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REVIEW AND SYNTHESIS

Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence

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Abstract

Plants interact simultaneously with each other and with soil biota, yet the relative importance of competition vs. plant–soil feedback (PSF) on plant performance is poorly understood. Using a meta-analysis of 38 published studies and 150 plant species, we show that effects of interspecific competition (either growing plants with a competitor or singly, or comparing inter- vs. intraspecific competition) and PSF (comparing home vs. away soil, live vs. sterile soil, or control vs. fungicide-treated soil) depended on treatments but were predominantly negative, broadly comparable in magnitude, and additive or synergistic. Stronger competitors experienced more negative PSF than weaker competitors when controlling for density (inter- to intraspecific competition), suggesting that PSF could prevent competitive dominance and promote coexistence. When competition was measured against plants growing singly, the strength of competition overwhelmed PSF, indicating that the relative importance of PSF may depend not only on neighbour identity but also density. We evaluate how competition and PSFs might interact across resource gradients; PSF will likely strengthen competitive interactions in high resource environments and enhance facilitative interactions in low-resource environments. Finally, we provide a framework for filling key knowledge gaps and advancing our understanding of how these biotic interactions influence community structure.

Keywords

Additive interaction, coexistence, competition, facilitation, meta-analysis, mutualist, pathogen, plant–soil feedback, resource gradient, soil biota.

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INTRODUCTION

Ecological theory and empirical studies indicate that competition is a dominant force influencing community structure and can be a major driver of species exclusions from communities (Lotka 1925; Volterra 1926; Grace & Tilman 1990; Gurevitch *et al*. 1992; Callaway *et al*. 1996). For plants, competition can strongly influence coexistence (Tilman 1982), individual plant fitness and community assembly (Aschehoug *et al*. 2016). There is also an increasing understanding that other interactions, such as associations with mutualists (van der Heijden *et al*. 1998), herbivores (Hulme 1996; Maron & Crone 2006) and pathogens (Bever *et al*. 2015) affect plant performance and community organisation. However, these interactions are generally studied separately from competition, and their relative strengths, combined effects and potential impacts on each other remain unclear.

In natural systems, plants often experience direct competition with neighbouring plants and simultaneous complex interactions with soil biota. Plants can shape communities of soil biota and alter soil structure and chemistry in ways that influence subsequent plant growth and survival. These plant–soil feedbacks (PSFs) have the potential to affect plant abundance, community assembly and succession as well as invasiveness of

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introduced exotics (van der Putten *et al.* 2013). Indeed, PSF theory predicts that when soil communities differentiate among host species and decrease the fitness of their hosts (i.e. negative PSF), dynamic plant–soil biota interactions can drive plant species coexistence even when strong resource competition would otherwise lead to exclusion (Bever *et al.* 1997; Bever 2003; Revilla *et al.* 2012). How the strength of PSFs compare with direct competitive interactions, however, is largely unknown. This is important because if the effect of PSF is small relative to competition and if PSF does not influence competitive strength, it is unlikely to change competitive outcomes and may play a relatively minor role in structuring communities (Kulmatiski *et al.* 2011, 2016). Alternatively, if the strength of PSF is comparable to competition, then including PSF responses may improve predictive models of plant communities and help explain how plants that differ in competitive abilities coexist (Bever 2003).

Another unknown is whether PSF and competition operate independently or interact in ways that exacerbate or ameliorate the effects of each other. There are indications that they may interact, as competitive effects are greater when focal plants also experience soil biota trained by conspecifics (Petermann *et al.* 2008; Pendergast *et al.* 2013). Alternatively, soil mutualists such as N_2-fixing bacteria may increase the availability of limiting resources, resulting in positive PSF and reduced competition (Bessler *et al.* 2012). Feedback strength and direction may differ predictably among plants with different nutrient acquisition strategies (Teste *et al.* 2017) and mycorrhizal associations (Bennett *et al.* 2017), but one major question is whether PSF differs among plant species that vary in competitive ability. For example, if strong competitors are more abundant and the accumulation of pathogens is density dependent, superior competitors may experience more negative PSFs than weaker competitors (Burdon & Chilvers 1982; Bell *et al.* 2006; Liang *et al.* 2016). PSF could then reduce the potential for competitive exclusion and promote coexistence (Bever 2003).

Recent studies have found that competitive ability, as inferred from variation in growth rate (*sensu* Kulmatiski *et al.* 2011), correlates negatively with effects of soil biota. In other words, early successional and fast-growing plant species are more likely to suffer from negative PSF, whereas late successional and slow-growing species have more neutral or even positive interactions with soil biota (Kardol *et al.* 2006; Lemmermeyer *et al.* 2015). Indirect tests of the relationship between competition and PSF can also be found in studies that have correlated plant abundance with the strength of negative feedback, since dominant species are often thought to be superior competitors. In some communities, dominant species generate more negative feedbacks than subordinates do (Maron *et al.* 2014; Heinze *et al.* 2016). In other communities, either the opposite occurs (Klironomos 2002; Diez *et al.* 2010; Mangan *et al.* 2010), or PSF is not associated with relative abundance (Reinhart 2012; Bauer *et al.* 2015). Collectively, these results suggest that there are gaps in our understanding of the relative importance of competition and PSF, the mechanisms by which they interact, as well as what factors determine outcomes of such interactions.

Here, we analyse data from 38 published studies to address the following questions: (1) What is the relative importance of competition and PSF? (2) Are the effects of competition and PSF additive or do they interact? (3) Is there a correlation between the measured strengths of competition and PSF? We then use results together with predictions of shifts in plant–plant interactions (Bertness & Callaway 1994) and PSF (Revillini *et al.* 2016) across resource gradients to generate a series of predictions for how the environment may influence the relative importance and joint effects of competition and PSF. Finally, we highlight critical knowledge gaps and suggest future research directions needed to better understand the overall effect of competition and PSF and their context dependency.

METHODS

Paper selection

We compiled a dataset that included studies where *both* competition and PSF were experimentally manipulated. We searched Web of Science on 5 January 2018 using the following broad terms: 'plant soil feedback AND competition', 'plant soil feedback AND diversity', 'soil microb* AND competition', 'soil bact* AND competition', 'soil fung* AND competition', 'soil microb* AND diversity', 'soil bact* AND diversity, soil fung* AND diversity'. Our search returned 23 001 publications, but the great majority of those were rejected in a preliminary screening because they were reviews, clearly addressed a separate topic or only focused on competition or PSF, but not both. We identified 143 potential papers that were screened more carefully and included if they modified soil biota and plant composition in the same study, and reported means, sample sizes and a measure of variance. Thirty-eight publications fit these criteria, and combined they included 150 focal plant species. Most of these studies (34) were greenhouse experiments involving faster growing, non-woody grassland species, whereas the remaining four studies were conducted in the field.

