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Relationships between plant–soil feedbacks and functional traits

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Abstract

1. Plant–soil feedbacks (PSF) and functional traits are two active but not well theoretically integrated areas of research. However, PSF and traits are both affected by life-history evolution, so the two should theoretically be related.
2. We provide a conceptual framework to link plant functional traits to two types of PSF metrics, and hypothesize that individual PSF (plant performance in conspecific vs. heterospecific soil) should be related to the fast–slow trait spectrum, whereas pairwise PSF (the sum of the individual feedbacks for two species growing in each other's soils) should be related to trait dissimilarity. We performed meta-analyses to test these hypotheses by compiling two datasets, one dataset consisting of individual PSF values and plant trait values (specific leaf area, SLA; leaf N concentration, LNC; specific root length, SRL; fine root diameter, FRD; plant height; seed mass), and the second consisting of pairwise PSF values and trait dissimilarity.
3. Our meta-analyses showed that individual PSF values were more negative in faster-growing species with greater SLA, LNC and SRL, supporting the growth–defence trade-off hypothesis. Plant height was positively correlated with individual PSF, perhaps because large, long-lived plants defend against pathogens better than smaller, shorter-lived plants. We also found that larger-seeded species had more positive or less negative PSF, likely reflecting greater tolerance of soil pathogens. The direction of relationships between trait dissimilarity and pairwise PSF varied with trait identity. Dissimilarities in SRL and FRD were negatively correlated with pairwise PSF while height dissimilarity was positively correlated with pairwise PSF. The contrasting relationships may reflect distinct links between trait dissimilarity and niche and fitness differences.
4. *Synthesis*. Our results demonstrate how an integration of PSF and trait-based approaches can advance plant community ecology.

KEYWORDS
functional traits, growth–defence trade-off, niche differentiation, phenotypic dissimilarity, plant–soil (below-ground) interactions, species coexistence, species-specialized pathogens/mutualists

1 | INTRODUCTION

Plant–soil feedbacks (PSF) express how plants interact with soil microbes and soil biogeochemical and physical properties. Negative PSF, where soil microbes and abiotic properties reduce plant performance, can theoretically contribute to species coexistence via conspecific negative density dependence (Bever et al., 2015; Kandlikar et al., 2019). This has provided a useful framework for evaluating the influence of soil microbes on community dynamics and biodiversity maintenance (Bever, 2003; Crawford et al., 2019; van der Putten et al., 2013). However, there is considerable variation in the strength of feedbacks observed across a broad range of species. This variation may reflect differences in local abiotic factors such as soil nutrients, moisture and climate factors (Bennett & Klironomos, 2019; De Long et al., 2019; Smith-Ramesh & Reynolds, 2017) or it could also be related to variation in plant functional traits (Bever et al., 2012; Ke et al., 2015). Although recent experimental studies tested the relationship between PSF and plant traits (Baxendale et al., 2014; Cortois et al., 2016; Kuťáková et al., 2018; Münzbergová & Šurinová, 2015; Semchenko et al., 2018; Teste et al., 2017; Wilschut et al., 2019), there remain gaps in the conceptual framework theoretically relating these two areas and a global test for this relationship.

Life-history evolution has produced distinct plant strategies that are positioned along the fast–slow trait spectrum. For example, plants can invest in traits that promote rapid growth (e.g. via nutrient acquisition) or in traits that provide defence against antagonists (Díaz et al., 2016; Weiher et al., 1999; Westoby, 1998) but not both to the same degree, which leads to a growth–defence trade-off. For seed traits, previous studies provide evidence for a trade-off between investment in numerous small seeds versus fewer larger seeds. The seed number–seed size trade-off predicts that small-seeded species have an advantage in fecundity and colonization, which may aid in pathogen escape through increased dispersal ability, whereas large-seeded species have greater seedling survival, competitive ability and pathogen tolerance (Bagchi et al., 2014; Dalling et al., 2011; Moles, 2018; Moles & Westoby, 2004; Muller-Landau, 2010). Plant height may indicate plant life span and competitive ability for light (Moles et al., 2009). A long-lived plant species, such as a tree, likely invests more in defence traits (e.g. structural traits, chemical defence) than a short-lived species, such as an herbaceous species, which should allocate more resources to nutrient acquisition or reproduction to maximize fitness (Kulmatiski et al., 2017).

Given the important roles of soil microbes in both nutrient acquisition and plant disease, we should expect relationships between PSF and the plant strategies traditionally linked with functional traits. Furthermore, plant traits should feed back to influence the composition and functioning of soil microbial communities by controlling the quality and quantity of resources entering into soil (Bardgett, 2017; de Vries et al., 2012; Delgado-Baquerizo et al., 2018; Legay et al., 2014). In other words, traits influence both the effect of a plant on the soil community and the response of the plant to the soil community. Based on the likely linkages between PSF and functional traits, we hypothesize a strong relationship between traits involved in the growth–defence trade-off and individual PSF (the absolute performance of a plant in conspecific soil vs. heterospecific soil; Figure 1a). Specifically, fast-growing plant species with traits, such as small seed size, short life span, high leaf N concentration (LNC), specific leaf area (SLA) and specific root length (SRL) and low fine root diameter (FRD), should experience more negative feedback effects than slow-growing plants with the opposite trait syndrome because the former have high growth rate/nutrient acquisition but low defence against natural enemies (Coley, 1988; Coley et al., 1985; Comas & Eissenstat, 2009; Laliberté et al., 2015; Lind et al., 2013; Teste et al., 2017).

