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Research

The soil microbial community predicts the importance of plant traits in plant–soil feedback

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Summary

- Reciprocal interaction between plant and soil (plant–soil feedback, PSF) can determine plant community structure. Understanding which traits control interspecific variation of PSF strength is crucial for plant ecology. Studies have highlighted either plant-mediated nutrient cycling (litter-mediated PSF) or plant–microbe interaction (microbial-mediated PSF) as important PSF mechanisms, each attributing PSF variation to different traits. However, this separation neglects the complex indirect interactions between the two mechanisms.
- We developed a model coupling litter- and microbial-mediated PSFs to identify the relative importance of traits in controlling PSF strength, and its dependency on the composition of root-associated microbes (i.e. pathogens and/or mycorrhizal fungi).
- Results showed that although plant carbon: nitrogen (C : N) ratio and microbial nutrient acquisition traits were consistently important, the importance of litter decomposability varied. Litter decomposability was not a major PSF determinant when pathogens are present. However, its importance increased with the relative abundance of mycorrhizal fungi as nutrient released from the mycorrhizal-enhanced litter production to the nutrient-depleted soils result in synergistic increase of soil nutrient and mycorrhizal abundance. Data compiled from empirical studies also supported our predictions.
- We propose that the importance of litter decomposability depends on the composition of root-associated microbes. Our results provide new perspectives in plant invasion and trait-based ecology.

Introduction

Understanding how species' traits, which are defined as measurable morphological or physiological characteristics of the species, influence community structure and ecosystem properties is a central concern for trait-based ecology (McGill *et al.*, 2006; Violle *et al.*, 2007; de Bello *et al.*, 2010; Adler *et al.*, 2013). Many studies have focused on the importance of plant traits in determining the strength of community-structuring forces, with particular interest in the aboveground components of terrestrial ecosystems (e.g. light availability, herbivore grazing and disturbance; Chave *et al.*, 2009; Adler *et al.*, 2013). However, interaction between plants and soil, a belowground process termed plant–soil feedback (PSF), was also found to have a strong impact on plant community structure (van der Heijden *et al.*, 2008; Bever *et al.*, 2010). Different plants can cultivate the soil environment differently, altering the soil properties and influencing the performance of individual plants nearby (Bever *et al.*, 1997; Binkley & Giardina, 1998). When a plant changes the soil environment such that the growth of individuals in conspecific-cultivated soils is larger (or smaller) compared with individuals grown in heterospecific-cultured soils, the feedback is defined as positive (or negative) PSF (Bever *et al.*, 1997; Brinkman *et al.*, 2010).

Past studies have revealed that PSF processes operate ubiquitously on various ecosystems and plant life-forms. Species vary greatly in their PSF strength, and such variation has been suggested to act as a structuring force of plant community (Bever *et al.*, 2010; van der Putten *et al.*, 2013 and references therein). For example, rare species have been shown to suffer from stronger negative PSF, implying that species' rarity can be predicted by its PSF strength (Klironomos, 2002; Mangan *et al.*, 2010). Variation in PSF also contributes to the invasiveness of exotic plants (Reinhart & Callaway, 2006). Compared with natives, invasive species may experience stronger positive PSF by leaving their belowground natural enemies behind (i.e. enemy release hypothesis; Klironomos, 2002; Mitchell & Power, 2003), or by altering nearby soil chemical properties (Miki & Kondoh, 2002; Farrer & Goldberg, 2009). However, despite the large body of evidence emphasizing the importance of PSF, a predictive relationship between species and its PSF strength is unavailable (van der Putten *et al.*, 2013). Understanding how species' traits are mechanistically linked with PSF strength, and which traits exhibit greater control on interspecific PSF variation, can provide this information and is crucial in plant community ecology.

Among the many mechanisms that can generate PSF, the two most highlighted have been plant-mediated nutrient cycling and

plant–microbial interactions. On the one hand, soil chemical properties are influenced by plants through its mediation of litter input, decomposition processes and nutrient depletion (Binkley & Giardina, 1998). Plants differ in their effects on local nutrient cycling, and studies often suggest litter decomposability as an important plant trait controlling plant-mediated nutrient cycling (Berendse, 1994; Miki & Kondoh, 2002). In particular, the production of quickly decomposing litter creates positive PSF by enhancing nutrient cycling, especially when the benefits have stronger effect on the plant itself. The difference in soil nutrient depletion by plants is also an important driver of negative PSF through nutrient cycling. For simplicity, we hereafter call PSF mediated by nutrient cycling litter-mediated PSF. On the other hand, the direct interactions between plants and soil microbes, termed microbial-mediated PSF, emphasize that plants differ in their local microbial communities and their response to particular microbial species (Bever *et al.*, 1997, 2010; van der Putten *et al.*, 2013). Although soil microbes are the main focus of this line of study, it should be noted that other soil-dwelling organisms may also cause biotic PSF as well (e.g. earthworms, Milleret *et al.*, 2009). Although diverse functional groups of microbes exist, past microbial-mediated PSF studies have focused primarily on groups that are directly associated with plant roots (i.e. root-associated microbes, such as pathogens, mycorrhizal fungi and certain nitrogen (N)-fixing microbes). Past studies often simplified the root-associated microbial community as a black box. Thus, they could only conclude that PSF was controlled by the overall impact of the root-associated microbial community. Positive (or negative) PSF can occur when the plant differentially facilitates (or suppresses) the population growth of beneficial microbes (e.g. mycorrhizal fungi) compared with detrimental microbes (e.g. soil-borne pathogens) during cultivation (Klironomos, 2002), or when facilitated detrimental (or beneficial) microbes have stronger effects on competitors than on the plant itself (Bever *et al.*, 1997, 2010).

However, the interdependency between litter- and microbial-mediated mechanisms is often neglected, which has hindered progress towards characterizing the major determinants of PSF strength. Some studies have attempted to link the two PSF mechanisms by addressing the direct role of saprophytic microbes in mediating litter decomposition (Knops *et al.*, 2002; Miki *et al.*, 2010). However, the indirect interactions between root-associated microbes and litter dynamics are rarely investigated, despite the potential ubiquity of such interactions (Manning *et al.*, 2008). For example, although root-associated microbes can cause PSF directly by affecting plant demography (e.g. growth and population dynamics), root-associated microbes can also indirectly influence nutrient cycling by controlling plant litter input and nutrient uptake (Mitchell, 2003; van der Heijden *et al.*, 2008). Similarly, a change in nutrient cycling due to litter-mediated PSF can influence population sizes of root-associated microbes by altering plant–microbe interactions (Wardle, 2006; Orwin *et al.*, 2011). Thus, a trait can influence PSF through both mechanisms due to the indirect interactions between litter dynamics and root-associated microbes. The relative importance of plant litter traits, traits mediating plant–microbial interactions and other population-level demographic traits (i.e. features that directly condition the population's finite rate of increase; Violle *et al.*, 2007) for plants and microbes in controlling PSF strength will remain unclear if the two mechanisms are examined independently.

The interdependency between the two mechanisms is characterized by the complexity of indirect interactions between litter dynamics and different root-associated microbes, but this feature has been neglected when treating the microbial community as a black box. Root-associated microbes from different functional groups (e.g. detrimental pathogens and beneficial mycorrhizal fungi) may affect litter dynamics through different processes. For example, pathogens may add dead plant materials to the litter pool by decreasing leaf longevity (Mitchell, 2003) and inducing additional plant mortality. By contrast, mycorrhizal fungi help the plant to deplete soil nutrients and can stimulate plant productivity (Read & Perez-Moreno, 2003; Orwin *et al.*, 2011). Changes in nutrient cycling processes can also result in variable indirect effects on pathogens and mycorrhizal fungi. For instance, increased nutrient availability might stimulate pathogen growth due to increased host plant productivity and tissue quality (Nordin *et al.*, 1998); however, the effects might suppress mycorrhizal fungi due to shifts in the nutrient limitation status of the microbes (Wallander, 1995; Treseder & Allen, 2002; Johnson, 2010). Because different root-associated microbes are involved in different indirect interactions with litter dynamics, the relative importance of traits could vary depending on the composition of root-associated microbes.

