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Research article

Plant–soil feedback relationships depend on nutrient availability and stoichiometry

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Plant–soil feedback (PSF) significantly influences plant species abundance and community composition. Negative PSF arises from pathogen accumulation, autotoxicity, and nutrient depletion, often being species-specific. Conversely, cultivating mutualistic microbes like mycorrhizal fungi can enhance PSF positively. While PSF relationships are typically studied in mesocosms under optimal nutrient conditions, natural ecosystems often face nutrient limitations, particularly nitrogen (N) and phosphorus (P). The impact of nutrient availability and N:P stoichiometry on PSF remains largely unexplored. In our study, we examined the PSF of six plant species across six nutrient treatments, combining three N:P ratios (3, 15 and 75) with two nutrient levels (high and low). The selected species represented distinct natural stoichiometric niches: two from P-limited soils, two from N:P co-limited soils, and two from N-limited soils. Our findings revealed that nutrient supply level and N:P ratio affected PSF in five out of six species. Two species exhibited more positive PSF at high nutrient supply, while one species showed a more positive PSF at low nutrient levels. Similarly, two species experienced higher PSF at low N:P ratios, and one at higher N:P ratios. Notably, the observed effects were not correlated with the species' natural stoichiometric N:P niches. In some cases, PSFs shifted from negative to positive within a single plant species, depending on nutrient levels and ratios. These results suggest that the effects of soil nutrient availability on PSF are common among plant species but are species-specific. Such nutrient-dependent PSF effects likely influence species coexistence in natural plant communities and are also impacted by human interferences in nutrient cycles, such as enhanced atmospheric N deposition rates.

Keywords: mycorrhizae, N:P ratio, plant pathogens, soil nutrients, species coexistence, stoichiometric niche

Introduction

Plants have the capacity to influence biotic and abiotic attributes of the soil, which can indirectly affect plant growth of themselves and conspecifics, i.e. intraspecific plant–soil feedback (PSF), or of heterospecifics, i.e. interspecific PSF (van der Putten et al. 2016). The importance of this phenomenon in explaining relative plant abundances

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and shaping natural communities is widely recognized (Klironomos 2002, van der Putten et al. 2013). Associations with pathogens and mutualists can result in either negative, neutral, or positive feedbacks (van der Putten et al. 2016, Luo et al. 2019). The most important driver of negative PSF is the accumulation of pathogens in the rhizosphere of the host plant (Luo et al. 2019). Because different plant species attract and support widely varying communities of soil pathogens, negative PSF is often species-specific (Crawford et al. 2019). This negative intraspecific PSF may prevent plant species from reaching or maintaining high densities through negative frequency dependency, and thus promote coexistence (Bonanomi et al. 2005, Hendriks et al. 2015, Goossens et al. 2023). Another mechanism of negative feedback is toxicity, which is the release of allelopathic compounds that are harmful for the species itself (autotoxicity, negative intraspecific PSF) or for other species (heterotoxicity, negative interspecific PSF). These compounds can enter the soil by root exudation or during organic matter decomposition (Bonanomi et al. 2005, Van De Voorde et al. 2012). Lastly, negative PSF may be caused by species-specific nutrient depletion. That is, plants can make the soil less suitable for conspecific individuals as a result of their shared nutrient acquisition strategies (Ke et al. 2015, Aldorfová et al. 2022), which include root architecture and acquired forms of nitrogen (N) (Kraiser et al. 2011). Positive PSF is often driven by the cultivation of mutualistic microbes in the rhizosphere, which are in general less species-specific than pathogens (Semchenko et al. 2022). Mycorrhizal fungi form associations with about 90% of plant species, facilitating the acquisition of nutrients from the soil (Revillini et al. 2016). In addition to providing limiting nutrients, some mycorrhizal fungi protect plant roots from pathogens and other enemies, resulting in positive or reduced negative PSF (Revillini et al. 2016, Bennett and Klironomos 2018). However, this effect depends on several other factors. For example, ectomycorrhiza protect the root more effectively from damage than arbuscular mycorrhizal fungi (AMF) (Bennett and Klironomos 2018). Furthermore, nutrient availability in the soil determines the dependency of plants on mycorrhizal associations (Bennett and Klironomos 2018).

