 2016; Ma *et al.*, 2018; McCormack & Iversen, 2019; Bergmann *et al.*, 2020). If a species must rely solely on its own roots for resource uptake (do-it-yourself strategy), then it is conceivable that this species will rely more on soil chemical compounds to obtain information about the surrounding biotic environment, such as the presence or absence of neighbours, in order to optimally position its roots. Root foraging of plants with a do-it-yourself strategy might therefore be more dependent on soil chemical cues than root foraging in outsourcing plants. Mycorrhizal status and other traits associated with the collaboration gradient were found to be poor predictors of root foraging precision across a large number of herbaceous plants (Stiblíková *et al.*, 2023). However, root traits and foraging precision were not measured in the same experiment, and simultaneous measurements and manipulation of mycorrhizal fungi may be needed to uncover the role of mycorrhizal symbiosis in root foraging precision. Also, to date, most studies of plant traits associated with efficient root foraging have focused on responses to the spatial distribution of nutrients, with little consideration for other forms of chemical legacies involving organic compounds. Further research and experiments are therefore needed to test the hypothesis that do-it-yourself species respond more strongly to the soil metabolome than outsourcing species.

**Hypothesis 4:** Species with efficient dispersal ability respond more strongly to the soil metabolome than species with poor dispersal ability (Fig. 3–H4).

Small-seeded species are more likely to disperse away from their parents than large-seeded species, so they can escape pathogens that accumulate near mother plants and hence experience weaker selective pressure to invest into pathogen defence. It was therefore proposed that species with small seeds and efficient dispersal would suffer from more negative PSF than species with large seeds and poor dispersal (Semchenko *et al.*, 2022). In a meta-analysis, Xi *et al.* (2021) found support for this hypothesis by showing that tall species with large seeds were associated with positive conspecific PSF, whereas short species with small seeds had more negative PSF.

Similar reasoning might predict how dispersal ability could affect plant responses to the soil metabolome. Since soil chemical compounds including root exudates and litter decomposition products can delay the germination of sympatric species and affect root growth across a range of plant species and functional types (Renne *et al.*, 2014; Mazzoleni *et al.*, 2015; Bonanomi *et al.*, 2017), species with large seeds and poor dispersal ability should be under greater selective pressure to react less strongly to the soil metabolome originating from their parents' litter and rhizodeposits. In addition, small-seeded species have lower energy stores in their seeds and hence are more affected by external resources at early seedling establishment, making them more likely to use belowground chemical signals to assess neighbour presence and the strength of the competitive landscape around them. Evidence for this biochemical recognition hypothesis has been found experimentally, and small-seeded species have indeed shown the strongest responses (Renne *et al.*, 2014). In another experiment manipulating litter type and decomposition stage, Bonanomi *et al.* (2017) showed that species with small seeds (and better dispersal ability) are more strongly inhibited by chemical compounds released into the soil by fresh and decomposing plant litter than species with large seeds. They observed that undecomposed plant litter inhibited root growth the most in annual species with small seeds, and this effect was mainly explained by the release of simple carbohydrates and condensed tannins that are rapidly degraded during decomposition (Bonanomi *et al.*, 2021). Altogether, these results suggest that seed size (as a proxy for dispersal ability) could be an important predictor of plant responses to the soil metabolome. Given that seed mass has been shown to be closely correlated to traits associated with the root collaboration gradient (Bergmann *et al.*, 2017), we expect species with light seeds (H4) and fine roots (H3) to be the most responsive to the soil metabolome.

## Conclusions and future directions

Plant–soil feedbacks are caused by complex interactions among resource uptake, litter decomposition, root exudation and changes in the structure and functioning of soil communities. Much progress has been made in understanding soil microbial legacies and how they affect plant population and community dynamics via PSF. In particular, several studies have linked plant functional traits to soil microbial legacies and their feedback effects on plant growth. However, despite the important role of soil organic metabolites in mediating belowground biotic interactions, the roles played by the soil metabolome in mediating PSF are still understudied.