Given the above lines of evidence, studying the determinants of interspecific PSF variation requires consideration of: (1) the indirect interactions between litter- and root-associated microbes; and (2) different microbial functional groups. Each trait should be investigated independently as a first step towards associating PSF with trait-based approaches. However, traits are often correlated and results are often confounded by the idiosyncratic nature of trait correlation, making experimental methods difficult. A modelling approach can circumvent this problem, which allows us to separate the effect of each trait without being confused by the different degrees of trait correlation. In this study, we present a model of plant–microbe–soil interactions coupling litter- and microbial-mediated PSFs. We considered detrimental soil-borne pathogens and beneficial mycorrhizal fungi to represent, respectively, the negative and positive extremes of direct plant–microbe interactions as these microbes are associated with the majority of plant species. Our goal was to identify which plant and microbial traits had the greatest effects on a species' PSF strength. We performed a simulation experiment to quantify the effects of each trait, and to examine how the relative importance of traits varies with the composition of root-associated microbes.

Description

Model framework

We develop a stage-structured plant–microbe–soil model, consisting of six state variables in an open ecosystem (Fig. 1; see

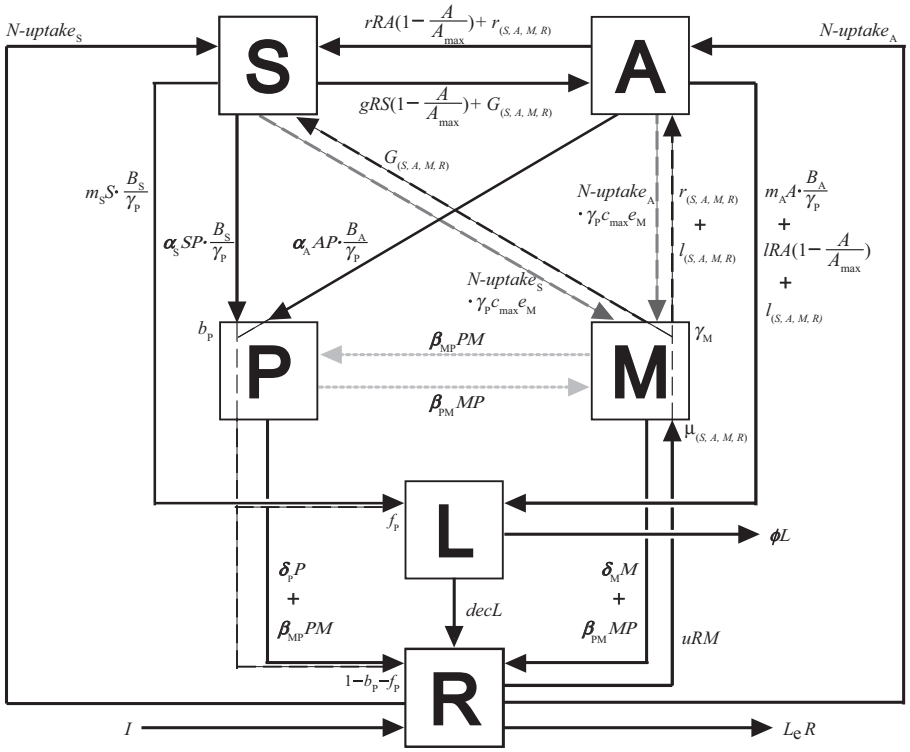

Fig. 1 Model flow diagram of the plant–microbe–soil model. Black lines represent N fluxes between various pools, including seedlings (S), adults (A), pathogens (P), mycorrhizal fungi (M), litter (L) and soil nutrient (R). Black dashed lines, nitrogen flux that flows to other pools after microbial assimilation. Dark grey dashed lines, carbon flux transferred from plants to mycorrhizal fungi. Light grey dotted lines, negative interactions between pathogens and mycorrhizal fungi. Symbols next to lines represent the magnitude of flux, whereas symbols next to state variables indicate the ratio of flux that is incorporated in the state variable. Plant N biomass and density are interchangeable by assuming fixed N content for each individual (i.e. B_S/γ_P and B_A/γ_P for individual seedling and adult, respectively, where B_S and B_A represent average seedling and adult individual C biomass, respectively, and γ_P is plant tissue C : N ratio). See Supporting Information Methods S1 and Table 1 for detailed model description, equations and parameters.

Supporting Information Table S1, and Methods S1 for detailed model description). The model includes two stages of plants, seedlings and adults (with densities S and A, respectively), as seedlings and adults interact with PSF drivers differently. We include pathogens and mycorrhizal fungi as representatives of direct microbial-mediated PSF, with nutrient content P and M, respectively. Nutrient content represents the nutrient biomass stored in microbes, and is used as the index for microbial abundance. To describe litter-mediated PSF, we consider nutrient content stored in organic litter (L) that is unavailable for plant uptake, and dissolved nutrients in soil solution that are available for plants (R). Due to N limitations often observed in terrestrial ecosystems, and the increased recognition of the role which mycorrhizal fungi (especially arbuscular mycorrhizal fungi) play in N uptake (Veresoglou *et al.*, 2012; Phillips *et al.*, 2013), we parameterize the dynamics of R and other flows within the model based on N cycling processes. N fluxes between various pools are represented by black lines in Fig. 1. The applicability of our model on phosphorus cycling (e.g. as proposed by Perring *et al.*, 2008) is discussed in Notes S1.

Here, we highlight key flows within our plant–microbe–soil model framework. Plants take up available soil N (i.e. $N\text{-}uptake_S$ and $N\text{-}uptake_A$ for seedlings and adults, respectively). Plant N uptake flux increases linearly with available-N (R), but decreases due to light competition following canopy closure (i.e. as adult density approaches A_{max}; see Table 1 for parameter definition). Seedlings allocate N uptake to biomass growth and mature to adults, whereas adults allocate N to reproduction and tissue production. The demographic trait per unit N uptake for growth, reproduction and tissue production is g, r and l, respectively. We assume that atmospheric carbon (C) is not a limiting factor for plant growth (but organic C is a limiting factor for microbes, discussed later). The amount of plant C fixation is determined by plant N uptake, light availability and plant tissue C : N ratio (γ_P).

Plants increase C fixation (i.e. to 1 + C_{max} times of the original value) when mutualistic associations are formed and release the additional fixed C as root exudations for benefit exchange (Cowden & Peterson, 2009; dark grey dashed lines in Fig. 1), whereas mycorrhizal fungi acquire N from the soil (uptake coefficient u) in exchange for plant photosynthetic C products. We exclude the case where plant–mycorrhiza interactions become parasitic to ensure mutualistic relationships (but see Johnson *et al.*, 1997 for studies related to the 'mutualism–parasitism continuum'), and assume that the exchange flux between the two organisms is determined by comparing the amount of mycorrhizal C demands (i.e. C requested by the fungi to maintain its C : N ratio, γ_M) and plant C supplies. Mycorrhizal fungi will transfer excess N to the plant (black dashed lines between mycorrhizal fungi and plants in Fig. 1) after meeting its own metabolic demands (i.e. C-limited status), but if the mycorrhizal fungi is also N-limited, the fungi will keep N for its own use (Treseder & Allen, 2002; Alberton *et al.*, 2007; Johnson, 2010; Näsholm *et al.*, 2013). After benefit exchange, mycorrhizal fungi utilize C for population growth (i.e. $\mu_{(S,A,M,R)}$ in Table S2), whereas plants allocate the N to further enhance seedling maturation, reproduction and tissue production (i.e. $G_{(S,A,M,R)}$, $r_{(S,A,M,R)}$, and $l_{(S,A,M,R)}$ in Table S2, respectively).