Publications included two types of competition treatments: (1) total plant density differed and focal plants were grown either with heterospecific plants or alone (referred to as $\text{Comp}_{\text{Multiple/Single}}$), or (2) plant density was kept constant and focal plants were exposed to either inter- or intraspecific competition (referred to as $\text{Comp}_{\text{Inter/Intra}}$). These are equivalent to the better-known additive and replacement designs commonly used in competition experiments (Gibson *et al.* 1999). The first competition treatment tests for the effect of interspecific competition but does not control for density. Thus, in these experiments, the difference between intra- and interspecific competition cannot be tested. In the second type of competition experiments, the strength of intra- vs. interspecific competition is explicitly compared. Including both types of competition treatments provided a broader exploration of various aspects of competition and reflects experimental approaches that are commonly used.

Soil biota were manipulated in three ways in our included publications: (1) soil biota were previously trained by the focal plant species or a competitor ($\text{PSF}_{\text{Home/Away}}$), (2) live or sterilised soil ($\text{PSF}_{\text{Live/Sterile}}$), or (3) soil untreated or treated with fungicide ($\text{PSF}_{\text{-Fungicide/+Fungicide}}$). For $\text{PSF}_{\text{Live/Sterile}}$ and

PSF$_{\text{-Fungicide/+Fungicide}}$ contrasts, we restricted the soil treatment to conspecific soils and/or soils cultivated by mixed communities where conspecifics occurred, as opposed to soil cultivated by heterospecifics. Thus, all PSF treatments in this meta-analysis focused on plant responses to conspecific-associated soil biota.

We included these three PSF treatments because they are commonly used in PSF research and address slightly different aspects of interactions between plants and soil biota. PSF$_{\text{Home/Away}}$ contrasts test the effect of soil biota cultured by a focal species or its competitor and therefore test for whether there are species-specific effects of soil biota. In contrast, PSF$_{\text{Live/Sterile}}$ comparisons test the net effect of all soil biota. Finally, PSF$_{\text{-Fungicide/+Fungicide}}$ tests for the effects of soil fungi (at least those that are suppressed by the fungicide). In some ways, the PSF$_{\text{Home/Away}}$ contrast is the most realistic in that plants do not grow in soils that have been sterilised or treated with fungicide naturally. However, we believe that all PSF treatments represent some simplifications of reality. For example, PSF$_{\text{Home/Away}}$ treatments can fail to assess the effect of more generalist soil biota (e.g. Augspurger & Wilkinson 2007; Thomidis *et al.* 2008; Sarmiento *et al.* 2017), including some virulent pathogens that can negatively impact > 1000 plant species (Burgess *et al.* 2017). Also, PSF$_{\text{Live/Sterile}}$ comparisons may more accurately describe situations where key soil biota (e.g. pathogens and mutualists) are present, ineffective or absent due to abiotic conditions, dispersal limitation and/or disturbance (Augspurger 1984; O'Hanlon-Manners & Kotanen 2004a,b; Hersh *et al.* 2012; Cardillo *et al.* 2018). Furthermore, the use of fungicide in PSF research can be an important experimental tool, especially in the field, as soil fungi arguably constitute one of the most important groups of soil-borne pathogens (Raaijmakers *et al.* 2009) and mutualists (Smith & Read 2008), even though non-target effects can occur (Paul *et al.* 1989; Van der Putten *et al.* 1990; Siddiqui & Arif-Uz-Zaman 2004).

The majority of publications (30 of 38) included a full factorial design with all treatment combinations (-Comp-PSF, +Comp-PSF, -Comp+PSF and +Comp+PSF), which allowed us to quantify the overall effects of competition and PSF as well as their potential interaction. The remaining eight publications tested competition and PSF using methods that were not directly comparable (e.g. PSF and competition treatments were conducted in different size pots). Data from these publications were included where possible to evaluate consistency of results across a broader range of experiments. Four of the 30 publications with a full factorial design were conducted in the field instead of the greenhouse (Callaway *et al.* 2004; Casper & Castelli 2007; Yelenik & Levine 2011; Bennett & Cahill 2016). In those studies, seedlings were either grown alone or transplanted into vegetation that had been established for at least 6 months, but typically much longer. Although the design was consistent with Comp$_{\text{Multiple/Single}}$, the effect was much stronger than in greenhouse experiments where competitors were the same age. Therefore, we placed field studies into a separate competition group resulting in three main moderator levels; Comp$_{\text{Multiple/Single}}$ field, Comp$_{\text{Multiple/Single}}$ greenhouse, and Comp$_{\text{Inter/Intra}}$ greenhouse. See Fig. 1 for a graphical outline of the various treatment combinations.

Data extraction

We extracted plant performance data from each publication, including total or shoot biomass, or for one publication, seed numbers (Tomiolo *et al.* 2015; Table S1). We recorded the type of competition and PSF treatment, and metadata specifying whether the experiment was conducted in the field or greenhouse, the identity and functional group (C_3 grass, C_4

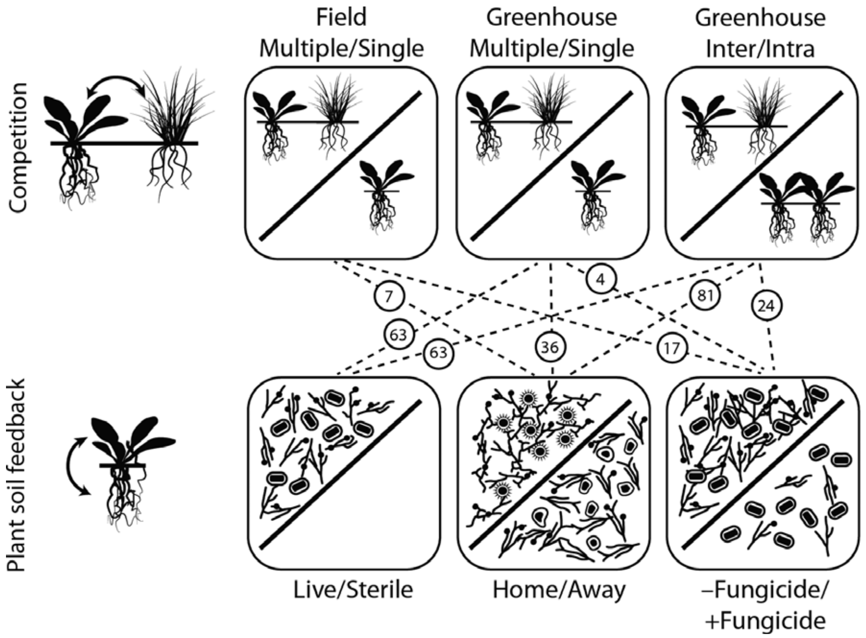

Figure 1 Graphical depiction of treatment combinations. Dashed lines and circles between icons show the number of independent experiments included in the meta-analysis estimating overall effects. Additional experiments were included in estimations of individual effects (Table S2).