In contrast to the individual PSF, pairwise PSF, which essentially represent the sum of the individual feedbacks for two species growing in each other's soils, should be related to ecological dissimilarity rather than absolute trait values. Negative values of pairwise PSF indicate that plants influence soils in a way that favours heterospecific over conspecific individuals, stabilizing coexistence through conspecific negative density dependence, whereas positive values indicate the opposite patterns (Bever et al., 1997). Crawford et al. (2019) recently showed that plant phylogenetic distance has a linearly negative correlation with pairwise PSF. However, Wandrag et al. (2020) showed that there was a divergent trend in feedback responses to soil biota with increasing phylogenetic distance, and thus it is difficult to predict feedback outcomes using phylogeny alone. This trend may reflect high trait similarity among closely related plants while trait similarity decreases—or at least becomes less predictable—with increasing phylogenetic distance. However, little is known about correlations between pairwise PSF and trait dissimilarity. Directly linking pairwise PSF to trait dissimilarity may be more powerful for understanding the role of PSF in species coexistence and biodiversity maintenance, but it remains a key knowledge gap.

Modern coexistence theory asserts that species coexistence depends on two non-exclusive processes, stabilizing differences, which promote coexistence, and average fitness differences, which promote competitive exclusion (Chesson, 2000, 2018). In theory, trait dissimilarity can reflect niche differences or average fitness differences, depending on the traits considered and the biotic and abiotic context (Kraft et al., 2015; Mayfield & Levine, 2010). If PSF and traits represent two aspects of a coordinated life-history strategy,