Both seedling and adult stages suffer natural mortality (with rate m_S and m_A) and pathogen infection (with infection efficiency

Table 1 Model state variables and parameters

Symbol	Interpretation	Units	Default
S	Seedling density	ind. m^{-2}	–
A	Adult density	ind. m^{-2}	–
M	Mycorrhizal fungi nitrogen content	g N m^{-2}	–
P	Pathogen nitrogen content	g N m^{-2}	–
L	Litter nitrogen content	g N m^{-2}	–
R	Soil nitrogen content	g N m^{-2}	–
r	**Plant reproduction rate per unit nitrogen uptake**	g N^{-1} m^2 d^{-1}	0.3
g	**Seedling biomass growth rate per unit nitrogen uptake**	g N^{-1} m^2 d^{-1}	9×10^{-7}
m_A	**Adult mortality rate**	d^{-1}	0.00005
m_S	**Seedling mortality rate**	d^{-1}	0.008
l	**Litter production rate of adults per unit nitrogen uptake**	ind.$^{-1}$ m^2 d^{-1}	0.008
dec	**Litter decomposition rate**	d^{-1}	0.006
γ_P	**Plant tissue carbon: nitrogen ratio**	g C g N^{-1}	60
α_S	**Pathogens infection efficiency of seedling**	g N^{-1} m^2 d^{-1}	0.008
α_A	**Pathogens infection efficiency of adult**	g N^{-1} m^2 d^{-1}	$\alpha_S \times 10^{-4}$
b_P	**Pathogen assimilation ratio of plant nitrogen**	dimensionless	0.6
δ_P	**Pathogen mortality rate**	d^{-1}	0.01
f_P	**Litter return ratio following pathogen infection**	dimensionless	0.35
u	**Mycorrhizal nitrogen uptake coefficient**	g N^{-1} m^2 d^{-1}	0.06
c_{max}	**Maximum carbon transfer ratio from plant**	dimensionless	0.3
e_M	**Mycorrhizal carbon assimilation ratio**	dimensionless	0.6
γ_M	**Mycorrhizal carbon: nitrogen ratio**	g C g N^{-1}	8
δ_M	**Mycorrhizal mortality rate**	d^{-1}	0.01
β_{MP}	**Competition coefficient of mycorrhiza on pathogen**	g N^{-1} m^2 d^{-1}	0.005
β_{PM}	**Competition coefficient of pathogen on mycorrhiza**	g N^{-1} m^2 d^{-1}	0.005
n_{min}	Minimum nitrogen transfer ratio of mycorrhiza	dimensionless	0.2
B_A	Carbon biomass of individual adult	g C ind.$^{-1}$	130 000
B_S	Carbon biomass of individual seedling	g C ind.$^{-1}$	10
I	Nitrogen deposition flux to the ecosystem	g N m^{-2} d^{-1}	0.005
L_e	Soil nitrogen leaching rate	d^{-1}	0.0002
ϕ	Litter leaching rate	d^{-1}	0.00008
A_{max}	Carrying capacity due to light limitation	ind. m^{-2}	0.5

ind., individual.

α_S and α_A), and dead plant material enters the plant-unavailable litter pool. The amount of N being transferred is calculated by the number of dead individuals multiplied by N content per individual (see Fig. 1 legend). The litter pool also increases due to turnover of adult plant tissue production (i.e. annual litter production). This flux is assumed to be produced only by adults, whereas the contribution from seedlings is negligible due to their relatively small size. For plant–pathogen interactions, we assume that adults suffered less from pathogen infection compared with seedlings due to their stronger physical protection (Reinhart *et al.*, 2010). Plants suffer additional mortality following pathogen infection (e.g. resulting in seedling mortality within a few weeks; Bagchi *et al.*, 2010; Alvarez-Loayza & Terborgh, 2011), and pathogens only acquire N by assimilating the N stored within plant material. A fraction of N within pathogen-induced dead plant material is incorporated into pathogen N content (i.e. pathogen assimilation ratio, b_P), whereas other fractions accumulate as litter or are mineralized back into the soil N pool (i.e. f_P and $1 - b_P - f_P$, respectively; black dashed lines between pathogens and litter pool in Fig. 1). By considering these linkages, our model explicitly couples litter- and microbial-mediated PSF together.

Nitrogen is released from biological components through litter decomposition, which is assumed to be determined primarily by plant physiological properties (Cornwell *et al.*, 2008) and follows first-order exponential decay (with plant litter decomposability denoted as dec). N stored within pathogens and mycorrhizal fungi is also released back to the soil N pool due to natural mortality (with rate δ_P and δ_M) and mortality caused by negative interactions between microbes (with competition coefficient β_{MP} and β_{PM}, represented by light grey dotted lines in Fig. 1; Wardle, 2006; Rasmann *et al.*, 2011). In our open ecosystem model, total N within the system is influenced by external forcing, including deposition (I), and N loss via leaching of both plant-available and -unavailable N, with leaching rates L_e and ϕ, respectively.

Model analysis and simulation experiments

We quantified the PSF strength by simulating a growth experiment in a glasshouse that compared seedling growth response in conspecific- and heterospecific-cultured soils (Klironomos, 2002; Brinkman *et al.*, 2010; Mangan *et al.*, 2010). This simple method successfully predicts community properties, especially when changes in soil environments are realized locally (Wakano, 2007; Ushio *et al.*, 2010) and when competition is less severe (e.g. seedlings in tropical forests, Paine *et al.*, 2008) (but see Hendriks *et al.*, 2013, for other calculation methods when these conditions are not met). More specifically, we considered two hypothetical plant species: a reference plant species (*ref*) with trait values calculated from empirical studies (Table 1; Methods S2) and a target plant species (*tar*).

We emphasized potentially important functional and demographic traits of both plants and microbes (bold typeface in Table 1), where microbial trait values represent the community-averaged value for the root-associated microbial group (i.e. pathogens or mycorrhizal fungi). The contribution of each trait to PSF strength was quantified by setting the target plant species to deviate only one trait value from the reference plant species at a time. A deviation of a microbial trait within the pathogen or mycorrhizal fungi community can be interpreted as a difference in dominant species within the pathogen or mycorrhizal fungi community

under the influence of the target plant species. Deviations for target trait values were set to either ± 50% or ± 20%, depending on the composition of root-associated microbes (discussed later).

The effects of different plant species (i.e. the *ref* and *tar* plant species) on the soil environment through cultivation were simulated by running the model numerically to equilibrium with parameters of both reference and target plant species (Methods S3; Stage 1 in Fig. 2). The equilibrium values of soil N (R_k^*) and root-associated microbes (P_k^* and M_k^*) were recorded to represent the specific properties of the soil cultivated by plant species k, and the difference between R_k^*, P_k^* and M_k^* when $k = ref$ or tar represents trait-specific effects on the soil environment.