The next critical step is to improve our understanding of how different species affect the soil metabolome via root exudation and litter decomposition, and how variation in chemical legacies ramifies to soil functions and affects the next generation of plants. To do this, research efforts should focus on determining the persistence and functions of root-emitted chemicals in the soil (Wen *et al.*, 2022), particularly species-specific specialised metabolites, and relate gradients in chemical legacies to the already known axes of variation in plant form and function.

To examine whether and how plants are affected by the soil metabolome, and whether certain plant traits may be more associated with negative, neutral or positive responses to the soil metabolome, we need experiments designed to measure how species with contrasting trait values respond to conspecific and heterospecific chemical legacies (Fig. 2). Additional manipulation of the soil biota may provide important insights about the direct and indirect effects of the soil metabolome in mediating plant–soil interactions. These PSF experiments would be ideal to test the trait-based framework described in this paper, as well as to test the extent to which greater phylogenetic or functional distance between a focal species and a species that produces the soil chemical legacy lead to stronger PSF effects (Semchenko *et al.*, 2022; Rutten & Allan, 2023).

In sum, the soil metabolome is an important component of soil legacies, and more work is needed to determine its importance as a driver of PSF. The framework and hypotheses outlined in this paper, which are not mutually exclusive, call for a new generation of PSF experiments to quantify the extent to which individual plant responses to soil microbial and chemical legacies matter for species coexistence and community dynamics across environmental gradients and biogeographic regions.

## Acknowledgements

BMD is supported by a grant from the German Research Foundation (project no. 470604360). RMC thanks the NSF EPSCoR program, OIA-1757351, for support. MS is supported by the European Union (ERC, PlantSoilAdapt, 101044424). The authors thank Inés M. Alonso-Crespo for making the plant illustrations used in Fig. 1. The authors also thank Dr Robin Heinen and other anonymous reviewers for their helpful comments and suggestions on earlier versions of our manuscript. Open Access funding enabled and organized by Projekt DEAL.

## Competing interests

None declared.

## Author contributions

BMD led the writing of the manuscript, with contributions from RMC and MS. All authors discussed ideas and contributed to the writing and editing of the manuscript.

## ORCID

Ragan M. Callaway  <https://orcid.org/0000-0001-7342-4312>  
Benjamin M. Delory  <https://orcid.org/0000-0002-1190-8060>  
Marina Semchenko  <https://orcid.org/0000-0001-6196-3562>

**Benjamin M. Delory<sup>1,2,\*</sup>** , **Ragan M. Callaway<sup>3</sup>**  and **Marina Semchenko<sup>4</sup>** 

<sup>1</sup>Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, 21335, Germany;

<sup>2</sup>Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, 3584 CB, the Netherlands;

<sup>3</sup>Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA;

<sup>4</sup>Institute of Ecology and Earth Sciences, University of Tartu, Liivi 2, 50409, Tartu, Estonia  
(\*Author for correspondence: email [b.m.m.delory@uu.nl](mailto:b.m.m.delory@uu.nl))