Together with water, light and carbon dioxide, mineral nutrients are the most important resources for plants, and therefore often growth-limiting in natural environments (Elser et al. 2007, Craine et al. 2012). In particular N and phosphorus (P) frequently limit terrestrial biomass production (Güsewell 2004). Although nutrient limitation is often considered at the community level, different species within a community may be limited by different elements because of their distinct adaptations (Verhoeven et al. 1996, Lannes et al. 2016, Wassen et al. 2021). First, there are contrasting nutrient acquisition mechanisms, including associations with rhizobacteria and mycorrhizal fungi for N and P uptake, respectively (Güsewell 2004, Luo et al. 2022). Second, nutrient conservation allows efficient use of acquired nutrients, and can therefore alleviate nutrient limitation. N and P can be resorbed from senescing plant tissues, and the relative resorption efficiency of both nutrients influences adaptation to N- or P-limited conditions (Güsewell 2004, Brant and Chen 2015). Distinct combinations of these adaptations lead to unique stoichiometric niches, each with a different optimal N:P ratio (Wassen et al. 2021).

The effects of plant–soil feedback and nutrients on plant growth are mostly considered separately in literature. PSF studies are often performed under optimal or standardized nutrient supplies, where nutrients are added to individual pots (Klironomos 2002, Brinkman et al. 2010). Natural ecosystems however are generally growth-limited by N, P or a combination of these nutrients (Harpole et al. 2011, Fay et al. 2015). In most other PSF studies, field soils with undetermined nutrient availabilities are used (Schnitzer et al. 2011, Van Nuland et al. 2017) as PSF is examined independently from soil nutrient load. However, nutrient availabilities in natural ecosystems can change over time, e.g. due to anthropogenic pressures (Peñuelas et al. 2011), and whether PSF depends on nutrient availability or on the type of nutrient limitation remains unknown. First, the type of resources that are limiting influences plant dependency on nutritional mutualists. That is, plants strongly limited by mineral nutrients are expected to allocate a high amount of resources to mutualists, possibly resulting in positive PSF. In contrast, limitation by other resources (e.g. light or water) will reduce this allocation, causing reduced protection against pathogens and thus more negative PSF (Revillini et al. 2016). Second, the aforementioned effect of species-specific nutrient depletion (Ke et al. 2015) is expected to become less important with increasing nutrient availability in the soil. Third, it is known that soil microbial communities are strongly influenced by nutrient levels (Van Der Heijden et al. 2008) and by the balance of N:P supply, with high N:P ratios resulting in greater fungal biomass relative to bacteria (Maaroufi and De Long 2020). Furthermore, P-limitation leads to dominance of mycorrhizal fungi, whereas N-limited conditions favour non-mycorrhizal fungi, including saprophytic, mutualistic and pathogenic species (Chagnon and Bradley 2013, Scheifes et al. 2024).

Limited studies have examined the relationship between nutrient availability and PSF. A greenhouse experiment by in 't Zandt et al. (2019) shows contrasting results for PSF based on above- and belowground biomass. Notably, PSF based on total biomass, which is most relevant, was not assessed. PSF based solely on above- or belowground biomass can differ due to variations in above–belowground allocation, influenced by nutrient availability and N:P stoichiometry (Olde Venterink and Güsewell 2010, Poorter et al. 2012). Another greenhouse study by Png et al. (2019) found that PSF was negative for N-limited soil from young dunes and neutral for P-limited soil from older dunes. However, since the soils differed in more parameters than only N and P concentration, no causal relationship was established. To date, no studies have formally tested the link between nutrient availability, nutrient ratios and PSF (Smith-Ramesh and Reynolds 2017).