The PSF strength for the target plant species was quantified by comparing its seedling growth in soils with different cultivation histories (i.e. the *ref*- and *tar*-cultivated soil). We formulated a submodel (Table S3) to simulate the seedling growth dynamics of the target plant species under glasshouse conditions (Stage 2 in Fig. 2). The submodel considers seedling growth, growth enhancement by mycorrhizal fungi, natural mortality and pathogen infection, which were all the same as the original model (in terms of model formulation and parameter value). However, in order to simulate seedling growth under glasshouse conditions, the submodel does not consider adult reproduction and shading effects from adults. In addition, as the dynamics of adult density only act as a surrogate for seedling growth response under glasshouse conditions, the submodel does not consider adult mortality and litter dynamics. Previously recorded equilibrium values (i.e. R_k^*, P_k^* and M_k^*) were used to replace the corresponding state variables (i.e. R, P and M) in the submodel, and were assumed to be constant during simulations. This assumption is based on observations that seedling growth is determined primarily by historical legacies, and that soil cultivation effects by seedlings are relatively small during its growth in glasshouse experiments (Kulmatiski & Beard, 2011). We ran the submodel simulation until all seedlings were either dead or had matured (i.e. until seedling density approaches zero; see Methods S4 for detailed numerical methods). The growth response of target plant species' seedlings (i.e. biomass produced) in soil k is represented by $A_{tar,k}^{**} \times B_A$, where $A_{tar,k}^{**}$ is the adult density in soil k. The PSF strength for the target plant was determined by comparing the growth response in the two different soils as follows:

$$PSF_{tar} = \log\left(\frac{A_{tar,tar}^{**} \times B_A}{A_{tar,ref}^{**} \times B_A}\right)$$

Positive (or negative) PSF_{tar} indicated that the growth of the target plant species was promoted (or suppressed) in conspecific-cultivated soils due to deviation of the specific trait from the reference plant species.

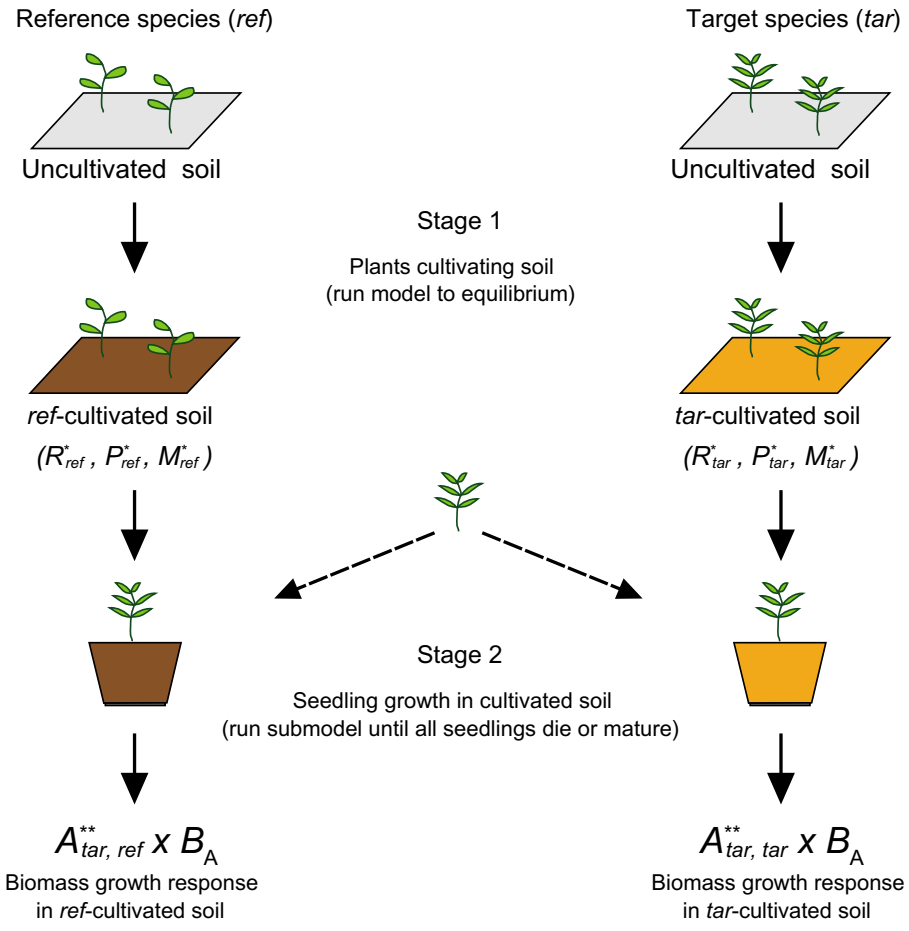

Fig. 2 Schematic diagram of plant–soil feedback (PSF) growth simulation experiment. Stage 1 represents plants cultivating nearby soils (run model to equilibrium), and Stage 2 represents growth dynamics of the target plant species' seedlings (run submodel to until all seedlings have either died or matured). Initial conditions for soil cultivation simulation (model in Supporting Information Table S1) were set as ($S(0)$, $A(0)$, $M(0)$, $P(0)$, $L(0)$, $R(0)$) = (10, 0.05, 5.0, 5.0, 10.0, 10.0) for all simulations, and no alternative stable state was detected within our parameter space. The initial condition for seedling growth simulation (submodel in Table S3) was set as ($S_{tar}(0)$, $A_{tar}(0)$) = (20, 0).

In order to investigate the effect of the composition of root-associated microbes on the relative trait importance, we performed the above analysis on each trait under the following hypothetical systems considering: (1) only litter-mediated PSF without any root-associated microbes ($P = M = 0$); (2) litter-mediated PSF and pathogens as representative of microbial-mediated PSF ($P > 0$, $M = 0$); (3) litter-mediated PSF and mycorrhizal fungi ($P = 0$, $M > 0$); and (4) litter-mediated PSF with both groups of root-associated microbes (P, $M > 0$), each with a different number of highlighted traits. By comparing the results across different scenarios, we investigated how the relative trait importance was dependent on the composition of root-associated microbes.

Deviations for target trait values were set to ± 50% or ± 20% for scenarios without or with mycorrhizal fungi, respectively. Trait deviation was smaller when mycorrhizal fungi were included in order to retain a realistic value for mycorrhizal C assimilation ratio (e_M) (i.e. C assimilation is imperfect and thus e_M should be < 1). We assessed the robustness of results by allowing larger deviation of each trait (i.e. −90% to +200%) if ecologically reasonable (Notes S2), which covered trait values across one order of magnitude and is representative for variation among some functional and demographic traits (Cornwell *et al.*, 2008; Poorter *et al.*, 2008). We also verified result robustness by changing environmental parameters (i.e. either ± 50% or ± 20%; Notes S1), and by randomly varying other trait values simultaneously (i.e. considering different degrees of trait correlation; Notes S2).

Empirical support of model predictions

We compiled a dataset to test our prediction that the composition of root-associated microbes (i.e. pathogens or mycorrhizal fungi) altered the relative importance of traits on PSF strength, with specific focus on changes in the influence of species' litter decomposability on PSF. The results from Schnitzer *et al.* (2011) (within their appendix D, Ecological Archives E092-026-A4) were applied, which independently quantified PSF strength generated by either the pathogen-only or mycorrhiza-only fraction of the cultivated soil, because litter decomposability data for many plants used in other PSF studies (e.g. Klironomos, 2002; Maron *et al.*, 2011) are not available. Based on plant species used in Schnitzer *et al.* (2011), we compiled a dataset of first-order decay constants for litter decomposition (i.e. *dec* in our model) from other publications (see Table S4 for detailed information on acquired data). When percentage mass loss within a given time period was presented in graphs, *Digital Curve Tracer* was used to digitize the mean value and *dec* was subsequently calculated by: $dec = -\log_e(1 - \text{percentage mass loss})/\text{time}$. The relationship between species' PSF (resulting from either the mycorrhizal fungi or pathogen fraction) and its litter decomposability was investigated separately using linear regression. The bias-corrected 95% bootstrap confidence interval was generated from 4999 iterations, and a relationship was considered significant if the confidence interval did not include zero (Adams *et al.*, 1997).