grass, N_2-fixing forb, forb, shrub, tree) of the focal and competitor species, whether species were native or invasive as defined by the authors, if soil biota used in the experiment was collected from natural communities in field or originated from a training phase, and the duration of the experiment. Similar to previous meta-analyses (e.g. Levine *et al.* 2004; Lekberg & Koide 2005; Hoeksema *et al.* 2010; Bunn *et al.* 2015), we extracted multiple experiments from individual publications. We considered experiments independent unless the same combination of plant species, soil biota and PSF treatments were used. In time series experiments, only data from the last harvest was extracted. If treatments differed in origin (e.g. seeds of invaders collected in the native or invasive range) or were exposed to different resources (water, nutrients), we included data as dependent 'trials' within experiments that were incorporated in our analysis as random permutations (Data S1). Overall, our analyses included 627 trials from 417 experiments presented in 38 publications. Means, measures of dispersion (standard error or standard deviation) and sample sizes were extracted from text and tables in main publication or supplemental material, and when results were presented in graphical form, we used WebPlotDigitizer (v 2.6 released 10/20/2013, author Ankit Rohatg, https://automeris.io/WebPlotDigitizer/) to extract data. In some cases where means across species were presented (e.g. Maron *et al.* 2016), we contacted authors directly to acquire means and standard deviations for individual species. Standard deviations were back calculated from standard errors and sample sizes ($\mathrm{SD} = \mathrm{SE} \times \sqrt{n}$). When replication varied among treatments, we used the smallest value. The data extracted from all of the included papers is presented in Table S1 and more information about the database is in Data S1.

Effect size calculations and statistical analyses

We report the response ratio (RR = treatment/control) as the effect size because it is easy to interpret; for example, RR = 1.4 means a 40% increase in plant biomass, while RR = 0.6 means a 40% decrease. However, we used the natural log of the response ratio (ln[RR]) for all analyses because it has less bias and a more normal distribution (Hedges *et al.* 1999). Thus, estimates of effect sizes reported here were back-transformed, which can generate asymmetrical confidence intervals. We considered the effect size significant when our estimates of the 95% confidence intervals excluded the value of no effect (RR = 1).

To understand the relative magnitude of competition and PSF as well as their potential interaction (questions 1 and 2), we estimated both overall and individual effect sizes *sensu* Morris *et al.* 2007 (Table S2). Overall effect sizes average the response of one factor across presence/absence of the other factor (analogous to main effects in a two-way ANOVA) and provide an estimate of the interaction between factors (Gurevitch *et al.* 2000). Individual effect sizes quantify the effect of one factor in the absence or presence of the other factor and allow quantification of the combined effect of both factors (i.e. joint effect size). If the factors interact, their joint effect cannot be predicted from the individual effects. Estimates of the overall and interaction effects require all treatment combinations and were thus restricted to data from full factorial experiments (325 trials in 295 experiments from 30 publications). We used the same dataset to estimate individual and joint effects. Lastly, we conducted an additional analysis of individual effects where we included the data that reported on some, but not all, treatment combinations and where PSF and competition were not directly comparable. We found that individual effect size estimates fell within, or in one case, very close to the 95% confidence interval of the overall effect size estimates. No matter which method we used, or which dataset we analysed, the patterns of competition and PSF effects were consistent (Table S2). Thus, for simplicity, we focus on results from the full factorial experiments.

All statistical analyses were completed in R (3.4.3; R Core Team, 2017) within the RSTUDIO environment (1.1.423; RStudio Team 2016). The calculations of overall effect sizes, interaction effect size and associated variances followed Morris *et al.* 2007 (equations B.9-B.12). Individual effect sizes, joint effect size and associated variances were calculated using the 'escalc' function and the 'ROM' measure (the log-transformed ratio of means) within the 'metafor' package (Viechtbauer 2010). Meta-analyses were conducted using 'rma.mv' in that same package. We ran multilevel random and mixed-effects models that accounted for random effects of focal plant species and estimated effect sizes of the different treatments within each factor (Table S2). We report mean values from 1000 permutations of the dataset where each permutation included a randomly selected trial of each experiment (see above independence criteria). We primarily report on results from analysis of the full factorial dataset, but two analyses (interaction and joint effects with moderators) were restricted to a smaller subset as we required at least 20 experiments from three publications for each moderator level (Data S1). To determine if the magnitude of competition differed from PSF, as opposed to just assessing the significance of each effect size, we completed additional meta-analyses on the difference in the overall effect size (Table S2). The associated variance for this difference was calculated following the rules of linear combinations of random variables (Barry & Lindgren 1995).

To assess the correlation between the measured strengths of competition and PSF (question 3), we calculated Pearson's correlation coefficient between the individual effect sizes of competition and PSF. To maintain independence among data, we used the same permutation approach described for the meta-analysis. We evaluated the two competition treatments $\mathrm{Comp}_{\mathrm{Multiple/Single}}$ and $\mathrm{Comp}_{\mathrm{Inter/Intra}}$, as well as field and greenhouse experiments separately because their effect sizes differed significantly (Fig. 2, Table S2). Also, because our objective with the correlation analyses was to assess the relationship between two variables, not to estimate the overall importance of factor levels, we relaxed the requirement of a minimum of three publications for inclusion. Where the correlations were significant, we assessed the individual PSF treatments separately to ensure that significant effects were not driven by different effect sizes among the various PSF treatments. We also used multiple linear regression to determine whether metadata could account for variation among

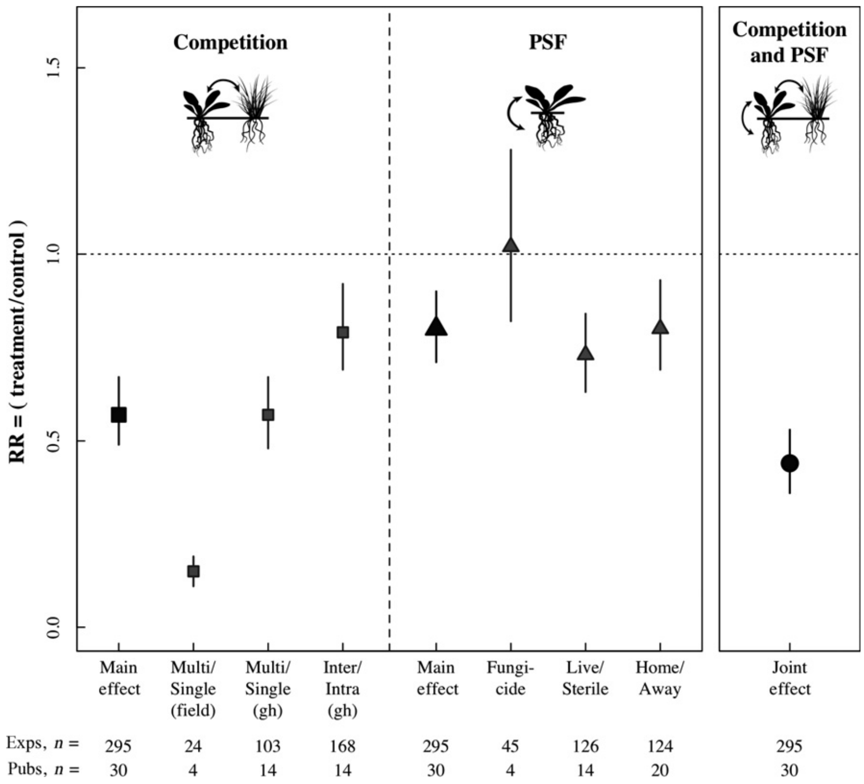

Figure 2 Overall (left) and joint (right) effects of competition and plant–soil feedback (PSF). Overall effects average the effect of competition across studies with and without PSF, and of PSF across studies with and without competition. The joint effect compares plants exposed to both competition and PSF to plants receiving neither. Overall effects were calculated across all experiments (Main effect) and broken by type of treatment. Competition treatments included target plants grown alone or together (Multiple/Single in field or greenhouse) or with different or the same species (Inter/Intra in greenhouse only). PSF treatments included plants grown without or with fungicides (Fungicide), in live or sterile soil (Live/Sterile), or in soil that had been cultured by a conspecific or heterospecific (Home/Away). The numbers along the *x*-axis show the number of experiments and publications included in the effect size calculations.

residuals in the correlation. More specific details about the statistical methods used in the meta-analysis as well as for the correlation and residual analyses are in Data S1.

