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RESEARCH ARTICLE

Plant phylogeny, traits and fungal community composition as drivers of plant–soil feedbacks

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Abstract

1. Plant–soil feedbacks (PSFs) are key drivers of plant community dynamics. However, our understanding of the factors moderating PSFs remains limited. We examined how plant phylogenetic relatedness and functional traits determine PSFs via their influence on rhizosphere fungal communities, especially arbuscular mycorrhizal fungi (AMF) and fungal pathotrophs.
2. We conducted a glasshouse PSF experiment using 21 temperate grassland plant species, where each focal species was exposed to soils conditioned by heterospecific plants of increasing phylogenetic dissimilarity. We tested whether phylogenetic distance between plant species, functional traits or the degree to which species associate with AMF or fungal pathotrophs, explained the magnitude and direction of PSF responses.
3. None of the measured plant traits explained PSFs, although the relative abundance of AMF was weakly and positively related to PSFs. Across all plant species, phylogenetic relatedness did not explain PSFs. However, species-specific effects of phylogenetic relatedness on the outcome of PSFs were detected. In particular, significant relationships with phylogenetic relatedness were observed only for species characterised by the highest rhizosphere relative abundance of AMF or fungal pathotrophs. For *Centaurea nigra and Vicia cracca* (both high AMF abundance) and *Anthoxanthum odoratum* (high pathotroph abundance), we found that PSF became more positive with increased phylogenetic distance between focal and conditioning species, showing a shift towards increased performance in conspecific than heterospecific soils. Meanwhile, as phylogenetic dissimilarity between *Poa trivialis* (high pathotroph abundance) and the soil conditioning species increased, more negative PSFs were observed, indicating improved performance in soils conditioned by increasingly distant heterospecific species.
4. *Synthesis*. Our results suggest that plant traits and phylogenetic relatedness are poor predictors of plant–soil feedbacks (PSFs) among temperate grassland plant species. Hence, despite known effects of these factors in shaping rhizosphere microbial communities, the way plant species respond to these microbial

communities is not related to the same characteristics. The occurrence of significant relationships between phylogenetic distance and PSFs in species with high relative abundances of mycorrhizal or pathogenic fungi suggests that the tendency to accumulate fungal mutualists or pathotrophs may be an important moderator of the relationship between plant phylogenetic relatedness and the magnitude and direction of PSFs.

KEYWORDS
arbuscular mycorrhizal fungi, fungi, pathogens, phylogeny, plant–soil feedback, traits

1 | INTRODUCTION

Plant–soil feedbacks (PSFs) are a key component of terrestrial ecosystem functioning and influence vegetation dynamics in many ways, such as: the maintenance of species coexistence (Crawford et al., 2019; Klironomos, 2002; Teste et al., 2017), plant invasiveness (Aldorfová et al., 2020; Levine et al., 2006) and successional changes in plant community composition (Bauer et al., 2015; Kardol et al., 2006). PSFs involve the modification of soil biological and abiotic properties by a given plant species that have downstream effects on the growth of future individuals in the same soil. These PSFs can be positive, negative or neutral, where plant performance is improved, reduced or unaffected, respectively, when grown in soil previously occupied by the same species compared with soil conditioned by other species (Bever et al., 1997; Van der Putten et al., 2013). Given this wide variation in PSF observed among species, there is considerable interest in developing a framework that can be used to predict the direction and magnitude of PSF responses as a function of plant species characteristics (de Vries et al., 2023; Rutten & Allan, 2023; Semchenko et al., 2022). However, despite an abundance of studies exploring individual aspects of PSFs, our understanding of how plant traits and phylogeny, via associated effects on soil microbial communities, shape PSFs is still limited by the lack of comprehensive empirical tests.

Plants modify their immediate environment in many ways and can shape the composition and diversity of microbial communities within their root zones (Grayston et al., 1998; Hu et al., 2018). This 'conditioning' of rhizosphere microbial communities can regulate PSFs, and, as such, PSF responses may be predictable based upon how a particular plant species modifies its root-associated microbiome (Fitzpatrick et al., 2018; Semchenko et al., 2018; Wilschut et al., 2019). Previous studies indicate that root-associated fungi, especially arbuscular mycorrhizal fungi (AMF) and fungal pathotrophs, play an important role in determining PSFs (Cortois et al., 2016; Semchenko et al., 2018). Several studies show that these fungal guilds are strongly influenced by plant species identity (Frac et al., 2018; Semchenko et al., 2018) and that increased associations with AMF (Cortois et al., 2016; Semchenko et al., 2018) or fungal pathotrophs (Semchenko et al., 2018; Wilschut et al., 2019) lead to more positive and negative PSFs, respectively. There is also evidence that AMF and pathotroph communities are strongly determined by plant phylogenetic relatedness (Barberán et al., 2015; Sweeney et al., 2021) and functional traits, particularly root traits (Bergmann et al., 2020; Eissenstat et al., 2015; Sweeney et al., 2021). This suggests, therefore, that the prediction of the direction and magnitude of PSFs requires better understanding of how soil microbial communities and their effects on plant performance are shaped by plant functional traits and phylogeny.

Several studies demonstrate that plant functional traits can act as important determinants of PSFs (Baxendale et al., 2014; Kardol et al., 2015; Rutten & Allan, 2023; Teste et al., 2017). Indeed, root traits known to influence AMF or pathotroph communities (Bergmann et al., 2020; McCormack & Iversen, 2019; Semchenko et al., 2018; Sweeney et al., 2021; Wilschut et al., 2019), including root diameter (Semchenko et al., 2018), percentage colonisation by AMF and specific root length (Cortois et al., 2016), have been shown to determine the outcome of PSFs. These traits represent the 'collaboration axis' of root resource economics (Bergmann et al., 2020), suggesting that a plant's strategy to partner with AMF for nutrient uptake is a key determinant of PSFs. However, the 'conservation axis' of the root economics space, reflecting the longevity and construction cost of root tissues, has also been found to determine the direction and magnitude of PSFs (Spitzer et al., 2022). Above-ground plant traits have also been linked to PSFs (Baxendale et al., 2014; Fitzpatrick et al., 2017; Semchenko et al., 2018), including shoot nitrogen content (Semchenko et al., 2018) and specific leaf area (Fitzpatrick et al., 2017). Importantly, these above-ground traits represent fast–slow plant resource economics and are independent of traits indicative of reliance on mycorrhizal fungi for nutrient acquisition (Bergmann et al., 2020). As both plant resource acquisition (Cortois et al., 2016; Semchenko et al., 2018) and resource conservation strategies (Baxendale et al., 2014) have been linked to PSFs (Rutten & Allan, 2023; Semchenko et al., 2022; Xi et al., 2021), further work is required to determine which plant traits determine PSF outcomes and the mechanisms behind these relationships.