## References

- Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology* 57: 233–266.
- Baxendale C, Orwin KH, Poly F, Pommier T, Bardgett RD. 2014. Are plant–soil feedback responses explained by plant traits? *New Phytologist* 204: 408–423.
- Bennett JA, Klironomos J. 2019. Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. *New Phytologist* 222: 91–96.
- Bennett RN, Wallsgrove RM. 1994. Secondary metabolites in plant defence mechanisms. *New Phytologist* 127: 617–633.
- Bergmann J, Ryo M, Prati D, Hempel S, Rillig MC. 2017. Root traits are more than analogues of leaf traits: the case for diaspore mass. *New Phytologist* 216: 1130–1139.
- Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM *et al.* 2020. The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* 6: eaba3756.
- Bever JD. 1994. Feedback between plants and their soil communities in an Old Field community. *Ecology* 75: 1965–1977.
- Biedrzycki ML, Jilany TA, Dudley SA, Bais HP. 2010. Root exudates mediate kin recognition in plants. *Communicative & Integrative Biology* 3: 28–35.
- Bilas RD, Bretman A, Bennett T. 2021. Friends, neighbours and enemies: an overview of the communal and social biology of plants. *Plant, Cell & Environment* 44: 997–1013.
- Bonanomi G, Cesarano G, Lombardi N, Motti R, Scala F, Mazzoleni S, Incerti G. 2017. Litter chemistry explains contrasting feeding preferences of bacteria, fungi, and higher plants. *Scientific Reports* 7: 1–13.
- Bonanomi G, Zotti M, Idbella M, Mazzoleni S, Abd-ElGawad AM. 2021. Microbiota modulation of allelopathy depends on litter chemistry: mitigation or exacerbation? *The Science of the Total Environment* 776: 145942.
- Bonanomi G, Zotti M, Idbella M, Termolino P, De Micco V, Mazzoleni S. 2022. Field evidence for litter and self-DNA inhibitory effects on *Alnus glutinosa* roots. *New Phytologist* 236: 399–412.
- Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R, Carmona CP. 2023. Reply to: the importance of trait selection in ecology. *Nature* 618: E31–E34.
- Bueno de Mesquita CP, Schmidt SK, Suding KN. 2019. Litter-driven feedbacks influence plant colonization of a high elevation early successional ecosystem. *Plant and Soil* 444: 71–85.
- Bukowski AR, Schittko C, Petermann JS. 2018. The strength of negative plant–soil feedback increases from the intraspecific to the interspecific and the functional group level. *Ecology and Evolution* 8: 2280–2289.
- Cahill JF, McNickle GG. 2011. The behavioral ecology of nutrient foraging by plants. *Annual Review of Ecology, Evolution, and Systematics* 42: 289–311.
- Cahill JF, McNickle GG, Haag JJ, Lamb EG, Nyanumba SM, St Clair CC. 2010. Plants integrate information about nutrients and neighbors. *Science* 328: 1657.
- Callaway RM, Li L. 2020. Decisions, decisions, decisions: plant roots detect and respond to complex environmental cues. *New Phytologist* 226: 11–12.
- Callaway RM, Ridenour WM. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436–443.
- Callaway RM, Thelen GC, Rodriguez A, Holben WE. 2004. Soil biota and exotic plant invasion. *Nature* 427: 731–733.
- Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R. 2021. Fine-root traits in the global spectrum of plant form and function. *Nature* 597: 683–687.