RESULTS AND DISCUSSION

What is the relative importance of competition and PSF?

Both competition and PSF reduced plant biomass as evidenced by their average negative effect sizes (Fig. 2, Table S2). Not surprisingly, the effect of competition was stronger when focal plants were grown with or without a neighbour ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$) than when plants were grown with a heterospecific vs. a conspecific neighbour ($\mathrm{Comp}_{\mathrm{Inter/Intra}}$ Fig. 2, Table S2). The relative importance of competition compared to PSF depended on the method used to assess competition. PSF was weaker than competition when competition studies manipulated plant density ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$, $P < 0.001$), but PSF and competition were similar when competition treatments involved inter vs. intraspecific contrasts ($\mathrm{Comp}_{\mathrm{Inter/Intra}}$ $P = 0.42$).

Although plant responses to PSF treatments were generally negative, the effect varied among treatments and whether plants were grown in competition. When averaged across competition treatments (i.e. overall effect sizes), the effects of $\mathrm{PSF}_{\mathrm{Live/Sterile}}$ and $\mathrm{PSF}_{\mathrm{Home/Away}}$ were both negative; plants grown in home and live soils were smaller than plants grown in away or sterilised soil (Fig. 2, Table S2). The overall negative PSF effect was likely due to a higher abundance of more specialised enemies present in the conspecific soil (home and live) compared to the away or sterilised soils. However, in the absence of competition (i.e. individual effect sizes), $\mathrm{PSF}_{\mathrm{Home/Away}}$ effects were more muted than $\mathrm{PSF}_{\mathrm{Live/Sterile}}$ and only marginally significant (95% CI: 0.78–1.01, $P = 0.08$; Fig. 3, Fig. S1). This is consistent with previous findings (Kulmatiski & Kardol 2008; Brinkman *et al*. 2010) and may occur because the away soil harbours biota that can influence the growth of focal plants both positively and negatively, whereas sterilised soils contain neither (e.g. Baker 1971; Mitchell 1978). The dampening of $\mathrm{PSF}_{\mathrm{Home/Away}}$ effects in the absence of plant competition (Fig. 2, Fig. S1) reflects synergistic effects of $\mathrm{Comp}_{\mathrm{Inter/Intra}}$ and $\mathrm{PSF}_{\mathrm{Home/Away}}$ (discussed in more detail below).

Fungicide applications did not affect plant performance (Fig. 2, Table S2). However, the large confidence intervals reflect variable measured effects and indicate potentially important, but opposing, effects in a subset of cases. For example, fungicides can be beneficial to plants (Maron *et al*. 2011) if pathogens are suppressed (Bagchi *et al*. 2010), but detrimental when fungal mutualists are reduced (Beare *et al*.

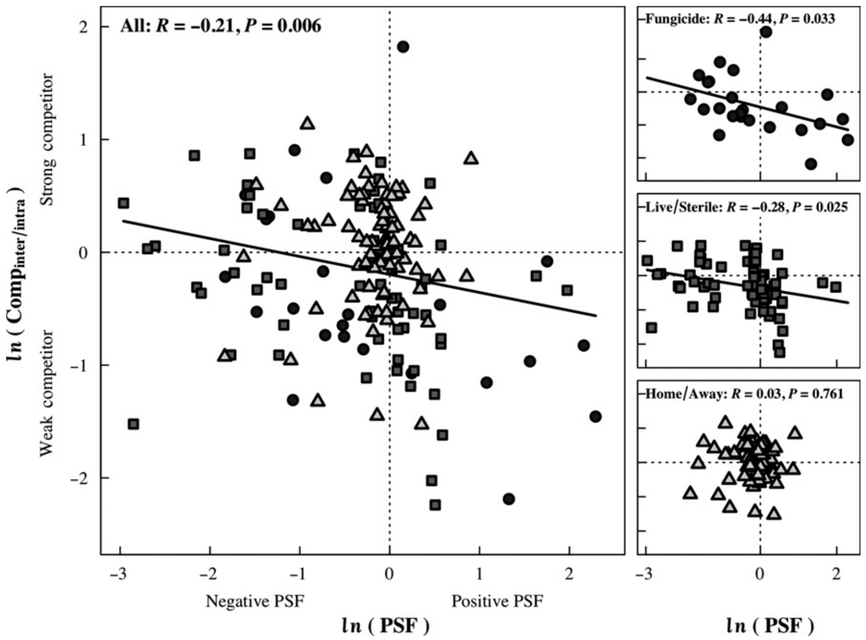

Figure 3 Correlation of individual effect sizes (ln-transformed) of competition and PSF for the subset of experiments where competition was evaluated by the inter- vs. intraspecific contrast. Where PSF values exceed zero, the effect of soil biota was positive on focal plants. Where competition values exceed zero, focal plants were larger when grown with other species than with themselves, that is, intraspecific competition was greater than interspecific competition. PSF, plant–soil feedback.

1993; Hartnett & Wilson 1999). Whether fungicide is beneficial or detrimental may be driven by where the experiment is conducted (greenhouse/field; Kulmatiski *et al.* 2008), successional stage of the community targeted (Kardol *et al.* 2006) and environmental conditions that may drive relative abundance of pathogens and mutualists (Revillini *et al.* 2016).

Are the effects of competition and PSF additive or do they interact?

Effects of competition and PSF were additive for most treatment combinations, implying that their combined effect can be predicted when competition and PSFs are known separately. In contrast, an interaction occurred when focal plants were grown with a heterospecific plant in home soil ($P < 0.001$ for $\mathrm{Comp}_{\mathrm{Inter/Intra}}$ x $\mathrm{PSF}_{\mathrm{Home/Away}}$; $P \geq 0.20$ for all other combinations). In this case, competition and PSF alone had slight to marginal effects on plant biomass (individual effects: $\mathrm{Comp}_{\mathrm{Inter/Intra}}$ $P = 0.045$; $\mathrm{PSF}_{\mathrm{Home/Away}}$ $P = 0.081$, Fig. S1, Table S2), but together they reduced the biomass of target plants to 61% of control plants (95% CI of joint effect: 0.50–0.76; Fig. S1, Table S2). These synergistic negative effects are consistent with PSF theory, where negative density-dependent effects manifest from the accumulation of harmful biota in the plant's root zone, which reduce plant growth and competitive ability. However, it is also possible that this interaction is the outcome of an unintended PSF effect on competitors, because in some experiments, the competitors were growing in their home soil (which was the away soil for the focal plant). Negative PSF experienced by competitors may have weakened competitive strengths and created disconnects between individual and joint effects contributing to the significant interaction observed. Whether the interaction resulted from synergism or unintended PSF effects, it attests to the interactive effect of soil biota and interspecific competition operating on the focal plant or its competitor.