The aim of this study was to determine the possible effects of soil N:P ratios and nutrient availability on species-specific plant–soil feedback (PSF) in species with different stoichiometric niches. For this purpose, plants were grown in soil conditioned by either the same or another species, and with different nutrient treatments. We hypothesized that both nutrient supply level and N:P stoichiometry would affect the direction and strength of PSF. Moreover, we predicted that:

1. PSF is generally more positive under low than under high nutrient levels, because of higher dependency of plants on mycorrhizal mutualists and reduced growth of pathogens under low nutrient levels (Ke et al. 2015, Van Der Heijden et al. 2015, McCarthy-Neumann and Kobe 2019);
2. a high ratio of N:P supply has a positive effect on PSF due the increased importance of AMF under P-limitation where AMF improve both P acquisition and plant resistance to pathogens (Laliberté et al. 2015); and
3. if the effects of the ratio of N:P supply differ among species, it may partially explain plant species' dependencies on stoichiometric properties of the soil; i.e. plant species naturally occurring under P-limited conditions will have a less negative PSF in soil with a high N:P ratio (i.e. P-limited soils), and vice versa for species from N-limited sites, explaining their natural distribution.

Material and methods

Experimental setup

Species selection

The experiment consisted of two phases: firstly, the conditioning phase where plants were subjected to the soil microbial communities and (species-specific) pathogens and mutualists could accumulate. Secondly the response phase, where plants were grown in the conditioned soil from the first phase (Fig. 1). Two families of plants (Poaceae and Asteraceae) were used in a greenhouse experiment, as a form of phylogenetic replication. From each family, three species were selected which occur in natural environments with contrasting nutrient limitations, i.e. they occur within their own 'stoichiometric niche' (Wassen et al. 2021). The three grass and forb species used were *Briza media* and *Centaurea jacea* (mostly occurring on P-limited soils), *Agrostis capillaris* and *Leucanthemum vulgare* (N and P co-limited soils as stoichiometric niche) and *Alopecurus pratensis* and *Achillea millefolium* (N-limited soils as stoichiometric niche). These preferences were based on the average of vegetation N:P ratios measured at sites where the species occur across eight European countries. The N:P optima were: *B. media,* 17.91 ± 6.88 (n = 48), *A. capillaris*, 11.22 ± 6.22 (n = 75), and *A. pratensis*, 6.74 ± 2.07 (n = 64) for the three grass species, and *C. jacea,* 20.45 ± 6.57 (n = 38), *L. vulgare,* 13.63 ± 6.56 (n = 24), and *A. millefolium*, 8.11 ± 4.87 (n = 34) for the forb species (mean ± standard deviation given, number of sites given between brackets). Data are from Roeling et al. (2018) and Wassen et al. (2021), provided by the authors. Stoichiometric niche groups were all statistically different from each other (Supporting information). All six species are known to involve in mutualisms with AMF (Allison 2002, Dixon 2002, Eschen et al. 2009, Mummey et al. 2009, Šmilauer et al. 2021).

Setup conditioning phase

For the conditioning phase, seeds were germinated in universal potting soil (Viano), 10–28 days before the start of the experiment, depending on the germination rate of the species. We then transplanted 60 seedlings per plant species (for a total of 360 plants) into separate 0.5 l pots, filled with a 95–5 vol% sand–inoculum mixture, for 8 weeks in a randomized setup within a greenhouse. The sand fraction consisted of dried white quartz sand (N and P concentrations below detection limits). Soil inoculum was collected from a moist, mesotrophic hay meadow (Doode Bemde, Belgium, 50°48'55.9"N, 04°38'41.2"E). A cylindrical soil core was used to collect soil samples of the upper 10 cm at 30 randomly selected locations within the meadow, which were then mixed.