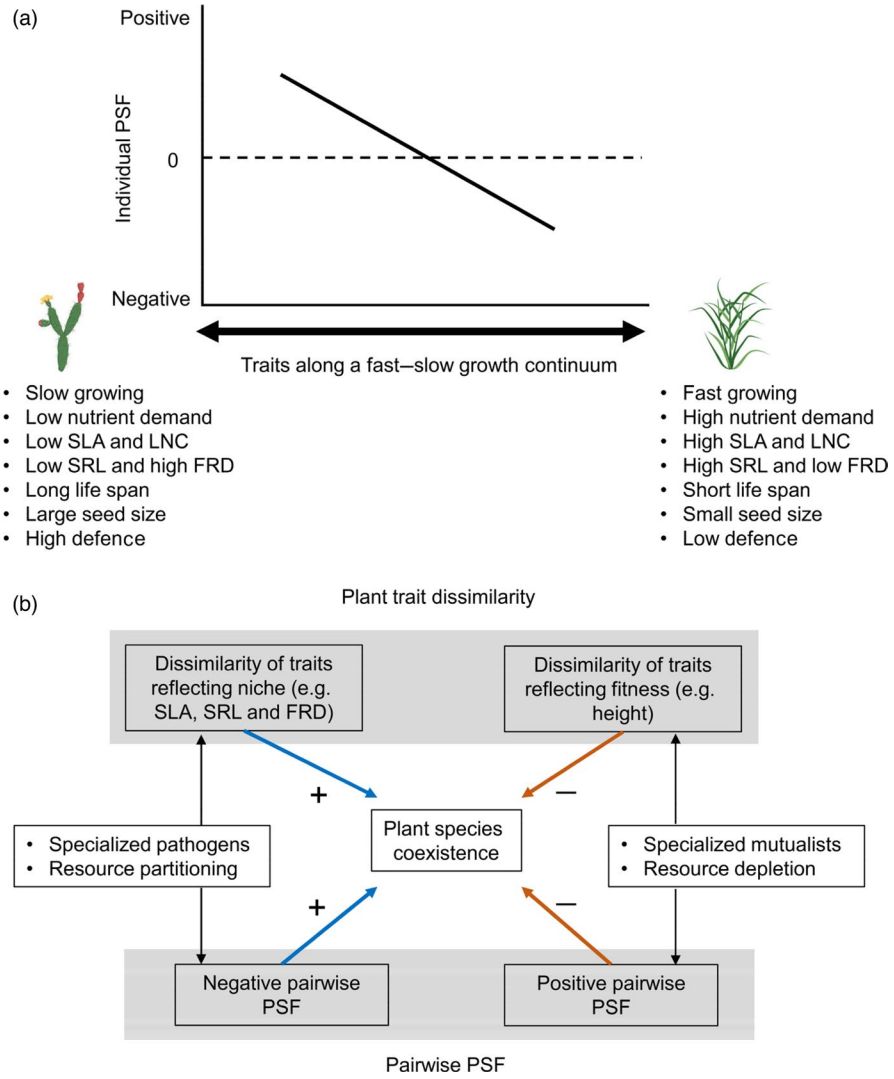

FIGURE 1 A conceptual framework connecting plant traits and plant–soil feedbacks (PSF) showing the key hypotheses tested in this study. (a) Individual PSF hypothetically varies with plant fast–slow growth continuum in accordance with the growth–defence hypothesis (Hypothesis 1). (b) Trait dissimilarity can lead to negative pairwise PSF when traits reflect resource niche partitioning or accumulation of specialized soil pathogens while they can correlate to positive pairwise PSF in cases where traits reflect average fitness differences driven by species-specialized mutualists or resource depletion. We predicted that trait dissimilarity is related to pairwise PSF (Hypothesis 2). The blue and red arrows indicate 'strengthening' (+) and 'weakening' (–) effects. SLA, specific leaf area; LNC, leaf N concentration; SRL, specific root length; FRD, fine root diameter

then their effects on coexistence should be reinforcing (Figure 1b): Negative pairwise PSF (i.e. species perform better in heterospecific than conspecific soil) should correlate with trait dissimilarities that contribute to niche differences by promoting use of different soil nutrients (such as SLA, SRL, Cadotte, 2017) or the accumulation of specialized soil pathogens (Smith-Ramesh & Reynolds, 2017). In contrast, positive pairwise PSF should correlate with trait dissimilarities that drive fitness differences favouring one competitor over the other regardless of their relative abundance, thereby reflecting competitive hierarchy (Chesson, 2000). For example, positive pairwise PSF have been observed in natural ecosystems such as ecto-mycorrhizal tree-dominated temperate forests (Nuñez & Dickie, 2014; Reynolds et al., 2003; Smith-Ramesh & Reynolds, 2017) because plant species associated with ecto-mycorrhizal fungi can gain competitive advantages over plants associated with arbuscular mycorrhizal fungi by efficiently capturing soil nutrients and lowering nutrient availability that is diminishing growth of arbuscular mycorrhizal species. Theoretically, trait dissimilarity reflecting average fitness difference/competitive hierarchy (e.g. height, a key trait for size-asymmetric competition for light, Cadotte, 2017) should correlate with positive pairwise PSF (Figure 1b).

Empirical support for these two hypotheses (Figure 1) would help explain the large variation of PSF for co-occurring plants, facilitate prediction of PSF for plant species for which no experiments have been conducted, and advance our understanding of the factors driving plant community dynamics. To meet this need, we conducted a comprehensive literature review and meta-analysis to test our hypotheses about plant traits and both individual and pairwise PSF. Specifically, we tested the hypotheses that (1) individual PSF will be negatively correlated with fast life-history traits and (2) pairwise PSF will be correlated with trait dissimilarity.

2 | MATERIALS AND METHODS

2.1 | Data compilation

In this meta-analysis, we calculated individual and pairwise PSF using two different datasets. For individual PSF, we searched ISI Web of Science on 3 August 2018 without restriction on publication year using the key search term 'plant soil feedback$'. We added extra studies from recent meta-analyses of Crawford et al. (2019)

and Lekberg et al. (2018), resulting in a total of 2,579 papers. We screened paper titles and abstracts to ensure that they were in the correct subject area, and thus 2,202 papers were removed. After this screening, 377 papers were assessed for eligibility using the following criteria: (a) plants were grown in conspecific and heterospecific soil; (b) conspecific soil had to be clearly influenced by one single plant species in the conditioning phase, and heterospecific soil was not affected by the focal species (we included studies where the authors stated that field soil was collected from certain species and used as soil inoculum); (c) PSF were tested for natural plants and studies for cultivated or crop plants were avoided; (d) studies reported means, standard errors or standard deviations or 95% confidential intervals and sample sizes for plant performance in the feedback phase. In total, 62 papers met these criteria (Figure S1). A list of data sources used in the study were provided in the Data Sources section.

Data were extracted from text, tables, figures or supplementary materials. We used ImageJ to extract means, standard errors or standard deviations of plant biomass from figures in the chosen papers (Schneider et al., 2012). Multiple experimental treatments from the same study were included in our analysis to take complete advantage of published results. Species names of focal plants and paper identity (authors and publication years) were recorded. In total, we constructed a dataset consisting of 2,108 observations and 216 plant species representing a variety of functional groups (e.g. herbs, trees and shrubs).

For pairwise PSF, we used the dataset complied by Crawford et al. (2019). This dataset consisted of 1,038 observations for 508 species pairs that were extracted from 69 peer-reviewed papers. The dataset included studies that conducted in forest and grassland ecosystems, and used laboratory or field experimental approaches. The plant species included trees and herbs. Effect sizes of pairwise PSF were calculated using species average performance in conspecific versus heterospecific soils, standard errors and replicates (see the following details) for each species pair and each observation. We obtained effect sizes, variances and species pairs for our meta-analysis.