Is there a correlation between the measured strengths of competition and PSF?

When competition was evaluated using plants grown at different densities ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$) in the greenhouse, soil biota effects were unrelated to competitive responses, both across ($P = 0.24$) as well as within PSF treatments ($P \geq 0.28$ in all three PSF treatments). In the field, competitive strength ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$) was negatively correlated with PSF responses ($R = -0.46$, $P = 0.02$) across all experiments. However, when examining this relationship closer, it was driven by different responses between $\mathrm{PSF}_{\mathrm{-Fungicide/+Fungicide}}$ and $\mathrm{PSF}_{\mathrm{Home/Away}}$ (there were no $\mathrm{PSF}_{\mathrm{Live/Sterile}}$ experiments in this subset of competition treatments), and was not significant ($P > 0.27$) when examined separately. It is possible that a relationship exists but that we lacked the power to detect it. However, it is also possible that the lack of relationship indicates that any effect of PSF is swamped by the much stronger effect of a competitor in the $\mathrm{Comp}_{\mathrm{Multiple/Single}}$ treatment (Fig. 2). In so far as this treatment reflects situations where plants may or may not compete with other plants (e.g. disturbed communities where establishment is somewhat stochastic), it suggests that negative density dependence is more likely driven by resource competition than PSF in sparsely populated communities.

When density was held constant and focal plants were exposed to either inter or intraspecific competition in the greenhouse ($\text{Comp}_{\text{Inter/Intra}}$; there were no field experiments with this competition treatment), competitive responses were negatively correlated with responses to soil biota across the three PSF treatments ($R = -0.21$, $P = 0.006$, Fig. 3). That is, strong competitors, which are plants that experienced stronger intraspecific than interspecific competition, or ln($\text{Comp}_{\text{Inter/Intra}} > 0$), were more likely to experience negative PSF. When PSF treatments were evaluated separately, the negative relationship persisted for the $\text{PSF}_{\text{Live/Sterile}}$ ($R = -0.28$, $P = 0.03$) and $\text{PSF}_{\text{-Fungicide/+Fungicide}}$ ($R = -0.44$, $P = 0.03$) treatments, but not the $\text{PSF}_{\text{Home/Away}}$ treatment ($R = 0.03$, $P = 0.76$). Whether the lack of a significant relationship in the $\text{PSF}_{\text{Home/Away}}$ treatment was due to biological reasons, methodological issues or a lack of power to detect a relationship is uncertain. For example, $\text{PSF}_{\text{Live/Sterile}}$ and $\text{PSF}_{\text{-Fungicide/+Fungicide}}$ treatments assess general differences in tolerance to pathogens and/or reliance on mutualists, which could be driven by the same traits that influence a plant's competitive ability, whereas the $\text{PSF}_{\text{Home/Away}}$ treatment quantifies the degree of host specialisation among microbial communities in ways that may not scale with plant competitiveness. As such, the different relationships observed among PSF treatments could be informative about underlying processes. On the other hand, the significant $\text{Comp}_{\text{Inter/Intra}}$ x $\text{PSF}_{\text{Home/Away}}$ interaction as well as the more muted responses in the $\text{PSF}_{\text{Home/Away}}$ treatment (indicated as a lesser range in PSF in Fig. 3c) could have obscured a negative relationship if such a relationship occurs. Furthermore, a few data points had considerable leverage on the correlation. For example, three points in the lower left-hand quadrant (depicting plants that were weak competitors and experienced strong negative PSF) had a large influence on the results. When they were removed, the correlation became negative and approached significance ($R = -0.18$, $P = 0.11$). It is clear that more experiments, preferably conducted under the same conditions, are needed to support or refute the different relationships observed here.

We do not know the underlying mechanism(s) for the negative relationship observed between competitive strength and PSF in some of the treatments. However, this relationship is consistent with the body of research indicating that plants with finite resources must trade-off between allocation to growth and defence (Coley *et al.* 1985) and suggests that a similar trade-off may exist between competition and PSF (Laliberté *et al.* 2015). That is, strong competitors may be more susceptible to pathogens than weak competitors, whereas weak competitors may benefit more from mutaulists (plants in upper left and lower right quadrants in Fig. 3 respectively). In contrast to a pattern indicative of trade-offs, some species were weak competitors and also suffered from negative PSF (lower left quadrant in Fig. 3), which may make them more susceptible to exclusion from communities where competition and PSF are strong structuring forces. Possible examples of such plants include early successional ruderals (Kardol *et al.* 2006). Plants in the upper right quadrant in Fig. 3, on the other hand, were strong competitors and also experienced positive PSF. The relatively few points in this quadrant across all three PSF treatments suggest that plants lacking trade-offs, coined 'Hutchinsonian demons' by Kneitel & Chase (2004) are proportionally rare. Invasive plants are sometimes thought of as 'demonic' because they may be less constrained by trade-offs between growth and defence (Ridenour *et al.* 2008; Kumschick *et al.* 2013). They can also be liberated from their co-evolved enemies (Elton 1958) and often experience weak negative, neutral or even positive PSF compared to co-occurring native plants that often suffer strong negative feedbacks (Agrawal *et al.* 2005; Kulmatiski *et al.* 2008; but see Anacker *et al.* 2014). This appeared to be true for the few invaders in our dataset, with the exotic invader *Acacia dealbata* (Rodríguez-Echeverría *et al.* 2013) having the most positive PSF and $\text{Comp}_{\text{Inter/intra}}$ (Fig. S2).

Limitations

Most studies in this analysis were short-term (< 5 months) greenhouse experiments involving competitive interactions among only two to three generally fast-growing, non-woody grassland species (Table S1). This low diversity could have overestimated true effects because increased diversity can moderate both competition and PSF (De Deyn & Van der Putten 2005; Aschehoug & Callaway 2015; Öpik & Davison 2016). Also, PSF is generally more negative for grasses and forbs compared with shrubs and trees, and both competition (Schoener 1983) and PSF (Kulmatiski *et al.* 2008) tend to be more negative in the greenhouse than in the field. Thus, we stress that results obtained in this analysis should not be extrapolated beyond these specific conditions.