Plant functional traits reflect the reliance of plants on mycorrhizal fungi and investment in overall defence against pathogens. However, PSFs are also strongly affected by host-specificity of plant–microbial interactions, which are likely determined by complex molecular mechanisms not reflected in commonly measured functional traits (Semchenko et al., 2022). Such interactions may be phylogenetically conserved, hence phylogenetic distance between plant species could be a key predictor of PSF outcomes (Fitzpatrick et al., 2017; Liu et al., 2012). Both AMF and fungal pathotrophs are known to exhibit host-specificity and preferences for closely related plant species (Dickie, 2007; Gilbert & Webb, 2007; Schroeder et al., 2019; Sweeney et al., 2021). Consequently, closely related plant species may share beneficial mutualist communities and plants may grow preferentially in soils conditioned by conspecifics or close phylogenetic relatives (Duell et al., 2023; Segnitz et al., 2020; Semchenko et al., 2018). Alternatively, growth in soil conditioned by increasingly phylogenetically dissimilar species may result in less exposure to specialised pathogens, resulting in pathogen release and improved plant growth (Aldorfová et al., 2020; Segnitz et al., 2020). Importantly, these potential outcomes oppose each other, and from this, we would expect phylogenetic relatedness to be positively and negatively correlated to PSFs, respectively, depending on whether AMF or pathogens are the primary drivers of PSF outcomes. Therefore, the relationship between phylogenetic relatedness and PSFs likely depends on the balance between AMF and pathogens in determining the net outcome of PSFs. This may lead to no overall effect of phylogenetic relatedness in moderating PSFs, should the opposing influences of AMF and pathogens be of equal importance and cancel each other out. This diversity of potential outcomes likely leads to the considerable uncertainty as to the role of plant phylogenetic relatedness in driving PSFs as many studies have provided evidence for (Anacker et al., 2014; Brandt et al., 2009; Crawford et al., 2019; Kempel et al., 2018; Wandrag et al., 2020) and against (Fitzpatrick et al., 2017; Lance et al., 2020; Mehrabi & Tuck, 2015; Wilschut et al., 2019) its significance. Although it is important to note that within the suite of studies reporting the effects of phylogenetic relatedness in determining PSFs, the effects sizes may be small (Crawford et al., 2019; Wandrag et al., 2020) or the results may be context specific and limited to regionally rare species (Kempel et al., 2018). As few studies have directly characterised the roles of AMF and fungal pathotrophs within the context of PSFs (Semchenko et al., 2018; Wilschut et al., 2019, 2023), there remains considerable uncertainty surrounding the microbial drivers of phylogenetic effects on PSFs.

Here, we examined how plant phylogenetic relatedness and functional traits act as determinants of PSFs via their influence on rhizosphere fungal communities, especially AMF and fungal pathotrophs. We hypothesised that both plant phylogenetic relatedness and plant traits determine PSFs and the direction, and magnitude of these relationships is mediated by the degree to which species accumulate AMF and fungal pathotrophs within their rhizosphere. We expect that plant species associating with an increased abundance or diversity of AMF or pathotrophs will experience more positive or negative PSFs, respectively. This was tested using soil from a glasshouse experiment of 21 common temperate grassland plant species representing a broad spectrum of life history strategies, in which we previously identified significant shifts in fungal community structure on the basis of plant phylogeny and functional traits (Sweeney et al., 2021). The present study builds on this work by using the conditioned soil in a PSF experiment in which a randomised phylogenetic gradient was generated between the focal species and the heterospecific species that conditioned the soil.

2 | METHODS

This experiment included two phases: an initial conditioning phase and a subsequent PSF phase. The conditioning phase, in which the soil fungal communities were shaped by the species present, is described in detail by Sweeney et al. (2021). Briefly, five replicates of 21 British grassland plant species (Tables S1 and S2), consisting of forbs, legumes and grasses, each represented by seven species, were grown in a field-collected soil and subjected to three environmental treatments (see below). This soil is a brown earth of the Malham series of Eutric Endoleptic Cambisols (Cranfield University, 2020) taken from a typical *Anthoxanthum odoratum–Geranium sylvaticum* meadow (Rodwell, 1992) at Colt Park, Ingleborough National Nature Reserve, in the Yorkshire Dales, northern England (54°10′47.9″ N, 2°20′11.1″ W). Plants were subjected to three different environmental treatments designed to induce trait plasticity, namely: (i) control—60% water holding capacity (WHC), no shade; (ii) shaded—60% WHC, 55% shade cover; and (iii) water limited, 45% WHC, no shade. These environmental treatments had no detectable impact on fungal community composition, or AMF and pathotroph abundance and richness, so the impact of these treatments is not considered further in this analysis, as detailed in Sweeney et al. (2021). The environmental treatments had no detectable effect on PSFs in this study (Table S3). Plants were grown for 12 weeks under glasshouse conditions and rhizosphere soil was collected and plant traits analysed.

Fungal communities were characterised using metabarcoding of the ITS2 region, using the universal primers ITS3F and ITS4R (White et al., 1990). Leaf and root traits measured included root diameter, volume, tissue density, dry matter content, carbon and nitrogen concentration, specific root length and, specific leaf area, thickness, dry matter content, carbon and nitrogen concentration and plant above and below-ground dry biomass. Soil biological and chemical variables measured were as follows: total, extractable and microbial biomass C, total, water extractiable and plant available N, nitrate, pH and soil moisture content (Sweeney et al., 2021). Detailed information on the methods used to measure plant traits and infer fungal community composition can be found in Sweeney et al. (2021). Within the conditioning phase (Sweeney et al., 2021), plant species identity was a significant determinant of the soil fungal community composition at the end of the conditioning phase, as assessed by permutational multivariate analysis of variance ($r^2 = 0.120$, $p < 0.001$). Furthermore, within these fungal communities, the relative abundance of fungal pathotrophs ($r^2 = 0.131$, $p = 0.003$) and AMF ($r^2 = 0.330$, $p < 0.001$) was strongly determined by plant species identity and structured by plant phylogenetic relatedness (AMF: Pagel's $\lambda = 0.836$, $p < 0.001$; Blomberg's $K = 0.571$, $p < 0.001$, pathotrophs: Pagel's $\lambda = 0.331$, $p = 0.060$; Blomberg's $K = 0.269$, $p = 0.082$). Detailed assessments of these results are found in Sweeney et al. (2021). Here, the feedback phase of the experiment that used the soil from the conditioning phase is reported.