2.2 | Effect size of individual PSF

Effect size of individual PSF was calculated using the natural log of response ratio (Brinkman et al., 2010; Hedges et al., 1999).

$$rr = Ln\left(\frac{X_e}{X_c}\right),$$

where X_e and X_c are plant biomass in conspecific and heterospecific soil, respectively. Variance of each effect size was estimated.

$$v_{rr} = \frac{(SD_e)^2}{n_e (X_e)^2} + \frac{(SD_c)^2}{n_c (X_c)^2},$$

where SD_e and SD_c are standard deviations of plant biomass in conspecific and heterospecific soil, respectively, and n_e and n_c are sample sizes for conspecific and heterospecific soil treatments, respectively.

2.3 | Effect size of pairwise PSF

To compare pairwise PSF across species that differ in their growth rates and sizes across experiments that differ widely in their methodologies, plant biomass was log-transformed (Crawford et al., 2019). The pairwise PSF for two plant species, A and B, and their respective soils, α and β, is.

$$rr(I_s) = Ln(\alpha_A) - Ln(\alpha_B) - Ln(\beta_A) + Ln(\beta_B),$$

where α_A is plant A performance in conspecific soil, α_B is plant B performance in heterospecific soil, β_A is plant A performance in heterospecific soil and β_B is plant B performance in conspecific soil. Variance of $rr(I_S)$ was estimated using the equation.

$$v_{rr(I_s)} = \frac{v_{\alpha_A}}{n_{\alpha_A}(\alpha_A)^2} + \frac{v_{\alpha_B}}{n_{\alpha_B}(\alpha_B)^2} + \frac{v_{\beta_A}}{n_{\beta_A}(\beta_A)^2} + \frac{v_{\beta_B}}{n_{\beta_B}(\beta_B)^2},$$

where v and n are variance and sample size of plant performances, respectively.

2.4 | Calculating species-level average individual and pairwise PSF

In our dataset, there were multiple observations (i.e. effect size values) for one plant species or one species pair. We did not consider variations within plant species or within species pair, and thus species-level average PSF values were calculated by one mixed-effect model using the METAFOR package (Viechtbauer, 2010) in R. In this model, species identity or species pair was used as the fixed effect and study as the random effect to overcome possible data dependence (i.e. from multiple effect sizes in single studies; Nakagawa et al., 2017). Average effect size and its variance for each species were calculated using the formulas in this model (Borenstein, 2009).

$$\overline{rr} = \left(\sum_{i=1}^{k} \frac{rr_i}{v_i + \tau^2}\right) / \left(\sum_{i=1}^{k} \frac{1}{v_i + \tau^2}\right),$$

$$\overline{v} = \frac{1}{\sum_{i=1}^{k} \frac{1}{v_i + \tau^2}},$$

where rr_i, v_i and τ^2 are effect size, within-experiment variance and between-experiment for experiment i within each subgroup (i.e. each species), respectively. τ^2 was estimated using the restricted maximum likelihood approach. We also computed average pairwise PSF value and its variance for each species pair by performing one mixed-effects

models with species pair as one fixed effect and study as one random effect and using the formulas mentioned above.

2.5 | Plant functional traits

To test linkages between PSF values and plant traits or trait dissimilarity, we chose six plant functional traits that are closely associated with plant life-history strategies: (SLA, the one-sided area of a fresh leaf divided by its dry mass, mm^2/mg), leaf nitrogen (N) concentration (LNC, the total amounts of N per unit of dry leaf mass, mg/g), specific root length (SRL, the ratio of root length to dry mass of fine roots, cm/g), (FRD, mm), plant height (the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, m) and seed dry mass (SM, the dry mass of an average seed of a species, mg). SLA, LNC, SRL and FRD are important plant economic traits that are related to carbon and soil nutrient acquisition and reflect trade-offs between growth and defence (Kong et al., 2019; Reich, 2014; Westoby, 1998; Wright et al., 2004). Plant height reflects plant size and life span. Seed mass reflects a trade-off between investment in numerous small seeds and fewer larger seeds.

We obtained all trait data from the TRY Database (Kattge et al., 2020). Trait values from different locations or populations were averaged to obtain mean values for each species; we did not consider intraspecific trait variability. Average trait values were natural log-transformed for each species and each trait prior to analyses because of large difference in orders of magnitude across plant species. Trait dissimilarity was calculated using the Euclidian distance for each species pair, and they were log-transformed prior to meta-analyses if needed to reduce the influences of differences in value sizes.

2.6 | Data analyses

A random effects model was used to estimate the overall weighted effect sizes using the *ram* function in the METAFOR package in R (Viechtbauer, 2010). A *Z* test was used to determine whether the weighted effect size was equal to zero. The total heterogeneity of effect size was tested using the *Q* statistic, which follows a chi-squared distribution under the null hypothesis that the effect size is the same for all experiments (Borenstein, 2009). Based on the results from this model, publication bias of non-significant results was tested by constructing a funnel plot to check for asymmetry or gaps in the data (Sterne & Egger, 2001).