While significant patterns emerged from the correlation analysis, much of the variation was not accounted for, resulting in large residuals in Fig. 3. Experimental metadata explained 25% of residual variation in our best-fit model ($R^2 = 0.25$, $F_{(7146)} = 7.15$, $P < 0.001$), and both evaluation phase and the functional group of the focal plant were significant ($F_{(4146)} = 6.50$, $P < 0.001$ and $F_{(3146)} = 12.47$, $P < 0.001$ respectively). The significance of evaluation phase was driven by a net positive departure of residuals in the longest experiments (16 weeks, 95% CI: 0.14, 0.55), whereas the residual distribution of shorter experiments all overlapped zero. This indicates, not surprisingly, that competition became stronger the longer experiments ran. Among functional groups (Fig. S3), the residual distributions were negative for N_2-fixing forbs (95% CI: −0.64, −0.13) and were positive for the grasses (CI = 0.09, 0.40; 0.07, 0.72). Why grasses may be more competitive than expected for any given level of PSF is uncertain, but the lower competitive ability by N_2-fixing forbs may be due to a lack of rhizobia when grown in sterilised soils or soil cultured by non-legumes.

To assess if plant functional group and experimental duration affected PSF, we examined the residual variation in PSF after competition was accounted for (i.e. the inverse of the residual analysis explained above). We found that residuals were positive for N_2-fixing forbs (CI = 0.43, 1.02), which experienced stronger positive PSF than predicted by the model. This could be due to the greater host preference in this symbiosis relative to other symbioses, such as AMF. We also found stronger evidence that experimental duration can affect the outcome of experiments. Interactions with soil biota changed from negative to positive with increasing experiment duration (Fig. S4), which means that short-term experiments can bias responses towards more negative PSF. This may result from young seedlings being more susceptible than adult plants to pathogens (Walker 1969; Augspurger 1984; Populer 2012). Furthermore, handling of soil inocula (e.g. collection, storage, sieving) for PSF experiments may have varying effects on different groups of soil biota. For example, soil sieving is likely to fragment roots and/or mycelium, which may increase the inoculum potential (i.e. colony-forming units per gram of soil) of soil-borne pathogens relative to mycorrhizal fungi (Petersen & Klug 1994), whereas longer duration experiments may be necessary for positive effects of AMF and N_2-fixers to manifest (Smith *et al.* 2009). It is also possible that nutrient depletion over time would favour mutualism rather than parasitism. However, even though our estimates of competition and soil biota may differ from those in mixed natural communities, these controlled experiments provide fundamental empirical data that demonstrate the relative importance and possible interactions between competition and PSF.

Another potential source of variation is whether soil biota was collected from naturally occurring plants or originated from a training phase in experimental field plots, mesocosms or greenhouse pots. The majority (76%) of experiments included in our analyses used a training phase, and, using the same meta-analysis model with conditioning method as the moderator, we found that soil biota origin mattered. Effects of soil biota collected from natural communities were neutral (RR = 1.00, $P = 0.94$), whereas soil biota originating from an experimental training phase resulted in negative PSF (RR = 0.72, $P < 0.001$). Because our dataset was restricted to PSF studies that also manipulated competition, we would not use this dataset on soil training to rule on PSF studies in general, and our replication of untrained studies was much lower than trained studies ($n = 71$ vs. 224 experiments respectively). However, the stronger effect of soil training observed here support earlier findings by Kulmatiski *et al.* (2008) and may be due to more exclusive interaction with focal plants relative to natural, mixed plant communities. Indeed, in experiments where focal plant abundance has been modified, PSF is more negative when soil biota originates from plots where focal plants are in higher abundance (Liao *et al.* 2015; Yang *et al.* 2015). Thus, plant traits, training period and focal plant abundance may all shape PSF responses and should be considered when planning experiments and interpreting results.

Some of the unaccounted variation in our residual analyses could also be a result of experimental factors that were not recorded, which reinforces the need to carefully document experimental conditions (e.g. soil nutrient availabilities), even those that do not appear to be directly relevant to the study. Such information would be very useful in future meta-analyses (Koricheva *et al.* 2013).

Synthesis

Our analyses indicate that the effect of competition depends on the type of competition. Not surprisingly, growing next to a plant compared to growing alone ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$) had a stronger negative effect on focal plants than when density was kept constant and comparisons were between inter or intraspecific competition ($\mathrm{Comp}_{\mathrm{Inter/Intra}}$, Fig. 2). The effects of soil biota also depended on the particular treatment, and except for $\mathrm{PSF}_{\text{-Fungicide/+Fungicide}}$, they were negative and most likely driven by somewhat specialised pathogens. Regardless of the way competition was measured, however, effects of soil biota and competition were additive or synergistic, and plants exposed to both were on average less than half the size of plants that were exposed to neither (Fig. 2). As such, efforts to incorporate PSF (and possibly also plant-phyllosphere feedback responses, Whitaker *et al.* 2017) into plant competition models (Bever 2003; Kulmatiski *et al.* 2011) appear warranted and could result in better predictions regarding the outcome of plant–plant interactions.

Our analyses also showed that interspecific competition was stronger than intraspecific competition (i.e. $\mathrm{Comp}_{\mathrm{Inter/Intra}} < 1$ in Fig. 2), which could lead to competitive exclusion due to a lack of self-regulation (Tilman 1982). Extrapolating our results from short-term greenhouse experiments to population dynamics in mixed communities is challenging for many reasons, partly because pairwise experiments can elicit unrealistically strong competitive effects (Aschehoug & Callaway 2015), and also because more complex communities can initiate interaction chains that make outcomes hard to predict (Levine *et al.* 2017). Nonetheless, if and when plants encounter strong interspecific competitors in the field, coexistence may depend on stabilising forces among competitors (*sensu* Chesson 2000a) such as resource partitioning (Tilman 1982), differential responses to spatial and temporal environmental variation (Chesson 2000b) and self-regulating effects due to density-dependent accumulation of natural enemies (Janzen 1970; Connell 1971). Negative PSF has the potential to prevent competitive exclusion (Bever 1994) and similar to a previous meta-analysis of PSF (Kulmatiski *et al.* 2008), we found significant and negative responses to soil biota overall (Fig. 2). We also found some support for a relationship between PSF responses and the competitive ability of plants, where stronger competitors were more likely to experience negative than positive interactions with soil biota (Fig. 3). This relationship was not significant in the $\mathrm{PSF}_{\mathrm{Home/Away}}$ treatment or where competition was much stronger than PSF ($\mathrm{Comp}_{\mathrm{Multiple/Single}}$), limiting our confidence in the biological significance and generality of this finding. However, several recent studies have shown similar negative relationships (Lemmermeyer *et al.* 2015; Chung & Rudgers 2016; Stanescu & Maherali 2017). If reflective of processes operating in natural communities, it implies that soil biota may moderate differences in competitive strength among plants by limiting strong competitors *and/or* by boosting weak competitors. This is significant, because PSF theory has primarily focused on the role of negative PSF for maintaining coexistence (Bever 2003), whereas positive PSF have often been regarded as a homogenising force driving communities towards low diversity (Reynolds *et al.* 2003).