- Cheng L, Chen W, Adams TS, Wei X, Li L, McCormack ML, DeForest JL, Koide RT, Eissenstat DM. 2016. Mycorrhizal fungi and roots are complementary in foraging within nutrient patches. *Ecology* 97: 2815–2823.
- Cortois R, Schröder-Georgi T, Weigelt A, van der Putten WH, De Deyn GB. 2016. Plant–soil feedbacks: role of plant functional group and plant traits. *The Journal of Ecology* 104: 1608–1617.
- Crawford KM, Bauer JT, Comita LS, Eppinga MB, Johnson DJ, Mangan SA, Queenborough SA, Strand AE, Suding KN, Umbanhowar J *et al.* 2019. When and where plant–soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters* 22: 1274–1284.
- De Long JR, Fry EL, Veen GF, Kardol P. 2019. Why are plant–soil feedbacks so unpredictable, and what to do about it? *Functional Ecology* 33: 118–128.
- De Long JR, Heinen R, Hannula SE, Jongen R, Steinauer K, Bezemer TM. 2023a. Plant–litter–soil feedbacks in common grass species are slightly negative and only marginally modified by litter exposed to insect herbivory. *Plant and Soil* 485: 227–244.
- De Long JR, Heinen R, Heinze J, Morriën E, Png GK, Sapsford SJ, Teste FP, Fry EL. 2023b. Plant–soil feedback: incorporating untested influential drivers and reconciling terminology. *Plant and Soil* 485: 7–43.
- Defossez E, Pitteloud C, Descombes P, Glauser G, Allard P-M, Walker TWN, Fernandez-Conradi P, Wolfender J-L, Pellissier L, Rasmann S. 2021. Spatial and evolutionary predictability of phytochemical diversity. *Proceedings of the National Academy of Sciences, USA* 118: e2013344118.
- Delory BM, Delaplace P, Fauconnier M-L, du Jardin P. 2016. Root-emitted volatile organic compounds: can they mediate belowground plant–plant interactions? *Plant and Soil* 402: 1–26.
- Delory BM, Schempp H, Spachmann SM, Störzer L, van Dam NM, Temperton VM, Weinhold A. 2021. Soil chemical legacies trigger species-specific and context-dependent root responses in later arriving plants. *Plant, Cell & Environment* 44: 1215–1230.
- Ehlers BK, Berg MP, Staudt M, Holmstrup M, Glasius M, Ellers J, Tomiolo S, Madsen RB, Slotsbo S, Penuelas J. 2020. Plant secondary compounds in soil and their role in belowground species interactions. *Trends in Ecology & Evolution* 35: 716–730.
- Endara M-J, Coley PD. 2011. The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology* 25: 389–398.
- Engelkes T, Morriën E, Verhoeven KJF, Bezemer TM, Biere A, Harvey JA, McIntyre LM, Tamis WLM, van der Putten WH. 2008. Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* 456: 946–948.
- Fang S, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN. 2013. Genotypic recognition and spatial responses by rice roots. *Proceedings of the National Academy of Sciences, USA* 110: 2670–2675.
- Fine PVA, Mesones I, Coley PD. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305: 663–665.
- Fitzpatrick CR, Gehant L, Kotanen PM, Johnson MTJ. 2017. Phylogenetic relatedness, phenotypic similarity and plant–soil feedbacks. *The Journal of Ecology* 105: 786–800.
- Freschet GT, Aerts R, Cornelissen JHC. 2012. A plant economics spectrum of litter decomposability. *Functional Ecology* 26: 56–65.
- Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao J, Cornelissen JHC. 2013. Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. *The Journal of Ecology* 101: 943–952.
- Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46: 1–23.
- Gavinet J, Prévosto B, Bousquet-Melou A, Gros R, Quer E, Baldy V, Fernandez C. 2018. Do litter-mediated plant–soil feedbacks influence Mediterranean oak regeneration? A two-year pot experiment. *Plant and Soil* 430: 59–71.
- Gfeller V, Thönen L, Erb M. 2023a. Root-exuded secondary metabolites can alleviate negative plant–soil feedbacks. *bioRxiv*. doi: 10.1101/2023.04.09.536155.
- Gfeller V, Waelchli J, Pfister S, Deslandes-Hérolf G, Mascher F, Glauser G, Aeby Y, Mestrot A, Robert CAM, Schlaeppli K *et al.* 2023b. Plant secondary metabolite-dependent plant–soil feedbacks can improve crop yield in the field. *eLife* 12: e84988.