Nutrient treatments

To disentangle the effects of nutrient levels and N:P ratio on biomass and PSF, three N:P ratios (3 i.e. N-limited, 15 i.e. balanced, and 75 i.e. P-limited) and two nutrient levels (high and low, with a difference of factor 5) were combined into six nutrient treatments in a full-factorial design (based on Güsewell 2005, Olde Venterink and Güsewell 2010; Supporting information). The combination of high nutrient level and balanced N:P ratio (15) corresponded with a half-strength Hoagland solution, for a total of 30.0 mg N, 2.00 mg P, 222 mg K, 55.2 mg Ca, 31.5 mg Mg, 4.94 mg Fe, 0.0342 mg Cu, 0.395 mg B, 0.237 mg Mn, 0.118 mg Zn, and 0.0691 mg Mo per plant in 8 weeks. To obtain different N:P ratios, only N and P concentrations were manipulated (Supporting information). The low nutrient level was realised by adding five times lower amounts of N and P than in the high nutrient level. Nutrients were added weekly in a stepwise way, i.e. each individual plant received 2.5 ml per week in the first 2 weeks, 5 ml per week in the next 4 weeks and 7.5 ml per week in the last 2 weeks. This was to take into account increasing nutrient demands during plant growth (Olde Venterink and Güsewell 2010). Plants were watered three times a week with deionized water. After the 8th week, plants were harvested and cut at the root–stem transition. Since the soil had to be retained in the pots for further use in the response phase, roots could not be harvested by washing, but rather by carefully breaking up the sand, taking out the roots and then placing back the sand into the pots. The remaining sand attached to the roots had to be washed off. After drying the plants for 48 h at 70°C, aboveground and belowground biomass was measured.

Response phase

During the response phase, the same six species were grown in soil conditioned during the first phase. Per species, again 60 plants were divided over the six different nutrient