2.1 | Establishment of plant–soil feedback phase

The second phase of the study, or PSF phase, consisted of individual plants being grown in soils conditioned by conspecific or heterospecific plants, as described above.

2.2 | Calculation of the phylogenetic gradient

To establish how plant phylogenetic relatedness affects PSF responses, we established a randomised phylogenetic gradient between the focal (species grown within the PSF phase) and conditioning (species that conditioned the soil inoculum) species. Replication from the conditioning phase was retained, meaning no soil was pooled for the PSF phase. Soil from each individual pot in the conditioning phase inoculated three pots in the feedback phase, of which one pot created a conspecific combination and the other two were used to create heterospecific combinations (Figure 1). The gradient of phylogenetic relatedness between the focal and conditioning species was established across the heterospecific pots. There were five replicates for each species (within each environmental treatment) in the conditioning phase, and soil from each pot inoculated two heterospecific pots in the feedback phase (see section below for details), resulting in a total of 10 pots that were used to create heterospecific plant–soil combinations (Figure 1). To create the phylogenetic gradient of plant–soil combinations for each focal species, soil conditioned by three randomly selected members of the same functional group as the conditioning species were selected alongside three or four randomly selected members of the other functional groups (either grasses and legumes or forbs), resulting in a total of 10 heterospecific combinations. For example, in the case of the grass *A. odoratum*, seedlings of the focal species were planted into soil of three other grass species, as well as three forb and four legume species, to assemble a total of 10 heterospecific plant–soil pots. As each species in the conditioning phase was subject to three different environmental conditions, the same

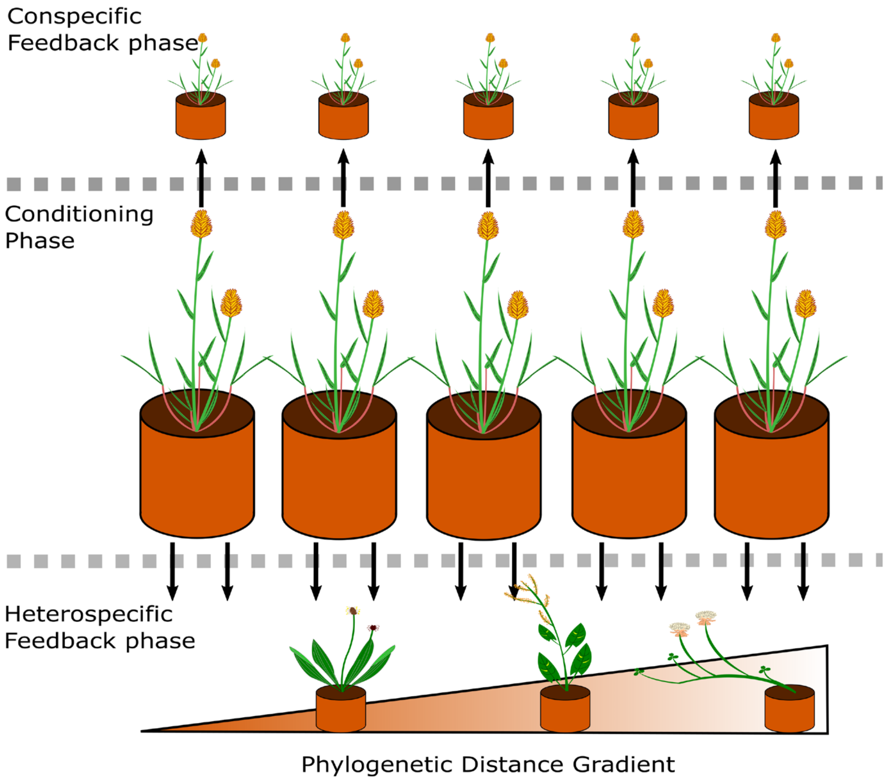

FIGURE 1 Schematic of the establishment of the phylogenetic gradient in the plant–soil feedback (PSF) phase. Each pot in the conditioning phase provided soil for three pots in the feedback phase consisting of one conspecific and two (different) heterospecific plant species. Each black arrow indicates a pot established in the PSF feedback phase. The heterospecific pots were used to create a phylogenetic gradient between each focal species and heterospecific soils conditioned by 10 randomly selected species. Random selection was restrained such that representatives of each functional group (i.e. grasses, legumes and forbs) were included in the selection to ensure a wide phylogenetic gradient. The same phylogenetic gradient and heterospecific soil combinations were replicated across the three prior environmental treatments that were used in the conditioning phase. However, environmental treatments were not further considered in this analysis as they had no detectable impact on the magnitude or direction of PSFs. Instead, they were used as independent replicates of each phylogenetic gradient.

phylogenetic gradient was imposed across soil of each species from each treatment. Thus, the gradient was replicated three times for each focal species. However, as mentioned previously, these environmental treatments had no detectable impact on the soil fungal communities in the conditioning phase (Table S3), so their influence on PSFs is not considered further. *Ranunculus repens* was excluded from this phase of the experiment as it failed to germinate, leaving 20 species within the PSF phase. In total, 836 plants were used in the final analysis.

To perform the experimental work, soil was collected from the same field site as described above, sieved (4 mm) and thoroughly homogenised. To examine the role of the conditioned soil biota in determining PSFs, we added conditioned soil to sterile soil as an inoculum (Ma et al., 2017; Pernilla Brinkman et al., 2010; Wubs et al., 2019). Sieved soil was autoclaved twice for 25 min at 134°C with a 24-h period between runs following Crawford and Knight (2017). To minimise the nutrient flush associated with autoclaving soil, soil was mixed in a 3:1 (v/v) ratio with sand sterilised under the same conditions. Five hundred grams of medium was added to each pot, made up of 400 g of sterile soil/sand mixture and 100 g of conditioned soil from the conditioning phase as inoculum. All materials used to transfer sterile and inoculum soil were washed with ethanol between samples. Seeds were surface sterilised by soaking in 5% (v/v) sodium hypochlorite solution for 5 min before rinsing in distilled water. Sterilised seeds were germinated upon the sterile medium and transplanted upon the emergence of the first true leaves, into 0.5 L pots (≈9 cm width × ≈9 cm length × 10 cm height), with one seedling per pot. Plants were watered liberally throughout and grown for 8 weeks under glasshouse conditions, prior to harvest. The above- and below-ground biomass was harvested, washed free of soil and dried at 60°C for a minimum of 72 h and dry weights were recorded.