- Grime JP, Mackey JML. 2002. The role of plasticity in resource capture by plants. *Evolutionary Ecology* 16: 299–307.
- Grman E, Suding KN. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology* 18: 664–670.
- Gundale M, Kardol P. 2021. Multi-dimensionality as a path forward in plant–soil feedback research. *The Journal of Ecology* 109: 3446–3465.
- Guyonnet JP, Cantarel AAM, Simon L, Haichar FEZ. 2018. Root exudation rate as functional trait involved in plant nutrient-use strategy classification. *Ecology and Evolution* 8: 8573–8581.
- Haichar FEZ, Santaella C, Heulin T, Achouak W. 2014. Root exudates mediated interactions belowground. *Soil Biology & Biochemistry* 77: 69–80.
- Han M, Chen Y, Li R, Yu M, Fu L, Li S, Su J, Zhu B. 2022. Root phosphatase activity aligns with the collaboration gradient of the root economics space. *New Phytologist* 234: 837–849.
- Han M, Chen Y, Sun L, Yu M, Li R, Li S, Su J, Zhu B. 2023. Linking rhizosphere soil microbial activity and plant resource acquisition strategy. *The Journal of Ecology* 111: 875–888.
- Han M, Zhu B. 2021. Linking root respiration to chemistry and morphology across species. *Global Change Biology* 27: 190–201.
- Hannula SE, Heinen R, Huberty M, Steinauer K, De Long JR, Jongen R, Bezemer TM. 2021. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nature Communications* 12: 5686.
- Heinen R, Biere A, Bezemer TM. 2020a. Plant traits shape soil legacy effects on individual plant–insect interactions. *Oikos* 129: 261–273.
- Heinen R, Hannula SE, De Long JR, Huberty M, Jongen R, Kielak A, Steinauer K, Zhu F, Bezemer TM. 2020b. Plant community composition steers grassland vegetation via soil legacy effects. *Ecology Letters* 23: 973–982.
- Heinen R, van der Sluijs M, Biere A, Harvey JA, Bezemer TM. 2018. Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects. *The Journal of Ecology* 106: 1217–1229.
- Hendriks M, Mommer L, de Caluwe H, Smit-Tiekstra AE, van der Putten WH, de Kroon H. 2013. Independent variations of plant and soil mixtures reveal soil feedback effects on plant community overyielding. *The Journal of Ecology* 101: 287–297.
- Henneron L, Cros C, Picon-Cochard C, Rahimian V, Fontaine S. 2020a. Plant economic strategies of grassland species control soil carbon dynamics through rhizodeposition. *The Journal of Ecology* 108: 528–545.
- Henneron L, Kardol P, Wardle DA, Cros C, Fontaine S. 2020b. Rhizosphere control of soil nitrogen cycling: a key component of plant economic strategies. *New Phytologist* 228: 1269–1282.
- Hierro JL, Callaway RM. 2021. The ecological importance of allelopathy. *Annual Review of Ecology, Evolution, and Systematics* 52: 25–45.
- Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, van der Heijden MGA *et al.* 2018. Root exudate metabolites drive plant–soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nature Communications* 9: 2738.
- Inderjit, Weiner J. 2001. Plant allelochemical interference or soil chemical ecology? *Perspectives in Plant Ecology, Evolution and Systematics* 4: 3–12.
- Kardol P, Cornips NJ, van Kempen MML, Bakx-Schotman JMT, van der Putten WH. 2007. Microbe-mediated plant–soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs* 77: 147–162.
- Kardol P, Veen GFC, Teste FP, Perring MP. 2015. Peeking into the black box: a trait-based approach to predicting plant–soil feedback. *New Phytologist* 206: 1–4.
- Kembel SW, Cahill JF. 2005. Plant phenotypic plasticity belowground: a phylogenetic perspective on root foraging trade-offs. *The American Naturalist* 166: 216–230.
- Kembel SW, De Kroon H, Cahill JF Jr, Mommer L. 2008. Improving the scale and precision of hypotheses to explain root foraging ability. *Annals of Botany* 101: 1295–1301.
- Klironomos JN. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67–70.
- Kong C-H, Zhang S-Z, Li Y-H, Xia Z-C, Yang X-F, Meiners SJ, Wang P. 2018. Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. *Nature Communications* 9: 3867.