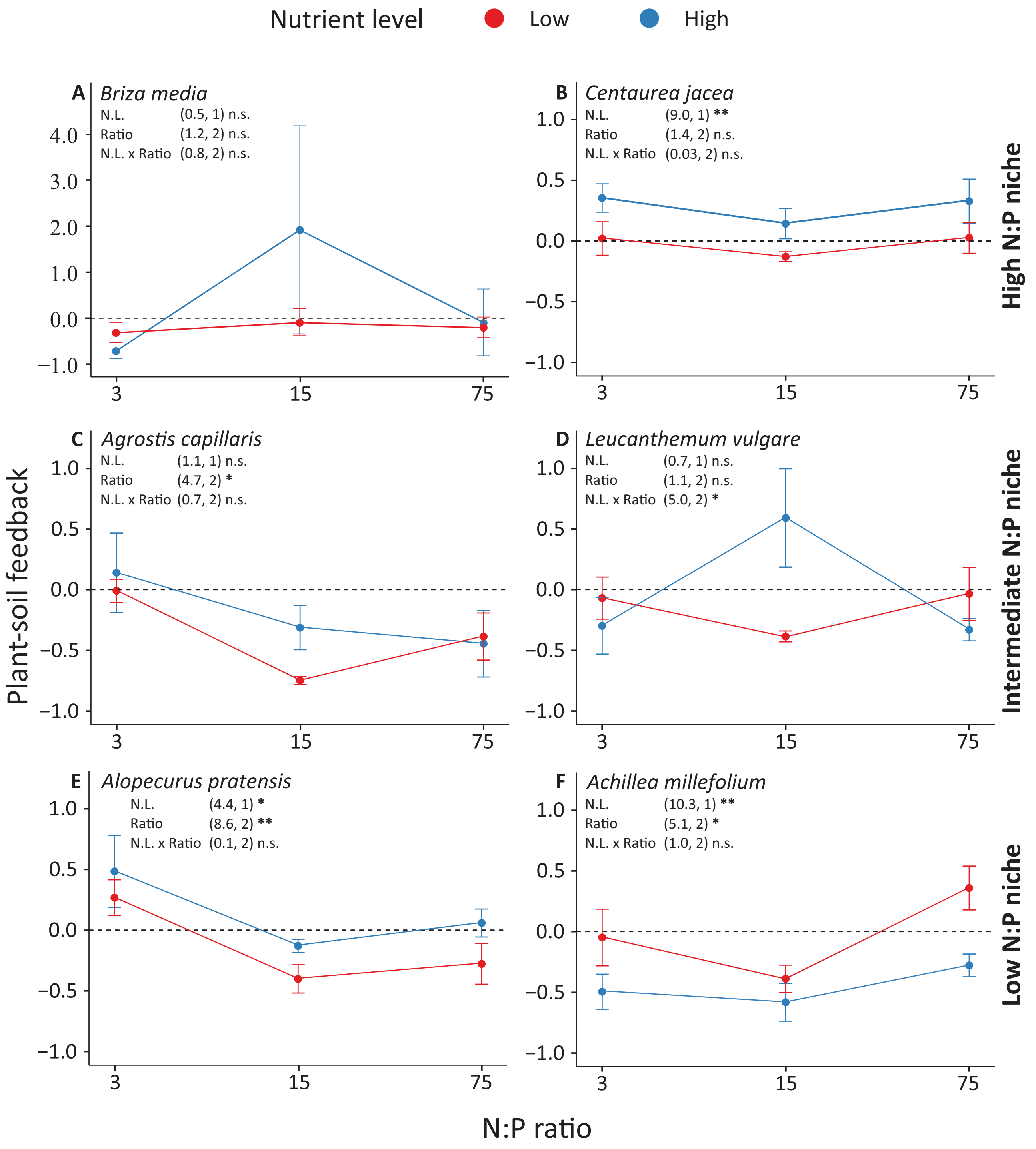

Figure 1. Relationships between nutrient level, N:P ratio, and PSF, calculated with total biomass, for each species. Columns correspond with plant families (A, C, E are Poaceae; B, D, F are Asteraceae) and rows with stoichiometric niches: high N:P niche (P-limitation), intermediate N:P niche (N and P co-limited), and low N:P niche (N-limited). Red: low nutrient level; blue: high nutrient level. For each of the species, F-values and degrees of freedom are given in brackets for the effects of nutrient level (NL), N:P ratio (Ratio), and their interaction (N.L. × Ratio) on PSF. Significant effects are indicated by asterisks. p-values: *** < 0.001 < ** < 0.01 < * < 0.05 < n.s. Bars represent standard errors and x axis is log transformed. For each combination of species, nutrient level and N:P ratio n = 5. Note that in *B. media* the y-axis has a different scale.

treatments (hence n = 10). In order to quantify the PSF each species experienced, half of all species were grown in soil conditioned by conspecific individuals during the conditioning phase (= 'self' plants; n = 5), and the other half were grown in soil conditioned by one of the other five species (= control plants; n = 5, repeated once for each species). For *B. media*, 40 instead of 60 seedlings were used because of poor germination (resulting in n = 3 or 4 for this species). Plants were again grown for 8 weeks, and water and nutrients were added as before. Finally, after harvesting all plants by washing and drying for 48 h at 70°C, aboveground and belowground biomass were measured. The six species, six nutrient treatments, and the conspecific versus heterospecific conditioning were combined in a full-factorial design for a total of 360 experimental units (6 species × 6 nutrient treatments × 2 soil conditioning treatments × 5 replications, Fig. 1).

PSF calculations

From the data of the response phase, PSF was calculated using the following equation:

$$\mathrm{PSF} = \frac{\mathrm{Biomass}_{\mathrm{self}} - \mathrm{Biomass}_{\mathrm{control}}}{\mathrm{Biomass}_{\mathrm{control}}} \qquad (1)$$

where 'Biomass' is the averaged total biomass, and 'self' and 'control' indicate that the plant is grown in soil conditioned by a conspecific or heterospecific plant (repeated for each of the five other species), respectively. Positive PSFs are obtained when plants grow better in soil conditioned by a conspecific than soil conditioned by a heterospecific plant, in the opposite case negative PSFs were obtained. Individual PSFs for all plants grown in conspecific soil were calculated by using individual biomass from the self-treatments and the averaged biomass for the controls in Eq. 1.

Statistics

Two linear mixed models were constructed with the function *lmer* from the R package 'lme4' (Bates et al. 2015). The first included PSF as response variable and nutrient level, N:P ratio, and stoichiometric niche as categorical fixed factors, along with their interactions, to assess whether nutrient availability and ratio influenced PSF and whether these effects varied based on the plant's stoichiometric niche. Plant species, nested within plant family, was included as a random factor.

To determine if the effects of nutrient level and N:P ratio were species-specific, a second model was created by swapping stoichiometric niche with plant species. Additionally, two-way ANOVAs were conducted for each plant species separately, followed by Tukey HSD post hoc tests to identify significant differences between N:P ratios. Assumptions of normality and homogeneity of variance were tested using the Shapiro–Wilk test and an F-test, respectively. Bonferroni corrections were applied to account for multiple comparisons in post hoc tests.