2.3 | Calculation of plant–soil feedback

The following equation was used to calculate PSF:

$$\text{Log}_e\,(\text{mean biomass in conspecific soil across the five conspecific replicates/individual plant biomass from a heterospecific soil}).$$

This metric is recommended for use when comparing PSFs between multiple species (Fitzpatrick et al., 2017; Klironomos, 2002; Petermann et al., 2008). Here, positive values show improved plant growth in conspecific compared with heterospecific conditioned soil (positive PSF), while negative values show enhanced performance in heterospecific relative to conspecific conditioned soil (negative PSF). The use of the mean biomass across the five conspecific replicates was necessary due to the experimental design of this study. The study was designed to maximise the phylogenetic gradient of species combinations across the heterospecific pots within the PSF phase (Figure 1). Consequently, the biomass of an individual plant in a conspecific soil could not be directly paired with the biomass of a plant grown in a particular heterospecific soil.

2.4 | Statistical analysis

All statistical analyses were carried out in R version 3.5.1 (R Core Team, 2018). Variables were log transformed when necessary to improve the distribution of the residuals in our models and approximate normality. All relationships $p < 0.1$ were considered to be of interest.

We built linear mixed effects models using the 'lmer' function in the lme4 package (Bates et al., 2015) to measure how plant species identity and functional group affected PSFs. Species identity or functional group were used as fixed effects with experimental block as a random effect. The 'r.squaredGLMM' function in the MuMIN package (Bartón, 2014) was used to calculate the conditional and marginal r^2 values.

To measure how phylogenetic relatedness between species affected PSFs, we used the phylogeny constructed in Sweeney et al. (2021), based on ribulose-bisphosphate carboxylase (rbcL) and maturase K (matK) genes, as published by de Vere et al. (2012), to derive plant phylogenetic distances (Figure S1). Individual accessions used to generate the phylogeny are recorded in Table S1. The parameters and models used to derive the phylogeny can be found in Sweeney et al. (2021). Pairwise distances between species were calculated by estimating the number of substitutions per site between sequences in the sequence alignment and phylogeny construction software, Mega X (Kumar et al., 2018). This metric provided greater resolution within the data than estimating time since divergence between species. A comparison between the two metrics is presented in Figure S2. We built linear mixed effects models, as above, with PSF as the response variable, phylogenetic distance as a fixed effect and species identity and experimental block as random effects. Furthermore, we tested the relationship between plant phylogenetic relatedness and PSFs for each individual species. To do this we built linear mixed effects models for each species tested, as above, with PSF as the response variable, phylogenetic distance as a fixed effect and experimental block as a random effect. Finally, we tested whether species average PSF responses were affected by plant phylogenetic relatedness. We took the mean PSF value per species and calculated Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) values to test for phylogenetic signal using the 'phyloSignal' function of the 'Phylosignal' package (Keck et al., 2016).

To assess the role of fungal community composition in determining PSFs, we first constructed a Bray–Curtis dissimilarity matrix of rhizosphere fungal communities from the soil harvested at the end of the conditioning phase to generate pairwise dissimilarities between species. We then subset the amplicon sequence variants (ASVs) to create Bray–Curtis dissimilarity matrices based upon rhizosphere AMF and pathotroph community composition. Dissimilarities in the fungal communities were based on the average fungal community associated with each species, within each environmental treatment—calculated using the 'merge_samples' function in the Phyloseq package (McMurdie & Holmes, 2013). Here, the mean relative abundance of each ASV present across each plant species-environmental treatment combination was calculated. PSF values were calculated using the mean biomass of the replicates grown in conspecific conditioned soil. Consequently, the fungal community composition of each individual conspecific plant could not be directly related to a given PSF value, as five conspecific replicates generated each PSF value. Therefore, the average fungal community composition for each species was generated and used. However, we acknowledge that this could lead to an overestimation of the effect of rhizosphere dissimilarity on PSFs through reducing intraspecific variation. The dissimilarity between the fungal communities between species was regressed against PSFs using linear mixed effects models, as above, with dissimilarity as a fixed effect and species identity and experimental block as random effects.

To assess how the relative abundance of AMF or fungal pathotrophs affects PSFs, we assigned the sequences identified in our analysis pipeline as pathotrophs using the FUNGuild database (Nguyen et al., 2016), as detailed in Sweeney et al. (2021). ASVs were assigned as pathotrophs at the lowest taxonomic rank available, up to a maximum of family. All Glomeromycota were classified as AMF and any uncategorised ASVs remained unclassified. The proportion of pathotrophs and AMF was calculated as the proportion of reads in the sample identified as belonging to a given functional guild relative to the total reads in a sample. The richness of pathotrophs and AMF was calculated as the number of ASVs assigned to each guild. We established the average relative abundance of AMF or pathotrophs for each focal species, using the data from the conditioning phase (Sweeney et al., 2021), and averages were calculated per species and per environmental treatment within the conditioning phase. We built linear mixed effects models, as above, with PSF as the response variable, the average proportion/richness of AMF or pathotrophs as fixed effects and species identity and experimental block as random effects. Overall, we identified 7528 ASVs from samples containing an average of 18,493 reads. Six hundred forty-three ASVs were identified as AMF and 98 as pathotrophs (Sweeney et al., 2021).

We assessed whether the traits of the focal species affected PSF outcomes and calculated average trait values for each species using data from each environmental treatment from the conditioning phase. For each trait, we built linear mixed effects models with PSF as the response variable, a given trait as a fixed effect and species identity and experimental block as random effects. Additionally, we tested whether trait similarity between species affected PSF outcomes by calculating phenotypic similarity between species and Euclidean distances between species using standardised (*z*-score) average trait data were calculated to generate pairwise phenotypic distances between conspecific and heterospecific species. We built linear mixed effects models with PSF as the response variable, phenotypic similarity as the fixed effect and plant species identity and experimental block as random effects.

We tested whether the species identity or functional group of the focal species affected PSF outcomes. For each focal species and functional group (grass, legume or forb), we built linear mixed effects models with PSF as the response variable, species identify or functional group as the fixed effect and experimental block as a random effect.

