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
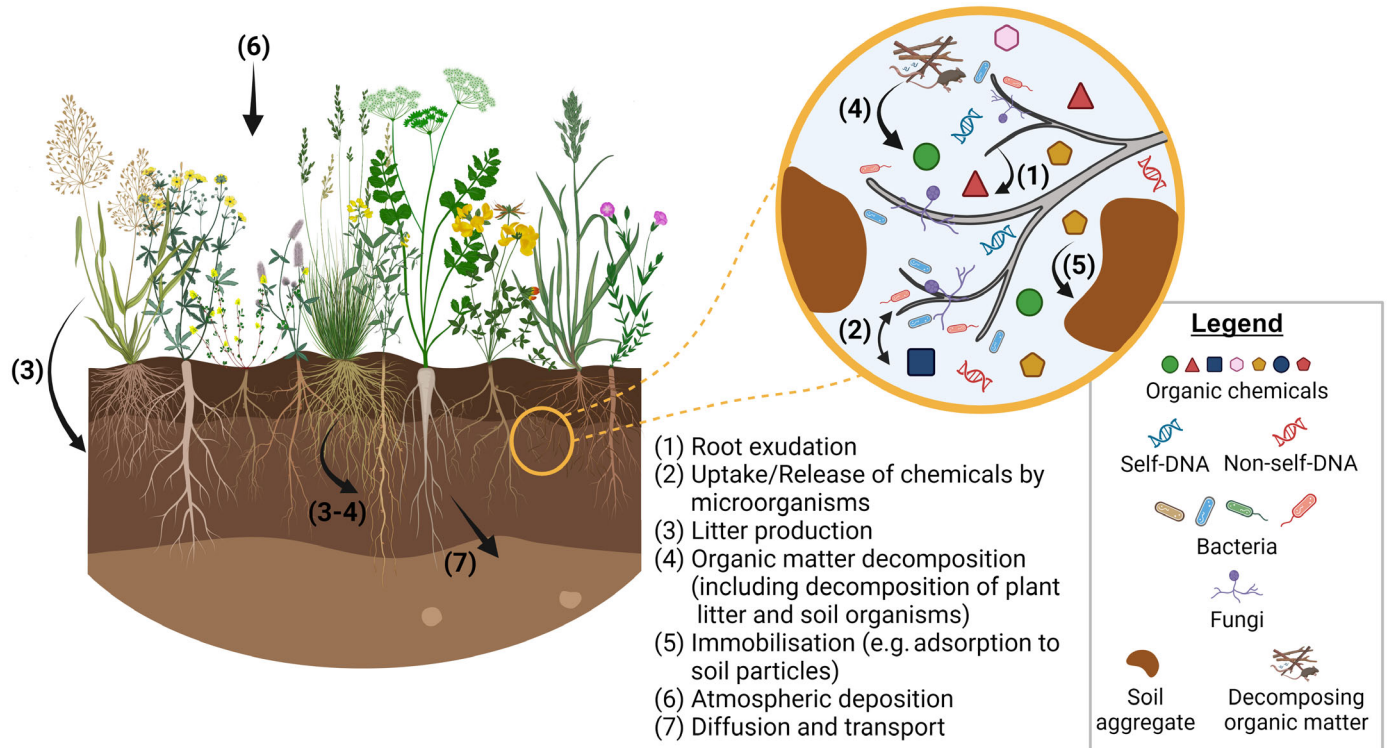

Fig. 1 Aboveground and belowground processes contributing to local changes in soil solution metabolome. This figure highlights seven dynamic, spatially variable and interconnected processes that contribute to soil chemical legacies by inducing variations in the quantity and composition of primary and 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 material 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.

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

predictor of PSF since weaker PSF is expected among closely related species if they accumulate similar biota in their rhizosphere. However, evidence for this is so far limited (Mehrabi & Tuck, 2015; Crawford *et al.*, 2019).