CONTEXT DEPENDENCY, KNOWLEDGE GAPS AND FUTURE DIRECTIONS

The studies included in these analyses were mostly conducted under benign greenhouse conditions. For field studies, however, a major challenge is predicting how the relative importance of interactions changes with environmental context (Agrawal *et al.* 2007; Maron *et al.* 2014; Louthan *et al.* 2015;

Smith-Ramesh & Reynolds 2017). To accomplish this, we need to better understand how environmental conditions select for particular plant traits, how different traits may shape interactions with soil biota and how soil biota directly respond to the environment. Unfortunately, we could not assess the effect of resources on competition and PSF in our analysis due to an insufficient number of experiments that varied resource levels, but it was encouraging to see that four of the five publications that did so were published during the past year (Table S2). In lieu of quantitative analyses, integrating results from our analysis with previously published models describing shifts in interactions among plants (Bertness & Callaway 1994) and their associated soil biota (Revillini *et al.* 2016) across resource gradients leads to several insights that we discuss below. We then highlight important knowledge gaps and potentially fruitful avenues for future research.

Individual and joint effects of plant–plant interactions and soil biota across resource gradients

Resource availability may play a central role in mediating both the traits that influence the outcome of plant interactions (defence: Coley *et al.* 1985; competition: Wilson & Tilman 1993; Besaw *et al.* 2011; ecological strategy: Cornwell *et al.* 2008) as well as the strength of the interactions themselves (Grime 1977; Haig & Westoby 1988; Maron *et al.* 2014; Louthan *et al.* 2015). One hypothesis for how abiotic gradients can influence the strength of interactions among plants is the Stress Gradient Hypothesis (Bertness & Callaway 1994). This posits that competition should generally be more frequent or important in high-resource, low-stress environments, whereas facilitation should be more common in low-resource, high-stress habitats. That is, resident vegetation in stressful environments is more likely to promote, rather than compete with, adjacent plants (He *et al.* 2013). Empirical support for this hypothesis is strong (Grime 1977; Callaway *et al.* 2002; Brooker *et al.* 2005; He *et al.* 2013; Cavieres *et al.* 2014).

Less is known about directional shifts in PSFs, but they may also vary predictably across gradients in resource availability and stress (Treseder & Allen 2002; Reynolds *et al.* 2003; Van der Putten *et al.* 2016; Smith-Ramesh & Reynolds 2017). Interactions with soil biota may be predominantly negative in resource-rich and productive environments (Revillini *et al.* 2016) because soil pathogens often thrive under such conditions (Reynolds *et al.* 2003; Hersh *et al.* 2012; Spear *et al.* 2015), whereas soil mutualists are less abundant or less mutualistic (Treseder & Allen 2002; Johnson *et al.* 2010). For example, nitrogen and phosphorus additions to grasslands worldwide reduce the abundance of ubiquitous, largely generalist AMF (Avolio *et al.* 2014; Leff *et al.* 2015), and nitrogen additions eliminate the positive PSF experienced by a native grass (Larios & Suding 2015) and reduce the soil biota-mediated competitiveness of a native against an invader (Shivega & Aldrich-Wolfe 2017). Alternatively, resource-poor habitats may favour mutualists and result in more neutral to positive PSFs if plants allocate resources to symbionts to acquire limiting resources (Reynolds *et al.* 2003; Revillini *et al.* 2016). Under extremely low resource availabilities, however, plants and soil biota may start competing for limiting resources (Treseder & Allen 2002), resulting in less positive PSF. Excluding very harsh conditions, we propose that individual interactions shift from predominantly negative in resource-rich habitats, where competition and negative PSFs predominate, to more positive in resource poor environments where plants may experience facilitation and obtain a net benefit from mutualists in the soil.

Assuming that the mostly additive effects documented in our meta-analysis persist across a resource gradient, then together the effect of plant–plant interactions and PSFs may amplify effects at both low and high resources (Fig. 4). In other words, plants may experience a ‘boost’ from facilitation and positive PSF in low-resource conditions and be similarly kept in ‘check’ by competition and negative density-dependent PSF when resource availabilities are greater. Similar to responses within communities where PSF may moderate differences in competitive abilities (Fig. 3), these additive effects could serve as a kind of equaliser across resource gradients in situations where the impacts of these two biotic interactions are similar in strength. While we have focused primarily on fertility gradients, these relationships may shift predictably across precipitation and temperature gradients as well, because non-nutritional benefits by mutualists can equal nutritional benefits (Delavaux *et al.* 2017) and soil biota may positively affect the fitness of plants by moderating the tolerance to pathogens (Newsham *et al.* 1995), drought (Jayne & Quigley 2014; Rubin *et al.* 2017), heat (Zhu *et al.* 2010) and freezing (Chen *et al.* 2013).

Future directions

We have provided estimates for the effects of competition and PSF and have suggested how their interactions may depend on resource levels. This conceptual framework and these analyses point to several research areas that may advance our understanding of biotic interactions and how they may influence the composition of plant communities. If responses to plant–plant interactions and PSF are linear and parallel (Fig. 4), one intriguing implication is that their relative importance may switch across resource gradients (Table 1). That is, the effect of competition would be stronger than PSF in high resource environments but PSF effects would surpass effects of facilitation in low resource environments. One obvious question is whether the negative trend between competitive strength and PSF observed in some greenhouse studies (Fig. 3) persists across resource gradients, especially in low-resource environments where we suggest that positive interactions dominate. Also, if plant–plant interactions and PSF change linearly from positive to negative with increasing resources, biotic interactions are predicted to be weak at intermediate resource levels (Table 1). What effect might this have on plant turnover rates, distributions and diversity across resource gradients, given that strong competition and negative PSF may result in high turnover among plants, whereas facilitation and positive PSF may have stabilising and homogenising effects (Reynolds *et al.* 2003)?

There are many uncertainties in what we propose above, and while many previous findings cited here support our predictions, some do not. For example, negative PSF can occur in

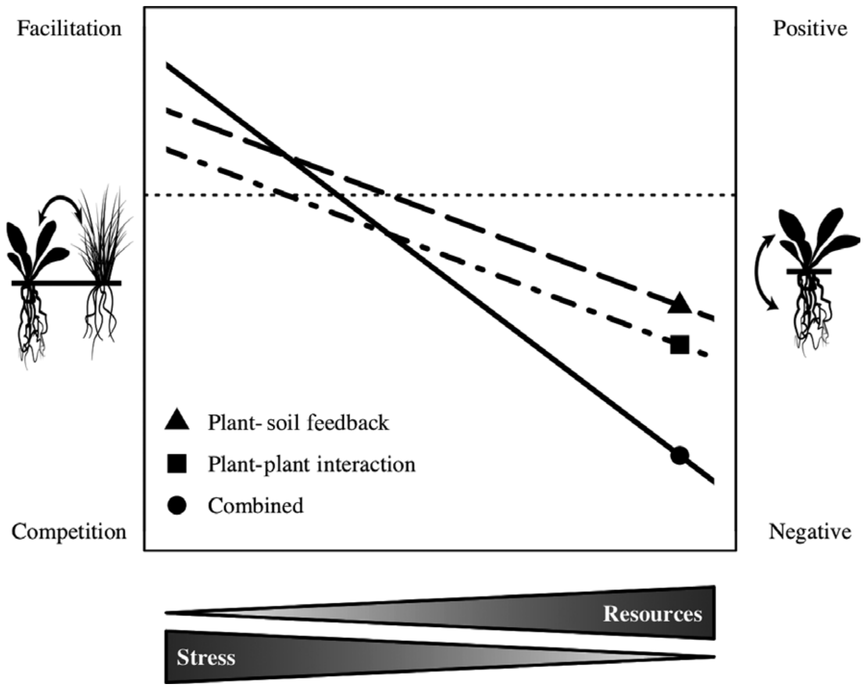

Figure 4 Responses of PSF predicted by the optimal resource allocation model (dashed line) and the stress gradient hypothesis (dot-dash line) and their combined effect (solid line) across resource and/or stress gradients. The horizontal dotted line depicts no net effects. The points plotted represent the meta-analysis results for PSF (triangle), competition (square) and their combined effect (circle), which were, for the most part, conducted under benign conditions. This figure portrays a 'typical plant' (one without specialised adaptations to low/high resources). PSF, plant–soil feedback.