We tested whether variation in the soil biological or chemical variables of the conditioned soil used as the inoculum explained variation in PSFs by conducting a principal component analysis (PCA) on the soil variables measured. We extracted the loadings of the main axes and used these as predictors of PSFs in linear mixed effects models and tested whether the properties of the heterospecific conditioned soil affected PSF outcomes. PSF was the response variable, and axis loadings were fixed effects, with species identity and experimental block as random effects. Finally, we tested whether the similarity of the soil properties between the conspecific and heterospecific soil inoculum explained PSFs and created a Euclidean distance matrix of standardised (*z*-score) average soil properties measured during the conditioning phase. We built linear mixed effects models with PSF as the response variable, soil properties similarity as the fixed effect and plant species identity and experimental block as random effects.

3 | RESULTS

3.1 | Plant phylogeny and species identity

When considering all species together, PSFs were unaffected by phylogenetic distance between species (Table 1; Figure 2a) and no significant interactions were detected with plant trait and fungal community metrics (Table S4). Species-specific relationships between phylogenetic distance and PSFs were observed (Table S5). For the grass *A. odoratum* ($r^2=0.218$, $p=0.039$; Figure 2b), forb *Centaurea nigra* ($r^2=0.101$, $p=0.092$; Figure 2c) and legume *Vicia*

TABLE 1 Results from linear mixed effects models describing the role of measured variables in influencing plant–soil feedbacks.

Variable	r^2_m	r^2_c	Coefficient	*p*
Phylogenetic distance	0.001	0.074	0.169	0.412
Phenotypic distance	0.001	0.069	−0.011	0.440
Fungal dissimilarity	0.001	0.071	−0.239	0.448
AMF dissimilarity	0.002	0.031	−0.248	0.203
Pathotroph dissimilarity	0.001	0.028	0.026	0.872
Proportion of AMF	0.007	0.087	1.524	0.056
AMF richness	<0.001	0.074	−0.006	0.674
Proportion of pathotrophs	0.002	0.082	−0.058	0.226
Pathotroph richness	<0.001	0.076	0.004	0.817
Focal species identity	0.074	0.098	—	0.011
Focal species functional group	0.002	0.028	—	0.470

Note: Each variable was a fixed effect with the species identity and experiment block as random effects (only experimental block was a random effect in models with plant species identity as a fixed factor). Marginal r^2 (r^2_m) values describe the effects of the fixed effects while the conditional r^2 (r^2_c) values describe the variance explained by both the fixed and random effects. No coefficient is calculated for species identity and functional group as they are categorical factors.

Abbreviation: AMF, arbuscular mycorrhizal fungi.

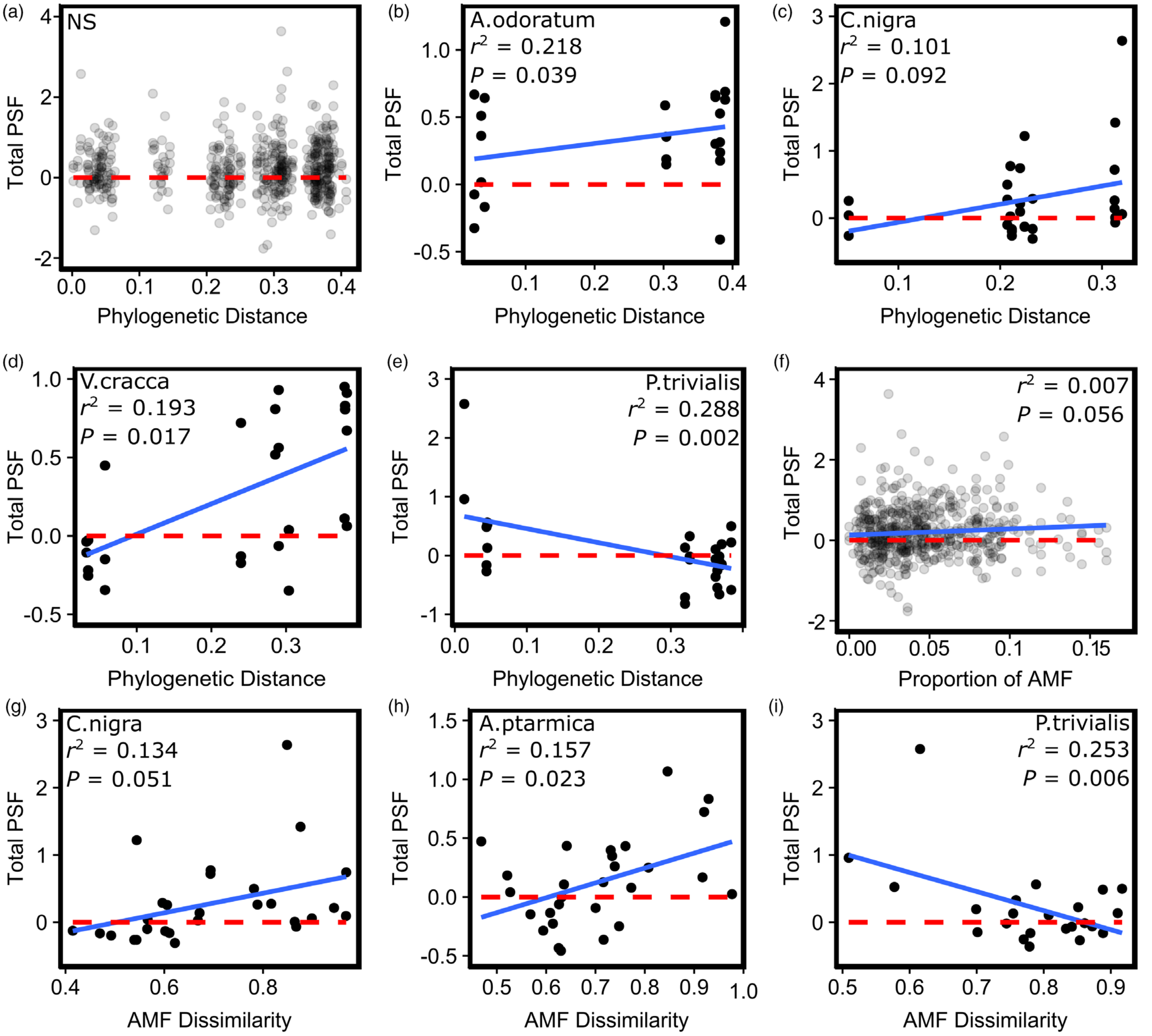

FIGURE 2 Drivers of plant–soil feedbacks. (a) Phylogenetic distance between species. (b–e) Species-specific relationships between phylogenetic distance and plant soil feedbacks (PSFs). (f) Average proportion of arbuscular mycorrhizal fungi (AMF) associated with a focal species. (g–i) Species-specific relationships between AMF community dissimilarity and PSFs. r^2 values are marginal r^2 values from linear mixed effects models describing the role of the x-axis variable in determining PSFs, with experimental block as a random effect; the blue line illustrates the fit of this model to the data. Red dashed line is at PSF = 0, where plant performance is equal in both conspecific and heterospecific conditioned soils.