Results

Litter-mediated PSF without any root-associated microbes

Litter and plant tissue quality traits were most important in determining PSF strength under the scenario with only litter-mediated PSF (Fig. 3a). A higher litter decomposability (*dec*) of the target plant species resulted in higher soil N content compared with soils cultivated by the reference plant species (i.e. $\Delta R^* > 0$, Fig. S1), thus creating positive PSF. A higher tissue C : N ratio (γ_P) also generated positive PSF for the target plant species. As we assumed fixed plant individual C biomass, and independency between plant tissue C : N ratio and litter decomposability rate, higher tissue C : N ratio implies lower N demand for plants and will cause more N to remain in nearby soils. By contrast, a target plant with a higher adult mortality rate (m_A) resulted in negative PSF as soil N availability decreased due to weaker light competition and greater plant N uptake (Notes S3; Fig. S2).

Litter-mediated PSF and pathogens

Traits related to plant defence against pathogens were most influential in determining PSF strength under the scenario with litter and pathogens. Higher values for the plant tissue C : N ratio, pathogen mortality rate (δ_P) and seedling biomass growth rate per unit N uptake (g) resulted in the strongest positive PSF for the target plant species (Fig. 3b). This result was due to the combined effect of increased soil N (i.e. $\Delta R^* > 0$, Fig. S3) and decreased pathogen N content (i.e. $\Delta P^* < 0$, Fig. S3) in the cultivated soil. A high pathogen assimilation ratio (b_P) of plant tissue resulted in the strongest negative PSF due to an increased pathogen N content, despite the accompanying increase in soil N. A greater plant reproduction rate per unit N uptake (r) also generated negative PSF due to increased pathogen N content and decreased soil N. However, litter decomposability had a small effect on PSF strength under this scenario, compared with other common traits shared in the scenario with only litter-mediated PSF. This is because the benefits of increased soil N caused by higher litter decomposability were offset by increased pathogen N content.

Litter-mediated PSF and mycorrhizal fungi

Traits related to plant tissue and litter quality, as well as those related to mycorrhiza nutrient acquisition were most influential in determining PSF strength under the scenario with litter and mycorrhizal fungi. Higher plant tissue C : N ratio, plant C transfer ratio (c_{max}) and mycorrhizal C assimilation ratio (e_M) (i.e. traits related to C exchange) resulted in strong positive PSF for the target plant species (Fig. 3c). The positive PSF was due to increased mycorrhizal N content (i.e. $\Delta M^* > 0$, Fig. S4), despite depleted soil N (i.e. $\Delta R^* < 0$, Fig. S4). Although the resulting PSF strength is weaker compared with that of plant tissue C : N ratio, litter decomposability showed higher relative importance compared with other common traits shared in previous scenarios (i.e. comparing Fig. 3b,c). The positive PSF for target plant species with higher litter decomposability resulted from a synergistic

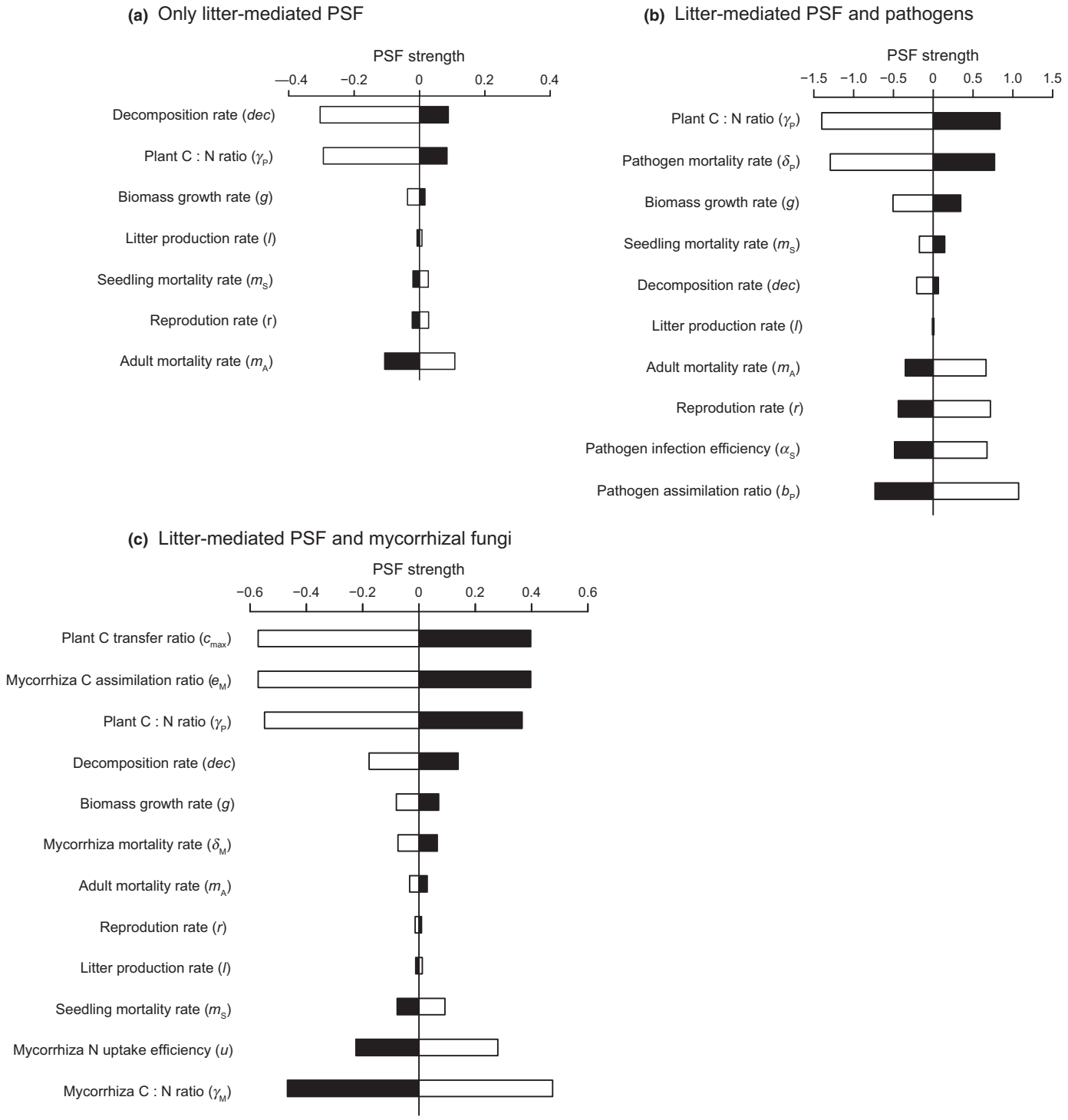

Fig. 3 Relative importance of traits for controlling plant–soil feedback (PSF) strength when considering (a) only litter-mediated PSF, (b) litter-mediated PSF with pathogens and (c) litter-mediated PSF with mycorrhizal fungi. Closed (or open) bars represent PSF strength when a specific trait was positively (or negatively) deviated from that of the reference plant. Trait deviations were set to ± 50% for scenarios (a) and (b), and ± 20% for scenario (c). Traits were sorted within each scenario by the PSF strength resulting from the positive deviation of each trait.

increase in both soil N ($\Delta R^* > 0$) and mycorrhizal fungi ($\Delta M^* > 0$). Positive deviations of other mycorrhizal traits, including mycorrhizal N uptake coefficient (u) and mycorrhizal C : N ratio (γ_M), demonstrated decreased soil and mycorrhizal N content, respectively, and were thus influential in determining negative PSF.