Table 1. The effect of nutrient supply level, N:P ratio, stoichiometric niche of the plants, and their interactions, on PSF. χ^2, effect size (as generalized Eta) and p-values of the mixed linear model are given. Predictors (nutrient level, N:P ratio, and Stoichiometric niche) are inserted as categorical factors with all interactions. Plant species, nested within plant family, are inserted as random factor. Significant effects are indicated in bold.

Variable	χ^2	η_g^2	p
Nutrient level	2.1	0.02	0.15
N:P ratio	0.6	0.002	0.73
Niche	4.6	0.24	0.10
Nutrient level × N:P ratio	**6.4**	**0.04**	**0.04**
Nutrient level × Niche	3.1	0.02	0.22
N:P ratio × Niche	8.1	0.05	0.09
Nutrient level × N:P ratio × Niche	2.1	0.01	0.71

All analyses were performed in R ver. 4.2.1 (www.r-project.org) and figures were made with ggplot (Wickham 2016).

Results

In both PSF models, PSF depended on the combination of nutrient level and N:P ratio, as indicated by a significant interaction (Table 1, Supporting information). The interaction of stoichiometric niche with N:P ratio was marginally significant ($p = 0.09$; Table 1), with the strength of PSF tending to become more positive when species were grown in soils near their optimum N:P ratio. Furthermore, the interaction between species and nutrient ratio had a strong significant effect on PSF ($p < 0.001$; Supporting information), showing that the influence of N:P ratio on PSF is species-specific. Excluding the three-way interaction term yielded results consistent with the original models, confirming that the main results were robust.

The species-specific models showed an effect of N:P ratio in three species (Fig. 1). For *A. capillaris* and *A. pratensis* (Fig. 1C, E), PSF was more positive under low N:P ratios (though not significantly different from N:P ratio 75 for *A. capillaris*). *Achillea millefolium* (Fig. 1F), on the other hand, had the most positive PSF under high N:P. In three species, there were opposite effects of nutrient level, with significantly more positive PSF at high level in both *Centaurea jacea* and *A. pratensis* (Fig. 1B, E) and at low level in *A. millefolium* (Fig. 1F). In *L. vulgare*, the interaction effect between nutrient level and N:P ratio on PSF was significant, showing a more positive PSF at high nutrient levels, but only for intermediate N:P ratios (Fig. 1D). The effects on PSF in *B. media* (Fig. 1A) were unclear and statistically not significant, likely due to insufficient replication.

Discussion

Generally, PSF studies are performed under optimal nutrient supply, assuming that these habitat conditions would be representative for the species response. However, our results show that PSFs are strongly affected by both absolute and relative nutrient availabilities. The plant species included in this study showed contrasting PSFs ranging from negative to neutral or positive, depending solely on the soil's N and P availabilities or stoichiometry. To our knowledge, this is the first study to establish a causal link between nutrient levels, soil N:P ratio, and PSF. Therefore, when designing PSF experiments to predict plant community dynamics, it is essential to consider both the absolute and relative nutrient levels within these plant communities, as neglecting them may lead to inaccurate or misleading conclusions. Our results also highlight the risk of generalizing conclusions from individual PSF studies, as the effects of PSF can vary significantly across plant communities, each with its own distinct nutrient availabilities.

Despite our results clearly showing that PSFs are affected by nutrient availability and stoichiometry, none of our three hypotheses were supported. Hence, the results were not in line with our expectations about the relative importance of low or high nutrient availability or N:P stoichiometry on mutualistic and pathogenic soil microbes for plant growth, nor on the plant species stoichiometric niches with respect to nutrient availability and stoichiometry. Instead, we observed a range of species-specific effects of nutrient ratios on PSF, suggesting that different mechanisms drive PSF in different species. In the following paragraphs we will discuss our results in the light of our three hypotheses, and will evaluate the importance of the species-specific rather than generalized effects of variation in nutrient supply and stoichiometry on PSF.