cracca ($r^2=0.193$, $p=0.017$; Figure 2d), increasing phylogenetic distance between species that conditioned the soil led to more positive PSFs. Meanwhile, positive PSF was recorded for the grass *Poa trivialis* when heterospecific soil was conditioned by a congener but PSFs became neutral with increasing phylogenetic distance ($r^2=0.288$, $p=0.002$; Figure 2e). Species average PSF responses were not phylogenetically conserved (Pagel's $\lambda=<0.001$, $p=0.999$; Blomberg's $K=0.070$, $p=0.689$). Plant species identity ($r^2=0.074$, $p<0.001$), but not functional group, was significantly related to PSF outcomes (Table 1). Here, the grasses *A. odoratum* and *Poa pratensis*, forbs *Achillea millefolium* and *C. nigra*, and legumes *Trifolium repens* and *Vicia sativa*, all experienced significantly more positive PSFs when compared to the remaining species (Table 2).

3.2 | Fungal communities

Dissimilarity in fungal community composition between species was unrelated to PSFs (Table 1), and no interactive effects were evident with phylogenetic or trait distance metrics (Table S4). Species with a higher average relative abundance of AMF within their rhizosphere experienced slightly more positive PSFs ($r^2=0.007$, $p=0.056$;

TABLE 2 Average plant–soil feedback (PSF) responses per species.

Species	Functional group	Estimate	Lower	Upper	*p*
Achillea millefolium	Forb	0.395	0.175	0.616	<0.001
Achillea ptarmica	Forb	0.099	−0.134	0.333	0.401
Centaurea nigra	Forb	0.302	0.066	0.542	0.012
Galium verum	Forb	−0.065	−0.282	0.152	0.551
Plantago lanceolata	Forb	0.238	0.014	0.463	0.387
Rumex acetosa	Forb	0.024	−0.217	0.266	0.84
Agrostis capillaris	Grass	0.013	−0.222	0.248	0.912
Agrostis stolonifera	Grass	0.253	0.122	0.495	0.039
Anthoxanthum odoratum	Grass	0.345	0.100	0.591	0.006
Dactylis glomerata	Grass	0.164	−0.081	0.409	0.187
Festuca rubra	Grass	0.088	−0.156	0.334	0.474
Poa pratensis	Grass	0.380	0.127	0.634	0.003
Poa trivialis	Grass	0.094	−0.143	0.333	0.431
Lathyrus pratensis	Legume	0.007	−0.242	0.257	0.95
Lotus corniculatus	Legume	0.115	−0.137	0.369	0.367
Lotus pedunculatus	Legume	0.055	−0.213	0.324	0.686
Trifolium pratense	Legume	0.166	−0.072	0.405	0.169
Trifolium repens	Legume	0.524	0.299	0.750	<0.001
Vicia cracca	Legume	0.186	−0.051	0.424	0.122
Vicia sativa	Legume	0.501	0.266	0.736	<0.001

Note: Average PSF values are estimated using least squares means from linear mixed effects models predicting how plant species identity affects PSFs, with experimental block as a random effect. Upper and lower refer to the respective 95% limits of the estimate. Functional group for each focal species is reported.

Figure 2f). However, the richness of AMF and pathotrophs and the relative abundance of pathotrophs associated with plant species did not affect PSF responses (Table 1). We recorded species-specific relationships between AMF community dissimilarity across focal and conditioning species and PSFs (Table S6). *C. nigra* ($r^2=0.134$, $p=0.051$; Figure 2g) and *Achillea ptarmica* ($r^2=0.157$, $p=0.023$; Figure 2h) exhibited more positive PSFs (improved growth in conspecific soils) with increasing AMF community dissimilarity. In contrast, *P. trivialis* ($r^2=0.253$, $p=0.006$; Figure 2i) exhibited the opposite pattern, showing the most positive PSF response when grown in soils with more similar AMF communities. With increasing AMF dissimilarity, *P. trivialis* trended towards more negative PSFs, or a preference for growth in heterospecific soils.

3.3 | Plant traits

We found traits of the focal species to be unrelated to PSFs (Table 3). Similarly, the phenotypic distance between species did not affect PSFs (Table 1), with no interactive effects evident with phylogenetic distance and fungal dissimilarity metrics (Table S4). However, we did find that increasing total ($r^2=0.011$, $p=0.012$), above-ground ($r^2=0.011$, $p=0.011$) and below-ground ($r^2=0.006$, $p=0.051$) biomass of plants in the conditioning phase was associated with slightly more negative PSFs (Table S7).

Overall, no significant interactive effects between phylogenetic distance, fungal community dissimilarity and the relative abundance and dissimilarity of AMF and pathogens were detected in our data (Table S4).

3.4 | Edaphic conditions

We performed PCA of the soil properties within the inoculum used for the feedback phase, which revealed two main axes of variation explaining approximately 60% of the variation in the soil data (Figure S3). Soil moisture content and pH loaded negatively on PC1, while water extractable total N, water extractable nitrate and plant available N loaded positively on PC1. Water extractable C, total soil C and N and microbial biomass C loaded positively on PC2. PC1 was weakly positively related to PSFs ($r^2=0.006$, $p=0.057$), but PC2 was unrelated to PSF outcomes (Table S7). Species-specific relationships between dissimilarity in soil properties across conspecific and heterospecific inoculum were observed (Table S6). Here, *A. odoratum* ($r^2=0.221$, $p=0.013$), *Dactylis glomerata* ($r^2=0.150$, $p=0.045$), *Plantago lanceolata* ($r^2=0.247$, $p=0.003$) and *Rumex acetosa* ($r^2=0.330$, $p=0.001$) all exhibited more positive PSFs with increasing dissimilarity in soil conditions between conspecific and heterospecific soil inoculum.