Litter-mediated PSF and both groups of microbes

We examined the relative importance of traits under two specific microbial interaction scenarios: symmetric negative effect between microbes due to competition (β_{MP}, $\beta_{PM} > 0$) (Fig. S5), and unidirectional impact of mycorrhizal fungi on pathogens via

the production of antimicrobial metabolites ($\beta_{MP} > 0$, $\beta_{PM} = 0$) (Fig. S6). Plant tissue C : N ratio and microbial nutrient acquisition ability were influential in both scenarios; however, the relative importance of some traits varied. We specifically emphasized the PSF strength resulting from higher litter decomposability (i.e. +50% in trait value) under different interaction strengths between the two groups of microbes (i.e. by continuous changes in β_{MP} and β_{PM}, Fig. 4a). This analysis allowed us to detect changes in the effect size of litter decomposability with alterations in the relative abundance of pathogens and mycorrhizal fungi (i.e. $M^*/(M^* + P^*)$, Fig. 4b). When negative effects between microbes were symmetrical (i.e. $\beta_{MP} \approx \beta_{PM}$), or the effects of pathogens on mycorrhiza were stronger (i.e. $\beta_{MP} < \beta_{PM}$), mycorrhizal fungi showed low relative abundance. Under these scenarios, the PSF strength resulting from higher litter decomposability was weak, corresponding to the pathogen-only system (Fig. 3b). Note that under these scenarios negative PSF could occur because the benefits of increased soil N – caused by higher litter decomposability – were accompanied by increased pathogen level. By contrast, the effects of litter decomposability were larger when the negative impacts of mycorrhizal fungi on pathogens were stronger (i.e. $\beta_{MP} > \beta_{PM}$). The relative abundance of mycorrhizal fungi was higher under these scenarios, resulting in a high importance of litter decomposability based on factors similar to the mycorrhizal fungi-only scenario (Fig. 3c).

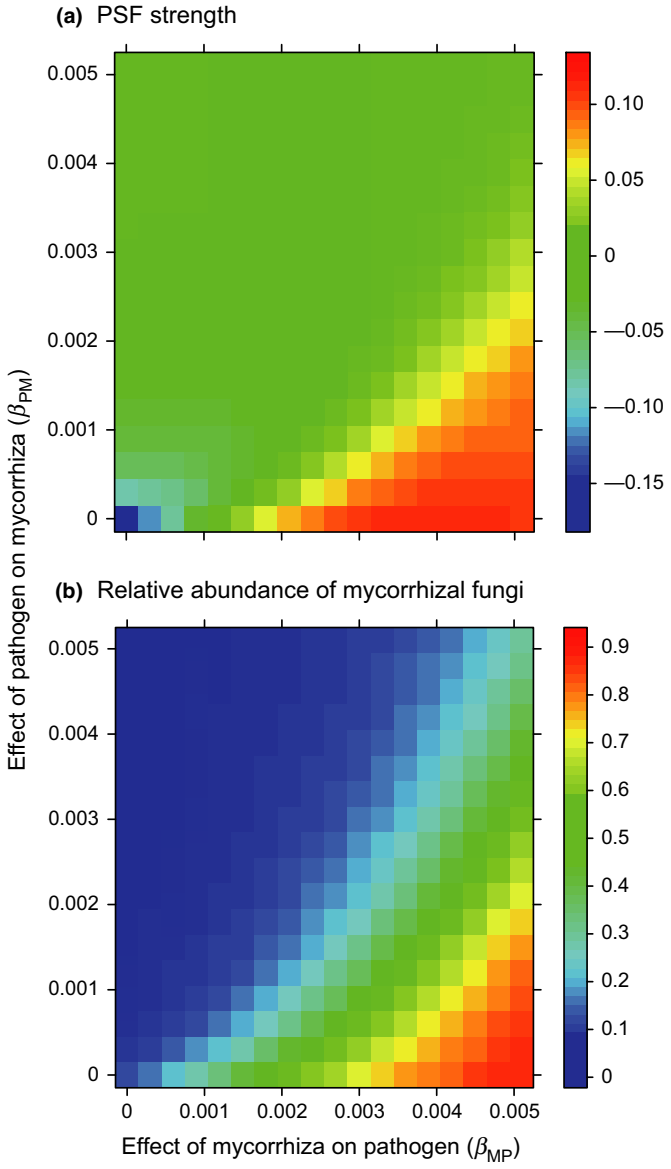

Fig. 4 Effects of higher litter decomposability on (a) plant–soil feedback (PSF) strength and (b) mycorrhizal relative abundance at equilibrium under different interaction scenarios between pathogens and mycorrhizal fungi. Warmer colours represent stronger positive PSF strength and higher mycorrhizal fungi relative abundance for (a) and (b), respectively. Litter decomposability was increased by +50% for the target plant species in this analysis.

Robustness of results

Overall, the results were qualitatively robust. Our results remained the same across a range (i.e. either ± 50% or ± 20%) of deposition flux (I), soil-N leaching rate (L_e), litter leaching rate (ϕ) and carrying capacity due to light-limitation (A_{max}) (see Notes S1 and Fig. S7 for corresponding fluxes of such variation). The most influential traits remained unchanged and did not show nonmonotonic patterns when we allowed larger, but realistic, trait deviations (i.e. −90% to +200%, corresponding to one order difference in trait value; Notes S2; Fig. S8). Important traits also remained influential when other trait values, in addition to the specific trait, were randomly assigned simultaneously (i.e. results were robust for randomly assembled target plant species; Fig. S9).

Empirical support of model predictions

Our modelling results suggested that the relative importance of species' litter decomposability on PSF strength would be stronger in mycorrhizal-dominated than in pathogen-dominated soils. Data compiled from multiple empirical studies (Table S4) showed a significant positive relationship between species' PSF and its litter decomposability when considering PSF strength generated by mycorrhizal fungi (95% CI for regression coefficient: 98.583–1218.247; Fig. 5a). However, no significant relationship was detected when only the pathogen fraction of the cultivated soil was included (95% CI: −323.991 to 863.101).

Discussion

Important traits under different microbial community composition

Ecologists have shown increasing interest in elucidating how functional and demographic traits of plants determine community properties and ecosystem processes (de Bello *et al.*, 2010). The present study aimed to identify the relative importance of traits on PSF strength by considering the interdependency between litter- and microbial-mediated PSF. In the absence of direct-interacting root-associated soil microbes, litter