We performed a series of univariate meta-regressions rather than single multivariate meta-regressions to test our hypotheses for fully exploiting our datasets. We are aware that it is of interest to assess the relative importance of different traits in driving the variation of PSF, but it is not the goal of this present study, and this study aims to generalize the relationships between PSF and key traits that reflect plant life-history strategy. Meta-regressions were then performed to evaluate the relationships between each individual plant trait, or each measure of trait dissimilarity, and species-average PSF effect sizes using random effects models. The random effects models in meta-analysis incorporate an assumption that the different studies are estimating different treatment effects, and these models allow us to test whether variables cause the heterogeneity of effect sizes (Borenstein, 2009). For each trait model, the total heterogeneity of effect sizes (Q_T) was partitioned into residual heterogeneity (Q_E) and variate-explained heterogeneity (Q_M; Borenstein, 2009). The Q_M statistic follows a chi-squared distribution under the null hypothesis that the effect size is the same for all subgroups. For data of traits or trait similarities, values were log-transformed, if necessary, to meet the requirements of regression analyses. All analyses were performed in R (R Core Team, 2020).

3 | RESULTS

3.1 | Linkages between plant traits and individual PSF

Across all studies, average individual PSF was negative (95% confidence interval = -0.1058 ± 0.0228, $Z = -9.1057$, $p < 0.001$). However, there was a significant variation in effect size (Q = 13,594.08, df = 2,107, $p < 0.001$). Without considering the influence of moderators (i.e. plant species identity and plant traits), 90.79% of total variance in the true effects was due to heterogeneity rather than sampling variance (i.e. I^2 = 90.77%), reflecting the inconsistency across the effect sizes that needs to be explained using moderators. Individual PSF values were inconsistent across plant species (Q_M = 4,302.00, df = 215, $p < 0.001$). We did not detect publication bias for this model because the funnel plot did not show asymmetry in effect size distribution (effect size vs. standard error, Figure S2).

Trait-based relationships with individual PSF were consistent with Hypothesis 1 (Figure 1a). PSF values decreased (i.e. they became more negative) with increased SLA (slope = −0.2269, Q_M = 7.42, p = 0.006, n = 134, Figure 2a), LNC (slope = −0.0099, Q_M = 4.21, p = 0.040, n = 152, Figure 2b) and SRL (slope = −0.0971, Q_M = 5.02, p = 0.025, n = 78, Figure 2c). Plant species with greater FRD (slope = 0.2995, Q_M = 5.16, p = 0.023, n = 64, Figure 2d), plant height (slope = 0.0844, Q_M = 23.35, $p < 0.001$, n = 171, Figure 2e) and seed mass (slope = 0.0267, Q_M = 4.68, p = 0.031, n = 181, Figure 2f) showed less negative or even more positive individual PSF values.

3.2 | Linkages between trait dissimilarity and pairwise PSF

Pairwise PSF values were associated with dissimilarity in SRL, FRD and height, but the direction of the relationship varied between these traits; these findings partially supported hypothesis 2 (Figure 1b). There was no relationship between PSF values and SLA dissimilarity (Q_M = 0.42, p = 0.516, n = 183, Figure 3a) or between PSF values