TABLE 3 Results from linear mixed effects models describing how plant traits determine plant–soil feedback responses.

Trait	r^2_m	r^2_c	Coefficient	p
Root diameter	<0.001	0.074	0.041	0.765
Specific root length	0.002	0.074	0.043	0.448
Specific root area	0.004	0.073	0.086	0.251
Root volume	<0.001	0.072	0.017	0.667
Root tissue density	0.010	0.075	−0.136	0.082
Root dry matter content	0.001	0.076	−0.125	0.379
Root nitrogen	0.001	0.074	0.038	0.593
Root carbon	<0.001	0.070	0.127	0.540
Leaf thickness	0.001	0.075	0.049	0.579
Specific leaf area	<0.001	0.073	0.015	0.859
Leaf dry matter content	<0.001	0.073	0.003	0.960
Leaf nitrogen	0.002	0.080	−0.160	0.317
Leaf carbon	0.003	0.081	−0.271	0.220
Total biomass	0.003	0.073	0.049	0.290
Above-ground biomass	0.005	0.074	0.072	0.143
Below-ground biomass	<0.001	0.073	−0.001	0.967

Note: Each variable was a fixed effect with experimental block as a random effect. Marginal r^2 (r^2_m) values describe the effects of the fixed effects, while the conditional r^2 (r^2_c) values describe the variance explained by both the fixed and random effects.

4 | DISCUSSION

In this study of 21 grassland plant species covering a broad spectrum of life history strategies, we found species-specific relationships between phylogenetic distance and PSFs, but no overall patterns across all plant species. Moreover, PSF outcomes across grassland plant species were unrelated to any of the measured functional traits. Likewise, dissimilarity in fungal community composition between plant species was unrelated to PSFs, though species with a higher proportion of AMF within their rhizosphere experienced slightly more positive PSFs. Additionally, we observed species-specific relationships between PSFs and dissimilarity in AMF community composition between conspecific and heterospecific soils.

Despite our finding that plant traits influenced fungal community composition and the relative abundance and richness of AMF and pathotrophs in the conditioning phase (Sweeney et al., 2021), no significant relationships between functional trait distances and PSF were detected. This lack of a relationship, which is in contrast to previous studies (Cortois et al., 2016; Fitzpatrick et al., 2017; Semchenko et al., 2018), may be a consequence of the low amount of variation in PSFs that was explained by either plant species identity or fungal community characteristics. This is likely to be a result of the design of the conditioning period, and specifically, the length of the conditioning phase and use of field-collected soil; a 12-week conditioning phase may not be sufficient to overcome the legacy of a diverse fungal community from the field. Field soil is commonly used in PSF experiments, but studies reporting significant trends may use several growing seasons (Semchenko et al., 2018) or expedite the conditioning period through the inoculation of a sterile soil base with a field sampled soil (Wilschut et al., 2019). Field soil may also provide functional redundancy within the microbial community structure that requires longer periods of soil conditioning to overcome. Our finding that the biomass of the plants that conditioned the soil was the only trait-based predictor of PSFs supports this suggestion, indicating that larger plants produced a stronger conditioning effect. Therefore, the intensity of soil conditioning may not have been sufficient to explain much of the variation in PSFs in this study.

Across all the grassland plant species, we found that phylogenetic distance did not determine PSFs. However, for four individual species, phylogenetic distance between species was related to PSFs; these species were the grasses *A. odoratum* and *P. trivialis*, the forb *C. nigra* and the legume *V. cracca*. Among the plant species tested, *V. cracca* and *C. nigra* had the first and second highest AMF relative abundance and second and first highest AMF richness, respectively (Figures S6 and S7). For both species, increasing phylogenetic dissimilarity with heterospecific soil conditioning led to more positive PSFs, that is improved growth in conspecific compared with heterospecific soils. Increasing phylogenetic distance between species reduces the likelihood that AMF taxa beneficial to specific host plants are present, reducing plant performance in distantly related heterospecific soils (Barberán et al., 2015; Semchenko et al., 2018). This is supported by the finding that *C. nigra* and *A. ptarmica* showed improved growth in heterospecific soils when dissimilarity in AMF community composition between conspecific and heterospecific soils was low, suggesting the need for a specific mycorrhizal community for optimal growth. Furthermore, during the conditioning phase of this study, we found that the AMF communities were structured strongly by plant phylogenetic relatedness (Sweeney et al., 2021). This pattern is reflected weakly in the positive relationship between the relative abundance of AMF and PSFs among all plant species tested and more specifically in the reported associations between PSFs and AMF dissimilarity for *C. nigra* and *A. ptarmica*.

The other two species that were significantly affected by the phylogenetic distance to species that conditioned the soil—*P. trivialis* and *A. odoratum*—stood out as the species with the first and second highest pathotroph relative abundance and the third and first highest rhizosphere pathotroph richness among studied species, respectively (Figures S4 and S5). In the case of *P. trivialis*, the two most positive PSF values were both observed at the shortest phylogenetic distance, when the species was grown on soil conditioned by its congeneric *P. pratensis*, while neutral PSF was observed at longer phylogenetic distances. It is possible, therefore, that *P. trivialis* is particularly vulnerable to the negative effects of biota of closely related species. As we did not observe a species-specific relationship between pathotroph dissimilarity and PSFs for *P. trivialis*, this finding may be related to the negative association between AMF dissimilarity between soils and PSFs for this species. This was a surprising result, since *P. trivialis* had one of the lowest rhizosphere AMF abundances in the conditioning phase (Figure S6). This preference for growth in soils of increasing AMF dissimilarity may be indicative of *P. trivialis* exhibiting a parasitic relationship with the AMF from closely related species (Bennett & Bever, 2009; Bever, 2002), or it could be a result of variables unaccounted for in this study. In contrast, when *A. odoratum* was grown in increasingly phylogenetically dissimilar heterospecific soils, more positive PSFs occurred, indicating reduced growth in heterospecific soil with increasing phylogenetic dissimilarity. While *A. odoratum* clearly has a high relative abundance of fungal pathogens, it may be adapted to tolerate its own pathotroph-rich communities. Potentially, exposure to novel biota in increasingly dissimilar heterospecific soils reduces plant performance leading to more positive PSFs. Overall, these species-specific findings suggest that a wide range of factors may determine how PSF changes with plant phylogenetic relatedness in a particular species. Besides the pathogen and AMF relative abundance and richness assessed in this study, phylogenetic distance may also reflect differentiation in other soil biota, such as oomycetes and nematodes (Domínguez-Begines et al., 2021; Wilschut et al., 2023), as well as differences in plant ability to regulate interactions with soil biota within roots and rhizosphere via root exudation (Bever et al., 2009; Kaur et al., 2022; Kiers et al., 2011; Sasse et al., 2018). This complexity of factors underlying phylogenetic effects may explain the idiosyncratic nature of our findings and considerable uncertainty in the literature as to the role of plant phylogeny in determining PSF outcomes (Anacker et al., 2014; Kempel et al., 2018; Lance et al., 2020; Wandrag et al., 2020; Wilschut et al., 2019).