- de Kroon H, Mommer L. 2006. Root foraging theory put to the test. *Trends in Ecology & Evolution* 21: 113–116.
- Kulmatiski A, Beard KH, Norton JM, Heavilin JE, Forero LE, Grenzer J. 2017. Live long and prosper: plant–soil feedback, lifespan, and landscape abundance covary. *Ecology* 98: 3063–3073.
- Kulmatiski A, Beard KH, Stevens JR, Cobbold SM. 2008. Plant–soil feedbacks: a meta-analytical review. *Ecology Letters* 11: 980–992.
- Lekberg Y, Bever JD, Bunn RA, Callaway RM, Hart MM, Kivlin SN, Klironomos J, Larkin BG, Maron JL, Reinhart KO *et al.* 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. *Ecology Letters* 21: 1268–1281.
- Lemmermeyer S, Lörcher L, van Kleunen M, Dawson W. 2015. Testing the plant growth–defense hypothesis belowground: do faster-growing herbaceous plant species suffer more negative effects from soil biota than slower-growing ones? *The American Naturalist* 186: 264–271.
- Li L, Li S-M, Sun J-H, Zhou L-L, Bao X-G, Zhang H-G, Zhang F-S. 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences, USA* 104: 11192–11196.
- Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* 555: 94–97.
- Mahall BE, Callaway RM. 1991. Root communication among desert shrubs. *Proceedings of the National Academy of Sciences, USA* 88: 874–876.
- Majumdar S, Kaur H, Rinella MJ, Kundu A, Vadassery J, Erbilgin N, Callaway RM, Cadotte MW, Inderjit. 2023. Synergistic effects of canopy chemistry and autogenic soil biota on a global invader. *The Journal of Ecology* 111: 1497–1513.
- Mao Z, Roumet C, Rossi LMW, Merino-Martín L, Nespoulous J, Taugourdeau O, Boukicim H, Fournier S, Del Rey-Granado M, Ramel M *et al.* 2023. Intra- and inter-specific variation in root mechanical traits for twelve herbaceous plants and their link with the root economics space. *Oikos* 2023: e09032.
- Maron JL, Klironomos J, Waller L, Callaway RM. 2014. Invasive plants escape from suppressive soil biota at regional scales. *The Journal of Ecology* 102: 19–27.
- Maron JL, Laney Smith A, Ortega YK, Pearson DE, Callaway RM. 2016. Negative plant–soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology* 97: 2055–2063.
- Mazzoleni S, Bonanomi G, Incerti G, Chiusano ML, Termolino P, Mingo A, Senatore M, Giannino F, Carteni F, Rietkerk M *et al.* 2015. Inhibitory and toxic effects of extracellular self-DNA in litter: a mechanism for negative plant–soil feedbacks? *New Phytologist* 205: 1195–1210.
- McCormack ML, Iversen CM. 2019. Physical and functional constraints on viable belowground acquisition strategies. *Frontiers in Plant Science* 10: 1215.
- Mehrabi Z, Tuck SL. 2015. Relatedness is a poor predictor of negative plant–soil feedbacks. *New Phytologist* 205: 1071–1075.
- Meier IC, Tückmantel T, Heitkötter J, Müller K, Preusser S, Wrobel TJ, Kändler E, Marschner B, Leuschner C. 2020. Root exudation of mature beech forests across a nutrient availability gradient: the role of root morphology and fungal activity. *New Phytologist* 226: 583–594.
- Metlen KL, Aschehoug ET, Callaway RM. 2009. Plant behavioural ecology: dynamic plasticity in secondary metabolites. *Plant, Cell & Environment* 32: 641–653.
- Mommer L, Cotton TEA, Raaijmakers JM, Termorshuizen AJ, van Ruijven J, Hendriks M, van Rijssel SQ, van de Mortel JE, van der Paauw JW, Schijlen EGWM *et al.* 2018. Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. *New Phytologist* 218: 542–553.
- Mommer L, Kirkegaard J, van Ruijven J. 2016. Root–root interactions: towards a rhizosphere framework. *Trends in Plant Science* 21: 209–217.
- Moore BD, Andrew RL, Külheim C, Foley WJ. 2014. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. *New Phytologist* 201: 733–750.
- Müller C, Junker RR. 2022. Chemical phenotype as important and dynamic niche dimension of plants. *New Phytologist* 234: 1168–1174.
- Nannipieri P, Hannula SE, Pietramellara G, Schloter M, Sizmur T, Pathan SI. 2023. Legacy effects of rhizodeposits on soil microbiomes: a perspective. *Soil Biology & Biochemistry* 184: 109107.