In a recent synthesis, Semchenko *et al.* (2022) proposed that the strength and direction of PSF could be predicted based on the position that a plant species occupies along the two main axes of the root economics space (i.e. collaboration and conservation gradients) and a third axis related to seed dispersal, which characterises the frequency of encountering conspecific soil legacies due to poor dispersal and correspondingly modulates the strength of selection for enhanced pathogen resistance or mutualist dependence. According to their framework, species with efficient dispersal (allowing pathogen escape), low mycorrhizal dependency (do-it-yourself strategy) and low tissue density (fast strategy) should experience strong negative PSF (i.e. negative effect on plant performance of soil biota from conspecific rhizosphere compared with sterile control) due to their overall greater susceptibility to pathogens. On the other hand, species with the opposite strategy – poor dispersal exposing plants to pathogen and mutualist effects of conspecifics, a slow strategy characterised by strong pathogen defence and outsourcing strategy relying strongly on mutualistic associations with mycorrhizal fungi – should experience positive PSF (i.e. better performance in live conspecific soil than in sterilised control). The potential for PSF to modulate species coexistence via species-specific microbial legacies is further predicted to depend on the distance between co-occurring species in functional trait space, with stronger feedbacks occurring among species with more contrasting trait values (Semchenko *et al.*, 2022; Rutten & Allan, 2023). These predictions are generally supported by several empirical studies (Lemmermeyer *et al.*, 2015; Fitzpatrick *et al.*, 2017; Kulmatiski *et al.*, 2017; Lekberg *et al.*, 2018; Xi *et al.*, 2021), although the strength of trait–PSF relationships varies between studies (Bukowski *et al.*, 2018; Heinen *et al.*, 2018) and evidence for root economic traits remains limited (Cortois *et al.*, 2016; Semchenko *et al.*, 2018; Spitzer *et al.*, 2022).

Although plant economic strategies and traits have been related to microbially-mediated PSF, whether or not differences in plant functional traits can also explain variations in soil metabolome and species responses to these chemical legacies remains to be tested (Delory *et al.*, 2021). To do this, we will first describe a possible experimental approach to quantify plant responses to the soil metabolome (Fig. 2). We will then present and discuss four hypotheses for how plant traits related to fine root construction could determine the impact of plant species on the soil solution metabolome and predict plant responses to these soil chemical legacies (Fig. 3). Given that traits related to seed dispersal (e.g. seed mass) have been proposed to be a strong evolutionary driver of PSF (Semchenko *et al.*, 2022), our framework also includes expectations on how dispersal ability may shape plant responses to the soil metabolome. By providing clear testable hypotheses, as well as a description of a possible experimental approach to test them, we aim to encourage exploration of the extent to which belowground chemical interactions cascade to PSF across species, environments and ecosystems.

An experimental approach to quantify plant responses to the soil metabolome

For a given response variable (e.g. plant dry weight), the strength of combined direct and indirect effects of the soil solution metabolome on a plant species can be estimated by comparing the value of that response variable between a plant individual that has been exposed to the soil metabolome of conspecifics or heterospecifics with the value measured on another individual of the same species grown without being exposed to this soil metabolome (i.e. net effect of the soil solution metabolome). Additional treatments manipulating soil microbial communities will disentangle the direct effects of the soil solution metabolome on plants from indirect effects mediated by microbial interactions (i.e. soil biota-mediated effect of the soil solution metabolome; Fig. 2). This approach is analogous to those used in PSF experiments focusing on microbial legacy effects (Pernilla Brinkman *et al.*, 2010; Semchenko *et al.*, 2022) and allows the calculation of effect sizes to estimate the net and soil biota-mediated effects of the soil solution metabolome for any variable of interest (Fig. 2). If the net effect of the soil solution metabolome deviates from zero, it would indicate that the soil solution metabolome has either a positive or a negative effect on the response variable of interest. Similarly, if the soil biota-mediated effect deviates from zero, it would indicate that the soil biota has either a positive or a negative effect on the response of a plant species to the soil solution metabolome. If the relationship between plant responses to the soil metabolome and plant traits is of primary interest, the relationship between calculated effect sizes and plant traits or trait axes can be modelled using appropriate statistical tools.

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

Hypothesis 1: 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 (Fig. 3 – H1).