While we have identified AMF and fungal pathotrophs as key drivers of PSFs in species-specific scenarios, we must acknowledge that this study utilised universal fungal primers (Lekberg et al., 2018) to characterise a broad spectrum of rhizosphere fungi and be able to assess the relative abundances of different functional guilds (Lekberg et al., 2018). Future PSF studies may benefit from the use of more specific primer sets or other sequencing techniques to get more detailed information on the composition of the AMF or pathotroph communities. Likewise, we also need to consider that the general direction of PSFs we observed in this study was positive (Table 2), which is in contrast to the negative PSFs commonly observed in other studies (Kulmatiski et al., 2008). This may be due to the environmental conditions during the experimental period. This experiment was conducted during a period of persistent hot and sunny weather. We hypothesise that this was conducive to more mutualistic rather than pathogenic effects within this study, leading to more positive PSFs. In our study, the relative abundance of AMF and pathotrophs was approximately 5% and 1%, respectively (Figures S4 and S6). In contrast, in the PSF study conducted by Semchenko et al. (2018), which used the same soil and seed source and was conducted in a period of cooler, wetter weather, fungal pathotrophs and AMF had an approximately equal relative abundance of around 4%. In their study, a range of both positive and negative PSFs were recorded (Semchenko et al., 2018). We surmise that the increased ratio of AMF to pathotrophs observed in our study is responsible for the overall positive direction of PSFs we detected.

We observed that the first principal component of soil biological and chemical properties, representing soil nutrient availability, was weakly and positively related to PSFs across all species. Here, increasing nutrient availability in the soil inoculum led to more positive PSFs and preferential growth in conspecific conditioned soils. While links between nutrient availability and PSFs are well documented (Bennett & Klironomos, 2019; Hobbie, 2015), this pattern is unlikely to be directly related to increased nutrient availability due to the excess of nutrients provided by the autoclaved media (Powlson & Jenkinson, 1976; Trevors, 1996). Soil abiotic properties also exhibited species-specific associations with PSFs. *A. odoratum*, *D. glomerata*, *P. lanceolata* and *R. acetosa* all exhibited improved growth in conspecific conditioned soils as abiotic dissimilarity between conspecific and heterospecific soils increased. This opposes what would be expected if these species exhibited resource niche differentiation and depleted specific soil resources (Bennett & Klironomos, 2019; Ehrenfeld et al., 2005). Therefore, these effects may be linked to other biotic soil properties correlated with these abiotic variables that are unaccounted for in this study (e.g. fungal saprotroph functioning).

Overall, our results suggest that the influence of phylogenetic relatedness on PSFs may be species-specific and dependent on the relative abundance of AMF and fungal pathotrophs associated with a given plant species. In reporting these idiosyncratic and species-specific PSF responses, our study builds on previous works by presenting data that may explain the considerable uncertainty surrounding the role of plant phylogenetic relatedness as a driver of PSF outcomes (Crawford et al., 2019; Fitzpatrick et al., 2017; Wandrag et al., 2020; Wilschut et al., 2019). We suggest that phylogenetic relatedness is a poor predictor of PSFs and that PSFs are primarily determined by how a given species interacts with AMF and pathotrophs. Furthermore, while our data support the role of AMF in determining PSFs (Semchenko et al., 2018), they raise questions about the importance of plant traits as drivers of PSFs. To conclude, we suggest that species-specific interactions between plants and the mycobiome are key determinants of PSFs. Finally, future studies should contextualise PSFs with measures of species associations with AMF and fungal pathotrophs to enhance our understanding of the role of these key fungal guilds in driving PSF outcomes.

AUTHOR CONTRIBUTIONS

All authors contributed to the framing and design of the study and interpretation of results. Christopher J. Sweeney conducted the experimental work and data analysis and wrote the manuscript with Marina Semchenko, Franciska T. de Vries, Bart E. van Dongen, Richard D. Bardgett.

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CONFLICT OF INTEREST STATEMENT

Richard D. Bardgett is executive editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. Marina Semchenko is an associate editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. Franciska T. de Vries is an associate editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Sequence data are available in the NCBI Sequence Read Archive (Bioproject: PRJNA641575, https://www.ncbi.nlm.nih.gov/bioproject/PRJNA641575). Plant biomass data used in PSF calculations and the fungal guild abundances and richness data are available in a Figshare repository at: https://doi.org/10.6084/m9.figshare.25036940 (Sweeney, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Table of accessions used for the phylogeny building and the average traits in this study by species.

Table S2: Species selection with average measured leaf trait values.

Table S3: Effect of the environmental treatments within the conditioning phase upon plant-soil feedbacks.

Table S4: Results from linear mixed effects models describing the role of measured variables in influencing plant-soil feedbacks.

Table S5: The role of phylogenetic distance between each response species and the heterospecific conditioning species in determining plant-soil feedbacks.

Table S6: The influence of dissimilarity between the influence of the plant-soil feedback (PSF) species and the conditioning species across various factors on PSFs.

Table S7: The role of principal components describing the biological and chemical properties of the soil inoculum and the conditioning plant biomass in determining plant-soil feedbacks.

Figure S1: Resolved phylogeny used in this study. Adapted from Sweeney et al. (2021).

Figure S2: Comparison of the phylogenetic distance used in this study (left) and estimates of divergence between species in millions of years (mya, right).

Figure S3: PCA of soil variables.

Figure S4: Average proportion of fungal pathotrophs per species, standard error presented.

Figure S5: Average richness of fungal pathotrophs per species, standard error presented.

Figure S6: Average proportion of arbuscular mycorrhizal fungi per species, standard error presented.

Figure S7: Average richness of arbuscular mycorrhizal fungi per species, standard error presented.

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