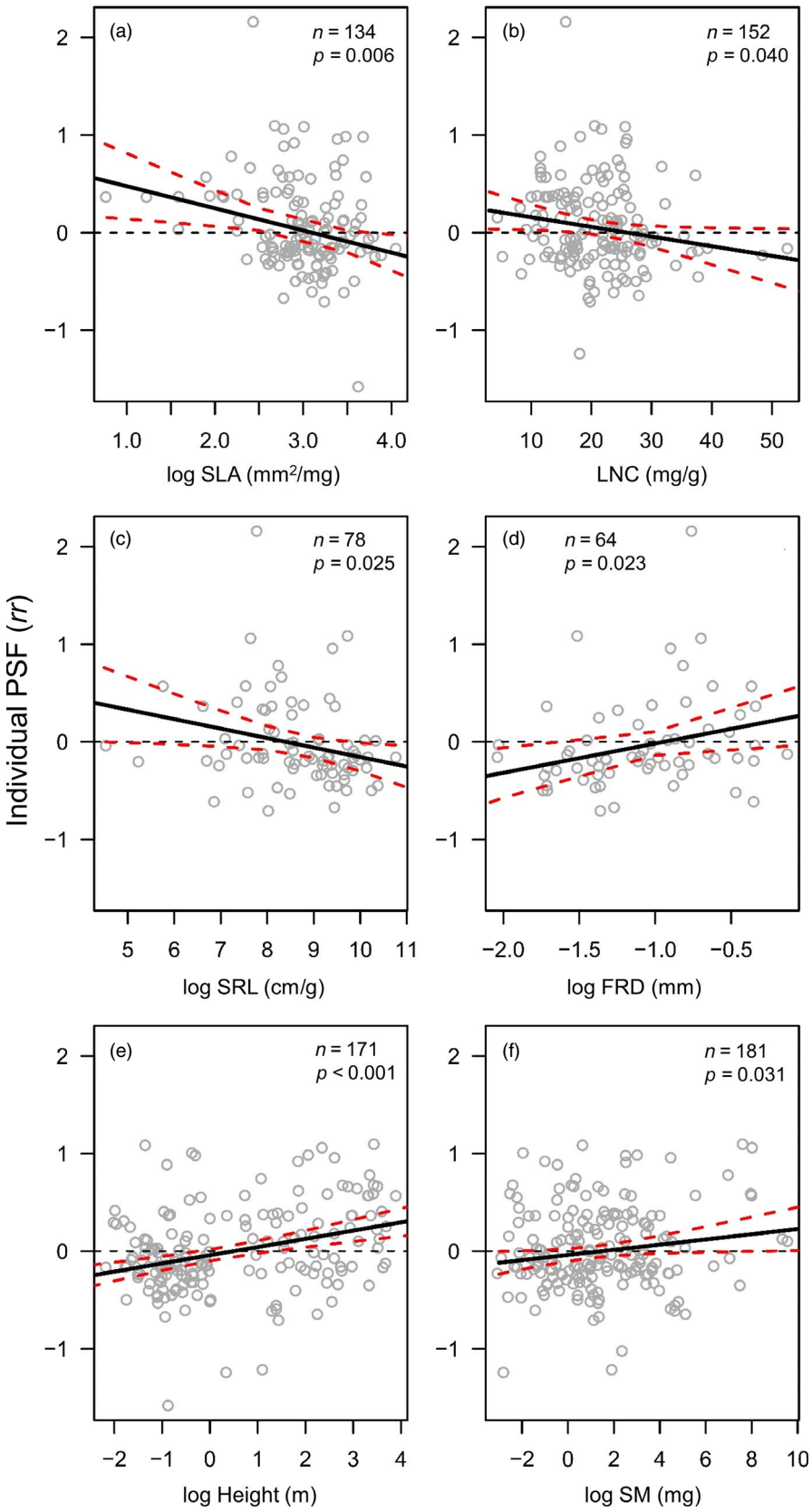

FIGURE 2 Relationships between individual plant–soil feedbacks and (a) specific leaf area, (b) leaf N concentration, (c) specific root length, (d) fine root diameter, (e) plant height and (f) seed mass, which test Hypothesis 1 (Figure 1a). The solid lines indicate the fitted relationships, and the dashed red lines indicate the 95% confidence intervals based on univariate regression analyses. SLA, specific leaf area; LNC, leaf N concentration; SRL, specific root length; FRD, fine root diameter; SM, seed mass

and LNC dissimilarity (Q_M = 0.48, p = 0.488, n = 197, Figure 3b). However, pairwise PSF values were negatively related to SRL dissimilarity (slope = −0.1091, Q_M = 6.39, p = 0.012, n = 103, Figure 3c) and FRD dissimilarity (slope = −0.5989, Q_M = 5.56, p = 0.018, n = 91, Figure 3d), and they were positively related to height dissimilarity (slope = 0.2012, Q_M = 4.41, p = 0.036, n = 224, Figure 3e). No relationship was detected between PSF values and SM dissimilarity (Q_M = 0.1862, p = 0.666, n = 230, Figure 3f).