The quantity and composition of root exudates are related to phylogeny, environmental conditions and plant traits (de Vries *et al.*, 2019; Meier *et al.*, 2020; Williams *et al.*, 2022). Species located on the fast side of the root economics space tend to have higher than average exudation rates expressed as total amount of C exuded into the soil per unit root dry weight per unit time (Guyonnet *et al.*, 2018; Sun *et al.*, 2021; Williams *et al.*, 2022). In particular, root tissue density appears to be a good and consistent predictor of root exudation: the lower the root tissue density, the higher the root C exudation rate (Guyonnet *et al.*, 2018; Sun *et al.*, 2021; Williams *et al.*, 2022). Root exudation of C also increases with respiration rate (Sun *et al.*, 2021), which is a physiological trait strongly related to the root conservation gradient (Han & Zhu, 2021). All these results suggest that root exudation rate might align with the root conservation gradient.
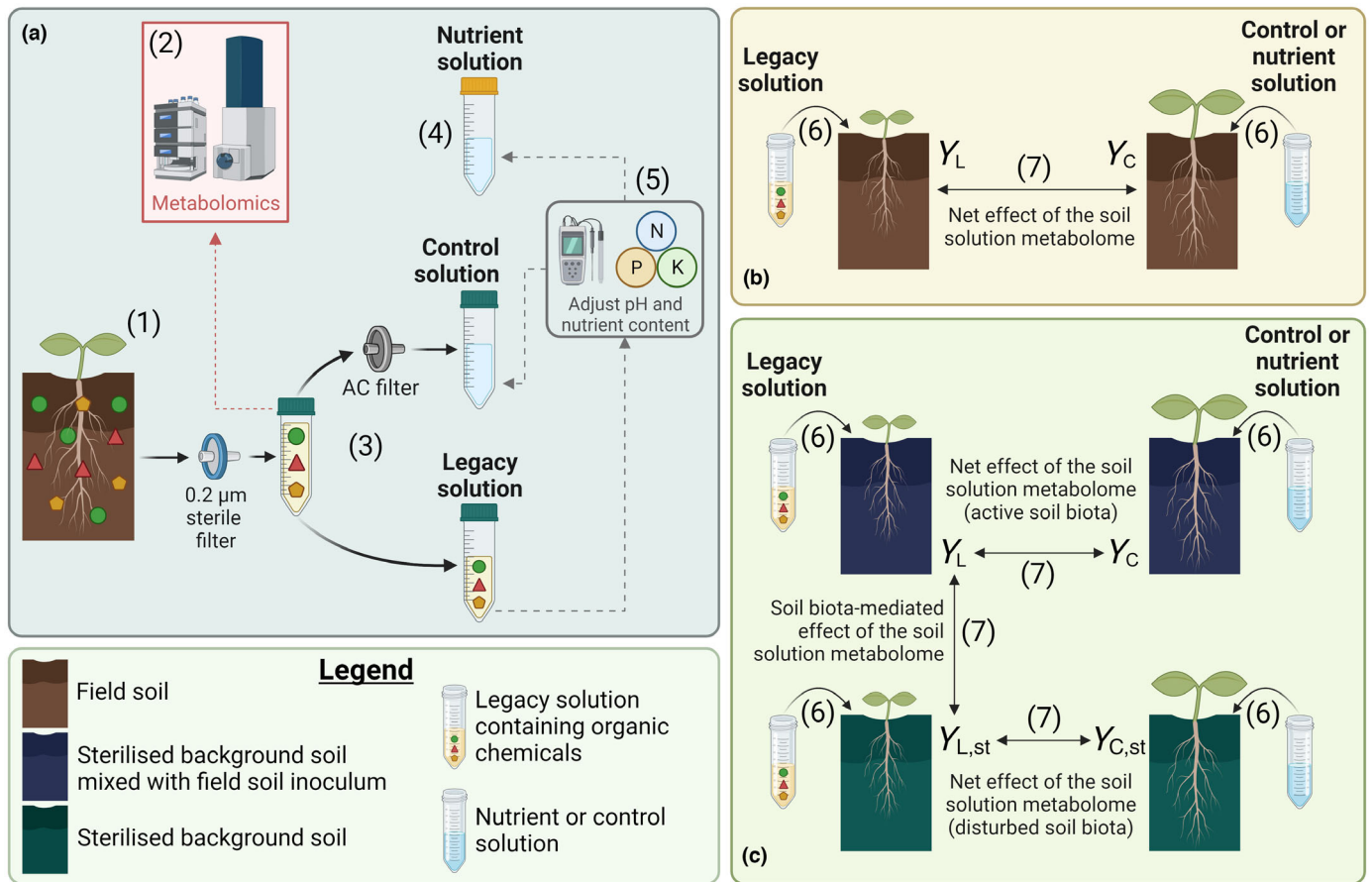