- Nettan S, Thetloff M, Lepik A, Semchenko M, Zobel K. 2019. Manipulation of vegetation with activated carbon reveals the role of root exudates in shaping native grassland communities. *Journal of Vegetation Science* 30: 1056–1067.
- Ninkovic V, Markovic D, Rensing M. 2021. Plant volatiles as cues and signals in plant communication. *Plant, Cell & Environment* 44: 1030–1043.
- Oburger E, Jones DL. 2018. Sampling root exudates – mission impossible? *Rhizosphere* 6: 116–133.
- Panda S, Kazachkova Y, Aharoni A. 2021. Catch-22 in specialized metabolism: balancing defense and growth. *Journal of Experimental Botany* 72: 6027–6041.
- Pernilla Brinkman E, Van der Putten WH, Bakker E-J, Verhoeven KJF. 2010. Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. *The Journal of Ecology* 98: 1063–1073.
- Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH. 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology* 11: 789–799.
- Pineda A, Kaplan I, Hannula SE, Ghanem W, Bezemer TM. 2020. Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. *New Phytologist* 226: 595–608.
- van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA *et al.* 2013. Plant–soil feedbacks: the past, the present and future challenges. *The Journal of Ecology* 101: 265–276.
- van der Putten WH, Bradford MA, Pernilla Brinkman E, van de Voorde TFJ, Veen GF. 2016. Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology* 30: 1109–1121.
- Reinhart KO, Callaway RM. 2006. Soil biota and invasive plants. *New Phytologist* 170: 445–457.
- Renne IJ, Sinn BT, Shook GW, Sedlacko DM, Dull JR, Villarreal D, Hierro JL. 2014. Eavesdropping in plants: delayed germination via biochemical recognition. *The Journal of Ecology* 102: 86–94.
- Rutten G, Allan E. 2023. Using root economics traits to predict biotic plant soil feedbacks. *Plant and Soil* 485: 71–89.
- Sasse J, Martinoia E, Northen T. 2018. Feed your friends: do plant exudates shape the root microbiome? *Trends in Plant Science* 23: 25–41.
- Semchenko M, Barry KE, de Vries FT, Mommer L, Moora M, Maciá-Vicente JG. 2022. Deciphering the role of specialist and generalist plant–microbial interactions as drivers of plant–soil feedback. *New Phytologist* 234: 1929–1944.
- Semchenko M, Leff JW, Lozano YM, Saar S, Davison J, Wilkinson A, Jackson BG, Pritchard WJ, De Long JR, Oakley S *et al.* 2018. Fungal diversity regulates plant–soil feedbacks in temperate grassland. *Science Advances* 4: eaau4578.
- Semchenko M, Nettan S, Sepp A, Zhang Q, Abakumova M, Davison J, Kalamees R, Lepik A, Püssa K, Saar S *et al.* 2019. Soil biota and chemical interactions promote co-existence in co-evolved grassland communities. *The Journal of Ecology* 107: 2611–2622.
- Semchenko M, Saar S, Lepik A. 2014. Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytologist* 204: 631–637.
- Spitzer CM, Lindahl B, Wardle DA, Sundqvist MK, Gundale MJ, Fanin N, Kardol P. 2021. Root trait–microbial relationships across tundra plant species. *New Phytologist* 229: 1508–1520.
- Spitzer CM, Wardle DA, Lindahl BD, Sundqvist MK, Gundale MJ, Fanin N, Kardol P. 2022. Root traits and soil micro-organisms as drivers of plant–soil feedbacks within the sub-arctic tundra meadow. *The Journal of Ecology* 110: 466–478.
- Steinauer K, Thakur MP, Emilia Hannula S, Weinhold A, Uthe H, van Dam NM, Martijn BT. 2023. Root exudates and rhizosphere microbiomes jointly determine temporal shifts in plant–soil feedbacks. *Plant, Cell & Environment* 46: 1885–1899.
- Stiblíková P, Klimeš A, Cahill JF, Koubek T, Weiser M. 2023. Interspecific differences in root foraging precision cannot be directly inferred from species' mycorrhizal status or fine root economics. *Oikos* 2023: e08995.
- Stotz GC, Salgado-Luarte C, Escobedo VM, Valladares F, Gianoli E. 2022. Phenotypic plasticity and the leaf economics spectrum: plasticity is positively associated with specific leaf area. *Oikos* 2022: e09342.
- Sun L, Ataka M, Han M, Han Y, Gan D, Xu T, Guo Y, Zhu B. 2021. Root exudation as a major competitive fine-root functional trait of 18 coexisting species in a subtropical forest. *New Phytologist* 229: 259–271.