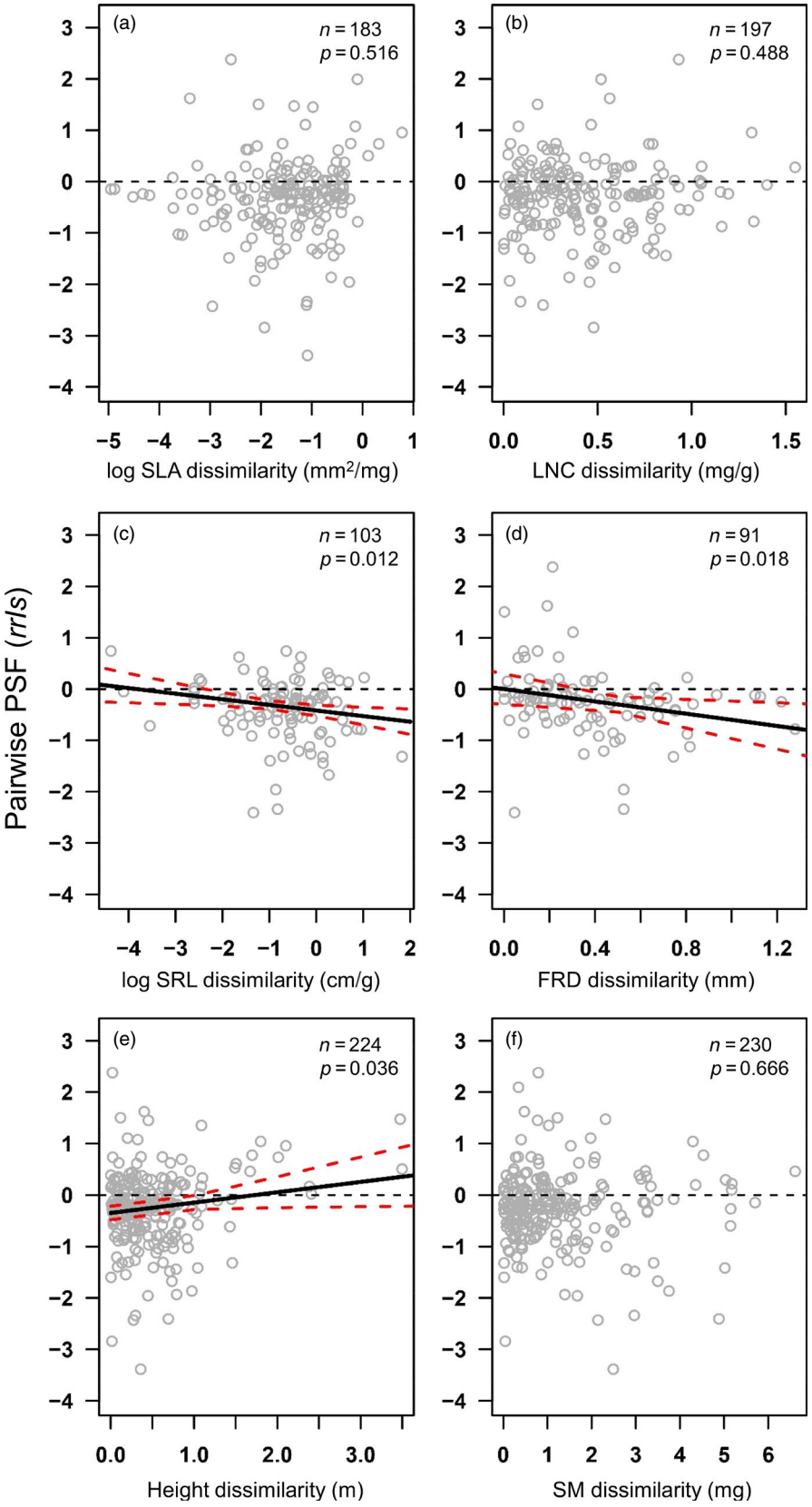

FIGURE 3 Relationship between pairwise plant–soil feedback and (a) SLA dissimilarity, (b) LNC dissimilarity, (c) SRL dissimilarity, (d) FRD dissimilarity, (e) Height dissimilarity and (f) SM dissimilarity, which test Hypothesis 2 (Figure 1b). The solid lines indicate the fitted relationships, and the dashed red lines indicate the 95% confidence intervals based on univariate regression analyses. Panels that do not show the trend lines imply there were not statistically significant relationships ($p > 0.05$). SLA, specific leaf area; LNC, leaf N concentration; SRL, specific root length; FRD, fine root diameter; SM, seed mass

4 | DISCUSSION

Plant–soil feedbacks and functional traits are two active research areas of ecology, but global evidence linking traits with PSF remains scarce. Integrating traits and PSF could explain variation in PSF among species in natural communities and advance our understanding of the role of PSF in generating niche and fitness differences and thus species coexistence. Our results help fill this

knowledge gap by demonstrating that (a) individual PSF were related to plant traits in directions consistent with known trade-offs between growth and defence or between seed number and seed size and (b) the direction of relationships between trait dissimilarity and pairwise PSF varied with trait identity, from negative, neutral to positive.

4.1 | Variation of individual PSF along the fast–slow trait spectrum

We tested the growth–defence hypothesis in the context of PSF (Hypothesis 1, Figure 1a) and found evidence of the negative relationships between PSF and traits associated with fast life histories, that is, SLA, LNC and SRL, and positive relationship between PSF and traits for slow life history, that is, FRD, seed mass and plant height (Figure 2), presumably because the fast-growing plants have lower defence against soil pathogens (Semchenko et al., 2018). This finding is consistent with evidence that slow-growing species with greater seed mass are more tolerant of conspecific neighbours (Lebrija-Trejos et al., 2016), and that plant–soil feedbacks are a key mechanism driving conspecific negative density dependence (Mangan et al., 2010; Maron et al., 2016). The plant height–PSF relationship may reflect the fact that taller plants have closer associations with mycorrhizal fungi than shorter plants because they are not limited by light and can exchange carbon for nutrients with mycorrhizal fungi (Cheeke et al., 2019).

Based on the trait–PSF relationships we observed, we can now make predictions about how PSF may vary across environmental gradients. Fertile habitats are usually dominated by plant species with fast traits, while slow-growing species dominate infertile habitats (Diaz et al., 2004; Reich, 2014; Wright et al., 2004). Under nutrient-rich conditions, negative PSF should be pervasive and play more important roles in community dynamics than that under nutrient-poor conditions; under nutrient-poor conditions, soil mutualisms (e.g. mycorrhizas, N_2 fixers) that drive positive PSF would be expected to be more important in community dynamics (Laliberté et al., 2015; Png et al., 2019). The same reasoning suggests that PSF should play a role in succession: early-successional plants that are characterized by fast growth, high nutrient acquisition, small seed size and short life span should be more negatively influenced by soil biota than late-successional plants with the opposite traits (Bauer et al., 2015; Kardol et al., 2006). Moreover, unpacking the relationship between fast-slow traits and individual PSF may enable us to better understand plant population ecology, including transient and stochastic dynamics (Stott et al., 2010; Thuiller et al., 2007), and can be used to inform vegetation management, such as restoration and species invasions (Suding et al., 2013; Wubs et al., 2016). Observed time lags between alien species arrival and dominance (Coutts et al., 2018) and alien population booms-and-busts (Simberloff & Gibbons, 2004) may be at least partly attributed to the time required for PSF to accumulate and take effect, with slow-growing and fast-growing plant invaders experiencing different effects.