Fig. 2 Experimental approach for the quantification of plant responses to the soil metabolome. This figure only illustrates how to estimate conspecific feedback effects due to water-soluble chemical compounds. Heterospecific feedback effects can be estimated using the same approach, except that the species 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
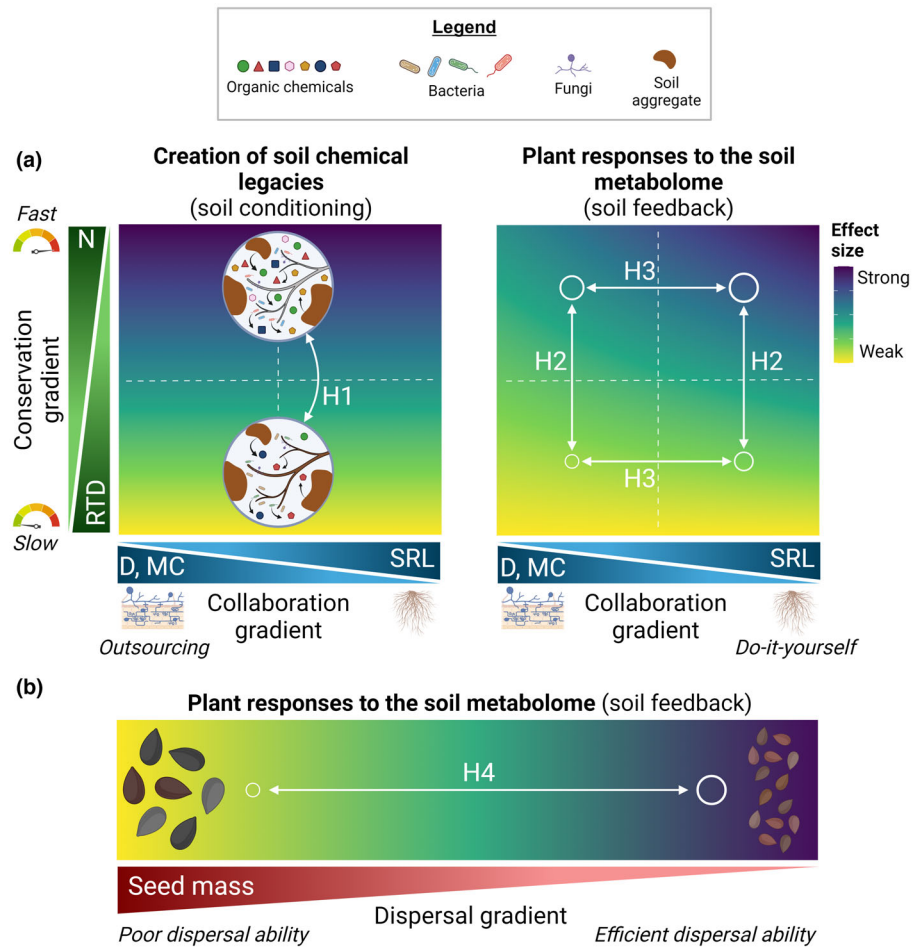
Fig. 3 Trait-based framework linking the soil metabolome to plant–soil feedbacks (PSF). Panel (a) focuses on root economics traits, whereas (b) focuses on traits related to seed dispersal. The proposed framework relies on the following hypotheses, which are not mutually exclusive: (H1) species on the 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. 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; Defossez *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; Gavinet *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 deltoides* 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. deltoides* 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.

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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.

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