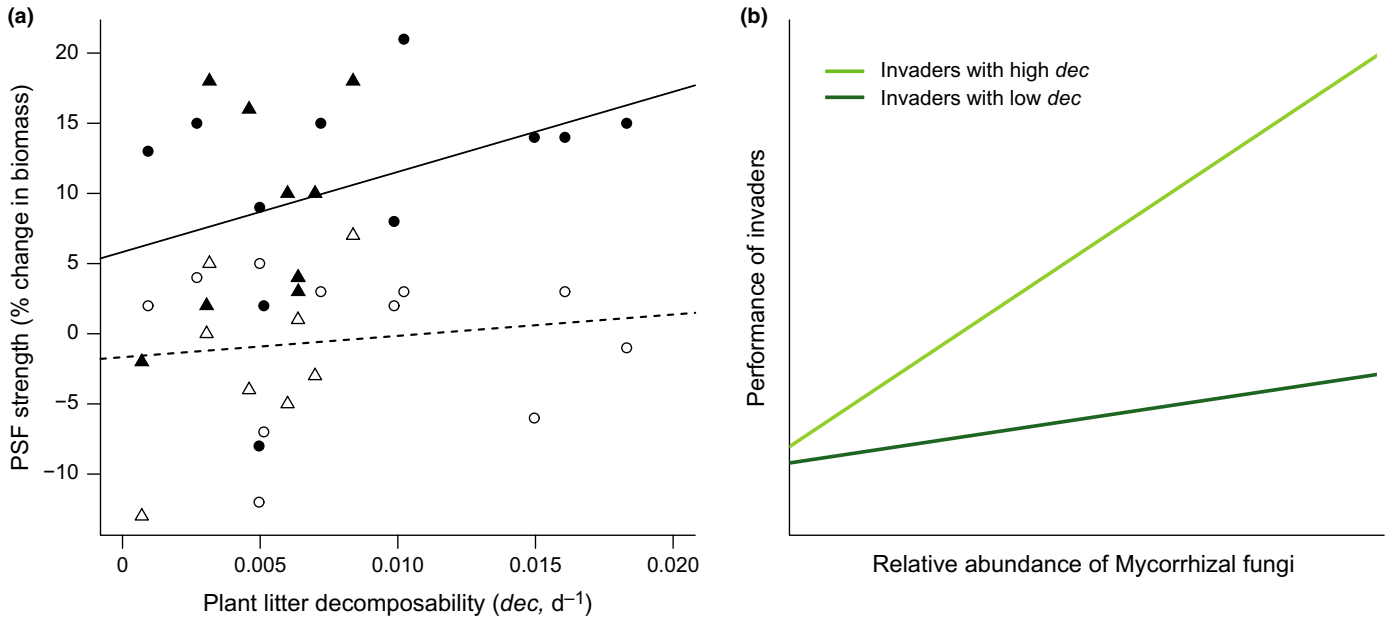

Fig. 5 Model predictions and empirical support. (a) The relationship between species' litter decomposability and plant–soil feedback (PSF) resulting from either mycorrhizal fungi (closed symbols and solid line) or pathogens (open symbols and dashed line). The average litter decomposability value was used when multiple data sources were found, whereas those of closely related species were used when data for the plant species was not available. Circles and triangles indicate litter decomposability obtained from the exact same plant as that used in Schnitzer *et al.* (2011) and from closely related species, respectively. (b) Predicted relationship between invader performance and relative abundance of mycorrhizal fungi. The performance difference between plants with high (light green) and low (green) litter decomposability would increase with increasing mycorrhizal fungi abundance.

decomposability was influential in determining PSF strength (Fig. 3a). Plant species that produce easily decomposing litter can accelerate N release from plant-unavailable organic matter, creating an N-rich environment and achieve growth advantages through positive PSF (Berendse, 1994; Miki & Kondoh, 2002; Farrer & Goldberg, 2009). Although plant tissue C : N ratio and litter decomposability can be negatively correlated, we examined the two traits independently (Kurokawa & Nakashizuka, 2008) to detect their effects. By assuming fixed plant C biomass, higher tissue C : N ratio implies a conservative uptake strategy and less N demand in order to put on the same amount of C biomass. As plant density in our model is limited by light, higher C : N ratio results in more N remaining and will benefit its own seedlings. Our model also predicted counterintuitive results that plants with higher adult mortality rates will experience strong negative PSF. Plants with such characteristics create a less dense canopy, which can stimulate plant N uptake as plants become less light-limited. Subsequently, less soil N will be remaining and have negative feedback on future seedling growth (Notes S3; Fig. S2). As plant N uptake was assumed to increase linearly with the soil N pool, we speculate that the impact of traits on PSF through soil N cycling would decrease when a saturating functional response is considered.

Plant defence traits are highly influential in determining PSF strength when the root-associated microbial community is dominated by pathogens (Fig. 3b). Plant roots can exhibit a notable variety of defence strategies (van Dam, 2009; Rasmann *et al.*, 2011), which can suppress soil pathogen levels by acting as a nutrient-insufficient resource (e.g. higher wood density and C : N ratio; Augspurger & Kelly, 1984; Chave *et al.*, 2009), by increasing pathogen mortality rate, or by decreasing pathogen assimilation ratio (Fig. S3). Our results also indicate that demographic traits can strongly influence PSF in pathogen-dominated soils. For example, faster seedling maturation can create positive PSF by shortening the time-period when plants are most susceptible to disease (Reinhart *et al.*, 2010), whereas higher reproduction rates will create negative PSF by supporting larger pathogen abundance (Bagchi *et al.*, 2010).

When mycorrhizal fungi are dominant, plants transferring higher ratios of C product to mycorrhizal fungi, and plants associated with mycorrhizal fungi with higher C assimilation ratios will experience strong positive PSF (Fig. 3c). Assuming that N is the limiting factor for plant photosynthesis, these traits would allow greater benefit exchange per unit N uptake and increase mycorrhizal abundance (Fig. S4) (Fellbaum *et al.*, 2012). Alternatively, plants experience negative PSF when plant–microbial interactions result in the dominance of mycorrhizal fungi with higher N uptake coefficients and C : N ratios. Such traits result in stronger N immobilization by the mycorrhizal fungi (Alberton *et al.*, 2007; Näsholm *et al.*, 2013) and larger C demand to maintain its stoichiometry (Wallander, 1995; Treseder & Allen, 2002; Johnson, 2010). This will lead to lowered mycorrhiza abundance due to mycorrhizal C starvation, resulting in inferior seedling growth in self-cultivated soils.

Effects of microbial composition on the relative importance of litter-mediated PSF

We found that different groups of root-associated microbes (i.e. pathogens and mycorrhizal fungi) were involved in different

indirect interactions with litter dynamics, and thus influencing the importance of litter decomposability differently. The relative importance of litter decomposability compared with other traits was low when pathogens were dominating (Figs 4, S5). This is because although a higher litter decomposability of the target plant can enhance nutrient cycling, the resulting increase of plant population (especially seedlings) will also increase pathogen levels thus cancelling out any beneficial effects. Our model considers the short-term mortality effect of pathogen infection on plant individuals (especially for seedlings, Bagchi *et al.*, 2010; Alvarez-Loayza & Terborgh, 2011), which may increase litter pool by increasing dead plant material. Our model also includes the long-term decrease in litter production at the population level. In particular, as pathogen infection increases plant mortality rate, it leads to shorter expected individual lifetime and smaller population size, thus causing reduced lifetime litter production. Although we neglected biomass reduction (i.e. poor growth) before infected individuals die, which operates at even shorter-term, the rapid mortality of seedlings following infection observed in empirical studies might suggest that this physiological response of seedlings is minor given its small size. Moreover, from our modelling results one can note that the relative importance of litter production rates (l) was generally low (Figs 3, S5, S6). Although further investigation should be made, these results imply that the effect of production change of infected plant individuals on soil properties may have a minor effect when focusing on the long-term impact of plant population on soil properties.

In contrast, litter decomposability had a stronger positive effect on PSF strength when mycorrhizal fungi were abundant (Figs 4, S6). Mycorrhizal hyphae can grow into soil micropores, allowing their hosts to further deplete soil nutrients (Veresoglou *et al.*, 2012). The mycorrhiza-enhanced nutrient uptake increases plant tissue production and litter accumulation (Orwin *et al.*, 2011). Under this scenario, plants producing rapidly decomposing litter allow faster nutrient release from the mycorrhiza-enhanced litter accumulation to the N-depleted soil, resulting in a synergistic increase of soil N content and mycorrhizal abundance. The benefits of higher litter decomposability are therefore amplified by the indirect interactions between mycorrhizal fungi and litter dynamics. Our prediction is supported by other studies demonstrating that mycorrhizal fungi can enhance soil C accumulation by increasing plant primary production and litter input (Read & Perez-Moreno, 2003; Orwin *et al.*, 2011).