4.2 | Correlations between trait dissimilarity and pairwise PSF are complex

Plant–soil feedbacks theory has clearly shown that predicting species coexistence requires measurement of pairwise PSF, that is, the relative performance of species on conspecific and heterospecific soil (Bever et al., 1997). Our results indicated that trait dissimilarity showed positive or negative or no correlations with pairwise PSF; greater SRL dissimilarity caused more negative PSF while the opposite pattern was observed for height dissimilarity (Figure 3). These findings partially supported our prediction that pairwise PSF is related to trait dissimilarity (Hypothesis 2, Figure 1b), but they indicated that the links between trait dissimilarity and pairwise PSF may be more complicated than previously expected. Our findings are consistent with the idea that many relationships between trait differences and coexistence are possible, with differing implications for competitive outcomes (Gross et al., 2015; Kraft et al., 2015).

The negative relationship we observed between SRL dissimilarity and pairwise PSF may reflect differences in plant strategies related to resource acquisition and defence. Plants with different SRL dominate habitats with different resource availability, and SRL dissimilarity is a predictor of niche difference across herb and tree species (Fort et al., 2015; Valverde-Barrantes et al., 2013). Fast-growing species with high SRL tend to condition soil with high abundance of pathogens and nutrient availability, and slow-growing species with low SRL produce soil with the opposite characters (Bagchi et al., 2014; Bever et al., 2015; Wardle et al., 2004). Consequently, fast-growing species are promoted in soil conditioned by slow-growing species because of low infection from pathogens, whereas slow-growing species are promoted in soil conditioned by fast-growing species due to high nutrient availability. Of course, we cannot rule out the possibility that fast-growing might not establish in soil conditioned by slow-growing species due to low nutrient availability or allelopathic chemicals.

In contrast, between-species difference in height was associated with increasingly positive PSF, which should promote competitive exclusion. Differences in this trait likely reflect the differential ability of species to pre-empt the same resources (e.g. light) or to form associations with ecto-mycorrhizal fungi, creating a competitive hierarchy and leading to average fitness differences (Cadotte, 2017; Gross et al., 2015; Herben & Goldberg, 2014; Kraft et al., 2015). The trait–PSF relationships we observed would further reinforce such competitive hierarchies. In principle, these patterns should help explain competitive exclusion and abundance patterns in natural ecosystems. For example, trees can outcompete herbaceous species because of size-asymmetric advantages concerning light competition in the early successional stage of forest ecosystems, and thus dominate the forests in the late successional stage. However, incorporating plant traits and PSF into modern species coexistence theory remains a considerable challenge due to limited experimental evidence and even theory (but see, Ke & Wan, 2020). Our work suggests that finding plant trait dissimilarity–pairwise PSF correlations can reduce the number of potential niche dimensions, if they reflect

one coordinated life-history strategy. Empirical research is needed to test whether PSF and trait dissimilarity mirror two aspects of a coordinated life-history strategy.

5 | CONCLUSIONS

Our analyses provided evidence for relationships between PSF and functional traits. The trade-off between growth and defence can drive variation of individual PSF. Individual PSF was more negative in faster-growing species, but taller and larger-seeded species have more positive or less negative individual PSF likely because of greater tolerance to soil pathogens. Pairwise PSF, normally used to deduce species coexistence, was related to trait dissimilarity in terms of some functional traits. However, our results showed SRL differences had negative relationships with pairwise PSF, and height differences had positive relationships with PSF, mediating distinct links between trait dissimilarity and species coexistence (niche difference vs. fitness difference). Together, these results suggest that PSF may reinforce the effect of trait dissimilarities on coexistence. However, knowledge of how trait dissimilarity affects species coexistence must improve before this conjecture can be rigorously tested. Extrapolating from our results, we suggest that considering PSF in modern species coexistence theory can help build a more comprehensive understanding of when PSF contribute to species coexistence (Ke & Wan, 2020).

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CONFLICT OF INTEREST

We confirm that there are no known conflicts of interest associated with this publication. Chengjin Chu is an Associate Editor and Jane A. Catford is a Senior Editor for Journal of Ecology, but they took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

N.X. conceived the idea and designed the research; N.X. and C.C. constructed the conceptual frameworks, with contributions from P.B.A., K.M.C. and M.B.; D.C., H.W. and K.M.C. conducted literature search and collected data; D.C. and N.X. performed the data analyses.; N.X., P.B.A., C.C., K.M.C., J.A.C., P.M.v.B. and M.B. discussed and interpreted the results; N.X. and P.B.A. wrote the manuscript, with inputs from C.C., K.M.C., J.A.C., P.M.v.B. and M.B.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.c59zw3r7f (Xi et al., 2021).

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DATA SOURCES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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