- Thakur MP, van der Putten WH, Wilschut RA, Veen GFC, Kardol P, van Ruijven J, Allan E, Roscher C, van Kleunen M, Bezemer TM. 2021. Plant–soil feedbacks and temporal dynamics of plant diversity–productivity relationships. *Trends in Ecology & Evolution* 36: 651–661.
- Tsunoda T, van Dam NM. 2017. Root chemical traits and their roles in belowground biotic interactions. *Pedobiologia* 65: 58–67.
- Uthe H, van Dam NM, Hervé MR, Sorokina M, Peters K, Weinhold A. 2021. Chapter Six – A practical guide to implementing metabolomics in plant ecology and biodiversity research. In: Pétriacq P, Bouchereau A, eds. *Advances in botanical research*. Cambridge, MA, USA: Academic Press, 163–203.
- Van der Putten WH, Van Dijk C, Peters BAM. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362: 53–56.
- Veen GF, Fry EL, Ten Hooven FC, Kardol P, Morriën E, De Long JR. 2019. The role of plant litter in driving plant–soil feedbacks. *Frontiers in Environmental Science* 7: 168.
- de Vries FT, Manning P, Tallwin JRB, Mortimer SR, Pilgrim ES, Harrison KA, Hobbs PJ, Quirk H, Shipley B, Cornelissen JHC *et al.* 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecology Letters* 15: 1230–1239.
- de Vries FT, Williams A, Stringer F, Willcocks R, McEwing R, Langridge H, Straathof AL. 2019. Changes in root-exudate-induced respiration reveal a novel mechanism through which drought affects ecosystem carbon cycling. *New Phytologist* 224: 132–145.
- Wang C-Y, Li L-L, Meiners SJ, Kong C-H. 2023. Root placement patterns in allelopathic plant–plant interactions. *New Phytologist* 237: 563–575.
- Wang N-Q, Kong C-H, Wang P, Meiners SJ. 2021. Root exudate signals in plant–plant interactions. *Plant, Cell & Environment* 44: 1044–1058.
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629–1633.
- Weigelt A, Mommer L, Andrzejek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J *et al.* 2021. An integrated framework of plant form and function: the belowground perspective. *New Phytologist* 232: 42–59.
- Weigelt A, Mommer L, Andrzejek K, Iversen CM, Bergmann J, Bruelheide H, Freschet GT, Guerrero-Ramírez NR, Kattge J, Kuyper TW *et al.* 2023. The importance of trait selection in ecology. *Nature* 618: E29–E30.
- Wen Z, White PJ, Shen J, Lambers H. 2022. Linking root exudation to belowground economic traits for resource acquisition. *New Phytologist* 233: 1620–1635.
- Weng J-K, Philippe RN, Noel JP. 2012. The rise of chemodiversity in plants. *Science* 336: 1667–1670.
- Wetzel WC, Whitehead SR. 2020. The many dimensions of phytochemical diversity: linking theory to practice. *Ecology Letters* 23: 16–32.
- Williams A, Langridge H, Straathof AL, Muhamadali H, Hollywood KA, Goodacre R, Vries FT. 2022. Root functional traits explain root exudation rate and composition across a range of grassland species. *The Journal of Ecology* 110: 21–33.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Xi N, Adler PB, Chen D, Wu H, Catford JA, van Bodegom PM, Bahn M, Crawford KM, Chu C. 2021. Relationships between plant–soil feedbacks and functional traits. *The Journal of Ecology* 109: 3411–3423.
- Xia M, Valverde-Barrantes OJ, Suseela V, Blackwood CB, Tharayil N. 2021. Coordination between compound-specific chemistry and morphology in plant roots aligns with ancestral mycorrhizal association in woody angiosperms. *New Phytologist* 232: 1259–1271.
- Yaffar D, Cabugao KG, Meier IC. 2022. Representing root physiological traits in the root economic space framework. *New Phytologist* 234: 773–775.
- Yang L, Maron JL, Callaway RM. 2015. Inhibitory effects of soil biota are ameliorated by high plant diversity. *Oecologia* 179: 519–525.
- Zhang N, Van der Putten WH, Veen GFC. 2016. Effects of root decomposition on plant–soil feedback of early- and mid-successional plant species. *New Phytologist* 212: 220–231.
- Zhang Z, Liu Y, Yuan L, Weber E, van Kleunen M. 2021. Effect of allelopathy on plant performance: a meta-analysis. *Ecology Letters* 24: 348–362.
- Zhou X, Zhang J, Khashi U Rahman M, Gao D, Wei Z, Wu F, Dini-Andreote F. 2023. Interspecific plant interaction via root exudates structures the disease suppressiveness of rhizosphere microbiomes. *Molecular Plant* 16: 849–864.

**Key words:** allelopathy, belowground interactions, functional traits, litter decomposition, plant–soil feedback, root exudates, seed dispersal.

Received, 29 March 2023; accepted, 30 November 2023.