Table 1 List of testable predictions for future, field-based research

1. If effects of competition and soil biota are additive (Fig. 2), then their combined effects are predicted from removal or alteration of competition and soil biota alone.
2. If stronger competitors are more likely than weaker competitors to experience negative PSF (Fig. 3), and if both biotic interactions are strong and equivalent drivers within communities (Fig. 2), removing soil biota will facilitate competitive exclusion and limit coexistence in both high- and low-resource environments.
3. If joint effects of plant–plant interactions and PSF are negative in high resource environments and positive in low resource environments, then removing neighbour plants and soil biota will have a positive effect on focal plants in high- but not low-resource environments (Fig. 4).
4. If plant–plant interactions and PSF change linearly from positive to negative with increasing resources, then these biotic interactions are weak at intermediate resource levels; removing neighbour plants and soil biota should have a small effect in those environments relative to gradient end points (Fig. 4).
5. If pathogens have a higher degree of host preference than mutualists do, then synergistic effects between PSF and competition in high-resource environments are more likely to occur than between PSF and facilitation in low resource-environments.
6. If plant–plant and PSF responses are linear and parallel across resource gradients (Fig. 4), then the relative importance of the two will switch along resource gradients; plant–plant interactions will have stronger effects than PSF under high resources, whereas the opposite will be true in low resources.

PSF, plant–soil feedback.

extremely low-resource environments (Chung & Rudgers 2016; Lambers *et al.* 2017; Teste *et al.* 2017) and positive PSF can help maintain monodominant stands of ectomycorrhizal trees in the highly productive tropics (McGuire 2007). Assessing the support for the predictions and questions outlined here (Table 1) and elsewhere (e.g. Treseder & Allen 2002; Smith-Ramesh & Reynolds 2017) will require research across natural gradients (e.g. rainfall, nutrient deposition or chronosequence) as well as studies that identify and manipulate key biogeochemical properties of gradients where plant density and PSF are explicitly measured or manipulated. Like others (Kulmatiski & Kardol 2008; Lou *et al.* 2014), we argue that advances in our understanding of linkages between PSF and plant community dynamics are likely to follow as researchers conduct more studies in the field using carefully conceived designs (see Smith-Ramesh & Reynolds 2017). Field experiments are challenging, in part because soil communities are complex and spatially variable, and unlike individual plants, soil biota are not easy to identify, isolate and manipulate. However, recent studies involving inoculation experiments on large (Wubs *et al.* 2016) and more moderate scales (Bennett *et al.* 2017), biocide applications (Reinhart & Clay 2009; Bagchi *et al.* 2014) and reciprocal transplants approaches (Reed & Martiny 2007; Yelenik & Levine 2011) illustrate that these challenges are not insurmountable and can provide unique insights into the relative importance of soil biota in more complex settings.

To fully understand and predict shifts in PSF, however, we need to consider individual responses of mutualists, pathogens and decomposers to resource conditions (Heinze *et al.* 2016; Van der Putten *et al.* 2016). There is a rich history in microbial ecology that needs to be better incorporated into PSF research. Plant pathologists have spent decades studying the factors that regulate disease (Hord & Ristaino 1992; Yanar *et al.* 1997), and mycorrhizal ecologists have long recognised that mycorrhizal function depends on resource supply and demand and can range from mutualistic to parasitic (Johnson *et al.* 1997; Treseder & Allen 2002). As such, PSF responses may not necessarily correlate with predictable shifts in abundances of various microbial groups. For example, AMF could conceivably be more abundant in high- than low-resource environments, because a large plant could allocate more carbon to these symbionts than a small plant, but a small plant would benefit more than a plant that is not as resource limited if AMF can help acquire limiting resources.

Recent advances in analytical tools, including high throughput sequencing and quantitative stable isotope probing (e.g. Drigo *et al.* 2010; Leff *et al.* 2015) are revealing the complexity and potential functionality of soil biota. Curated databases, such as MycoDB, FunGuild and MaarjAM (Öpik *et al.* 2010; Chaudhary *et al.* 2016; Nguyen *et al.* 2016) can inform on potential function of sequenced microbial communities and generate species distribution maps to estimate shifts across environmental gradients (Kivlin *et al.* 2017). This information could be combined with metagenomics methods that track shifts in functional genes associated with pathogenicity and nutrient acquisition. This could be particularly interesting for AMF given that they can aid in nutrient acquisition as well as pathogen protection (Sikes *et al.* 2009), which means that the function of this group of soil biota may shift across resource gradients.

CONCLUSIONS

Our analyses show that PSF effects, while variable among different treatments, can rival the effects of competition. Combined, PSF and competition can have additive and sometimes synergistic effects and result in plants that are less than half the size of plants that experience neither. As such, incorporating PSF into plant competition models will likely improve predictions of plant–plant interaction outcomes. We also found that when plants experience moderate, but not strong competition, PSF has the potential to reduce differences in competitive abilities among plants and promote coexistence.

Extrapolating from our analytical results, we suggest that the combined effects of plant–plant interactions and PSFs are likely to amplify negative interactions in high-resource environments and enhance positive biotic interactions in low-resource environments. Exploring these interactions in field conditions with greater biotic complexity will provide empirical tests of the ideas presented here on how plant interactions and PSF affect the organisation of plant communities, as well as help us predict responses of plant communities to rapid anthropogenic global change.

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AUTHORSHIP

YL coordinated the writing and coded the papers included in the meta-analysis. RB conducted the meta-analyses with input from JB, SK and YL, and BL ran the correlation and residual analyses and made all figures except Fig. 1, which was provided by Emily Harrington. SK did the original Web of Science search and screened abstracts for the meta-analysis, and YL, KR, MH, JM and BL screened potential papers more carefully for inclusion. All co-authors participated in generating the ideas presented here and actively partook in the writing of this manuscript.

DATA ACCESSIBILITY STATEMENT

Data required to repeat the analyses presented here are available in the Dryad Digital Repository (doi:10.5061/dryad.487fq3m).

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SUPPORTING INFORMATION

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

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