Our findings suggest that the community of root-associated microbes can be viewed as a spectrum, with pathogen- and mycorrhiza-dominated soils at the two extremes. The positive effects of higher litter decomposability, and potentially its relative importance to determining PSF, would increase with the relative abundance of mycorrhizal fungi (Fig. 4). This prediction was supported by data compiled from empirical studies, which showed that species' PSF strength was significantly correlated with its litter decomposability in mycorrhizal-dominated soils, but not in pathogen-dominated soils (Fig. 5a). When detailed trait information is unavailable, examining differences in the interspecific PSF variation among different microbial compositions can be a less rigorous test. As trait variation among plants is fixed but influences PSF strength differently depending on the composition of root-associated microbes, the resulting variation in species' PSF would vary among different microbial fractions. Klironomos (2002) reported PSF strength for five invasive and five rare native species resulting from either mycorrhizal fungi or pathogen filtrate of the cultivated soil. Results found that invasive species exhibited greater PSF variation in mycorrhizal fungi soils compared with pathogen soils, whereas native species showed similar variation in the two soils (Fig. 2 in Klironomos, 2002). These empirical results support our prediction that the composition of root-associated microbes alters the importance of traits on PSF strength. In addition, comparing PSF between plant species with and without mycorrhizal associations is an additional approach to test our prediction. Further information on plant and microbial traits, as well as the relative abundance of different microbial functional groups, can facilitate better predictions of interspecific PSF variation.

Insights for exotic plant invasion success

Interactions between plant and soil have been increasingly recognized as an important factor determining the invasiveness of exotic plants (Reinhart & Callaway, 2006). Higher litter decomposability has been frequently suggested as a promising trait that promotes invasion (Liao *et al.*, 2008; Farrer & Goldberg, 2009) (although it is also possible that both high decomposition rate and invasion result from disturbance, Mack *et al.*, 2001). However, opposite observations have been reported (Drenovsky & Batten, 2007; Kurokawa *et al.*, 2010). Based on our results, we propose that plants with higher litter decomposability are most likely to become invasive when the invaded ecosystem has a higher abundance of mycorrhizal fungi compared with pathogens (e.g. the case when the invader is enemy-released and pathogens in the invaded ecosystem are specialist, thus not interacting with the invader; Klironomos, 2002; Mitchell & Power, 2003; Reinhart & Callaway, 2006). In contrast, higher litter decomposability is irrelevant in promoting invasion when the invaded ecosystem supports abundant pathogens (e.g. the case when pathogens in the invaded ecosystem are generalists, or the specialized pathogen of the invader accompanied the invasion; Eppinga *et al.*, 2006; Reinhart & Callaway, 2006), or when the invader in nonmycorrhizal (Pringle *et al.*, 2009). Our results can also be applied to plant restoration management. In particular, we would suggest that when mycorrhizal fungi are more abundant, plants with higher litter decomposability might be restored more readily (Eviner & Hawkes, 2008; Funk *et al.*, 2008).

A viable means to test our predictions is a comparison of the performance of invaders with different litter decomposability across multiple invaded sites. The performance of invaders with higher litter decomposability is predicted to increase more than invaders with lower litter decomposability as the relative abundance of mycorrhizal fungi increases (Fig. 5b). MacDougall *et al.* (2011) quantified microbial-mediated PSF strength for seven invasive species, and linked species' PSF strength with species relative abundance. Their results indicate that although both *Poa pratensis* and *Cytisus scoparius* experienced similar degrees of

enemy-release (i.e. suffered less from microbial-mediated PSF), *P. pratensis* was notably more abundant than *C. scoparius*. These results suggest that microbial-mediated PSF alone cannot fully predict the invasiveness of invaders. Other studies suggested that *P. pratensis* has higher litter decomposability (with $dec = 0.03\ d^{-1}$, averaged over three studies; Kemp *et al.*, 1994; Müller *et al.*, 2003; Vahdat *et al.*, 2010) than *C. scoparius* ($dec = 0.001\ d^{-1}$; Ganjegunte *et al.*, 2005). Together, these results support our prediction that plants with higher litter decomposability show increased benefit and are more invasive in enemy-released soils. A predictive test could also be developed to compare mycorrhizal and nonmycorrhizal plant species.

Future work and conclusions

While we considered the interdependency between litter- and microbial-mediated PSF specifically for pathogens and mycorrhizal fungi, other interactions and microbial groups can be incorporated into our framework. Past studies have shown how the functional diversity of saprophytic microbes influenced litter-mediated PSF (Miki *et al.*, 2010). Our model can be expanded to examine the diversity within the pathogen and mycorrhizal fungi group, and their differences in saprophytic ability. For example, ectomycorrhizal fungi may interact with litter-mediated PSF differently compared with arbuscular mycorrhizal fungi due to their higher saprophytic ability (Read & Perez-Moreno, 2003; Phillips *et al.*, 2013). Other microbial groups (e.g. nitrifying and N fixing microbes) may also change the relative importance of litter traits on PSF through their impact on nutrient cycling (Ehrenfeld, 2003; Hawkes *et al.*, 2005). In particular, N-fixing microbes provide plants with an alternativee pathway to obtain N (Stock *et al.*, 1995; Ehrenfeld, 2003), and thus they benefit the plant differently compared with mycorrhizal fungi and may weaken the importance of litter decomposability. Future studies can extend our framework to include competitive interactions among multiple plant species and their combined effects on soil properties (Miki & Kondoh, 2002; Bever *et al.*, 2010). This would be important when cost–benefit relationships are asymmetric for microbial-mediated PSF (Bever, 2002), and when consequences of litter-mediated PSF are also realized by the competitor (Yelenik & D'Antonio, 2013). Finally, in this study we focused on interspecific trait variation under the assumption that interspecific variation is greater than intraspecific variation (McGill *et al.*, 2006). However, with the increasing recognition of intraspecific trait variation (Albert *et al.*, 2010; Violle *et al.*, 2012), our approach of evaluating the relative importance of traits by altering single trait values can also be applied to discuss the role of intraspecific trait variation in plant–soil interactions.

To the best of our knowledge, this study is the first attempt to link plant and microbial traits with PSF strength using a modelling approach. We believe that integrating various PSF mechanisms (i.e. litter- and microbial-mediated PSF) and their related traits can shed new light on future PSF studies. Our approach can allow better predictions of the determinants of interspecific PSF variation and how important PSF processes are in structuring plant communities.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Trait-specific effect on soil N content for the scenario only considering litter-mediated PSF.

Fig. S2 Effects of adult mortality rate on plant N uptake and soil-N leaching dynamics when only considering litter-mediated PSF.

Fig. S3 Trait-specific effect on soil N content and pathogen N content for the scenario considering litter-mediated PSF and pathogens.

Fig. S4 Trait-specific effect on soil N content and mycorrhizal fungi N content for the scenario considering litter-mediated PSF and mycorrhizal fungi.

Fig. S5 Relative importance of traits for the scenario with litter-mediated PSF and both microbial groups when negative effects are symmetric between microbes.

Fig. S6 Relative importance of traits for the scenario with litter-mediated PSF and both microbial groups when the negative effect is unidirectional from mycorrhizal fungi on pathogens.

Fig. S7 Robustness of results under different environmental settings.

Fig. S8 PSF strength resulting from larger trait deviation from the reference plant species.

Fig. S9 Relative importance of traits for randomly assembled target plant species under different microbial compositions.

Table S1 Model equations and descriptions

Table S2 Model equations for plant demography enhancement by plant–mycorrhiza associations and growth of mycorrhizal fungi under different nutrient limitation status

Table S3 Submodel equations used for simulating PSF experiments

Table S4 Characteristics of studies and litter decomposability data included in the analysis

Methods S1 Details model description and equations.

Methods S2 Analytical and empirical justifications of parameter values for the reference plant species.

Methods S3 Submodel equations and detailed method used for simulating PSF experiments.

Methods S4 Processes of numerical simulation.

Notes S1 Effects of environmental parameters on the relative importance of traits.

Notes S2 Result robustness based on larger trait deviation and randomly assembled target plants.

Notes S3 Effects of adult mortality rate on soil N fluxes when only considering litter-mediated PSF.

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