Contrary to our first hypothesis, PSF was not consistently more positive under low nutrient availability (Table 1, Supporting information). Hence, our findings differ from those of in 't Zandt et al. (2019) who observed that PSF was generally eliminated under high nutrient level, but perhaps the difference can be ascribed to the relatively low replication applied in that study, which likely prevented capturing of the diverse species-specific responses to nutrient increases. We based our hypothesis on the expectations that AMF would be more important under low nutrient availability (Van Der Heijden et al. 2015), while high nutrient availability would result in increased pathogen growth (Nordin et al. 1998, Wei et al. 2018) and thus more negative PSFs. Furthermore, the association with mycorrhizal fungi at high nutrient availability can become less beneficial and in some cases even detrimental, as the cost of providing C to the fungi increases relative to the benefit of receiving phosphorus (Grman et al. 2012). Although *A. millefolium* indeed showed a more positive PSF under low nutrient availability (Fig. 1F), the opposite was found for three out of six species (Fig. 1B, D, E). Possible explanations are a decrease in species-specific depletion of nutrient forms (Ke et al. 2015, Aldorfová et al. 2022) due to reduced nutritional stress (Gustafson and Casper 2004, Smith-Ramesh and Reynolds 2017), or increased production of chemical defenses against pathogens (Coley et al. 1985, Lou and Baldwin 2004) at higher nutrient availabilities. Thus, we propose that the net effect of nutrient availability on PSF is driven by a complex interplay of mechanisms and manifests as a highly species-specific response that can range from beneficial to detrimental, or have little to no impact.

Our findings do not support our second hypothesis, nor the results of Png et al. (2019), that PSF would be generally less negative in P-limited soils than in N-limited or N:P-balanced soils. We expected a less negative PSF under high N:P, assuming that arbuscular mycorrhiza would be most important under these N:P stoichiometric conditions to improve P acquisition (Smith et al. 2003, Ceulemans et al. 2011, Ma et al. 2021), which would also strengthen plant resistance to pathogens (Laliberté et al. 2015). Although we did observe this for *A. millefolium* (Fig. 1F), the opposite was found for *A. pratensis* (Fig. 1E) and *A. capillaris* (Fig. 1C). AMF may have had a minimal impact on PSF in our experiment due to their broad host range (cf. Semchenko et al. 2022). In our study, we compared intraspecific PSF (plants growing in soil conditioned by conspecifics) with interspecific PSF as control group (soil conditioned by heterospecifics). Differences in AMF abundance between soils conditioned by conspecifics and those conditioned by heterospecifics may have been limited because of this broad host range. This generalist characteristic suggests that the presence and activity of AMF are less likely to vary significantly across different plant species, leading to comparable PSF outcomes regardless of the plant species present. Instead of AMF, pathogens may be responsible for the observed changes in PSF in our study, as pathogens are more often species-specific (Crawford et al. 2019). Indeed, Ebeling et al. (2022) found greater damage by pathogens in response to nitrogen addition in grasses but not in forbs, although the authors did not ascribe these effects to variation in N:P ratios. Our results correspond to their findings with two out of three grasses having more negative PSF at higher N:P ratios (Fig. 1C, E), while this is not observed for forbs.

Our third hypothesis – that variation in PSF among species would align with their natural stoichiometric niches – was not supported by our findings. *Leucanthemum vulgare* and *A. pratensis* exhibited more positive PSFs at an intermediate N:P ratio and under N-limitation, respectively (Fig. 1D, E), consistent with their known stoichiometric niches. In contrast, *A. capillaris* and *A. millefolium* showed PSF optima at low and high N:P ratios, respectively (Fig. 1C, F), which do not correspond with their typical stoichiometric niches in natural communities – N and P co-limitation for *A. capillaris* (though it can dominate under P-limitation) and N-limitation for *A. millefolium*. We had expected that species with high N:P stoichiometric niches – typically considered more dependent on mycorrhizal symbioses, i.e. 'outsourcing' (Ceulemans et al. 2011, Tedersoo and Bahram 2019, Bergmann et al. 2020) – to show more positive PSFs under P-limitation due to increased reliance on AMF. However, our findings do not support this pattern: species from high N:P niches did not consistently experience more positive PSFs at P-limitation compared to those from intermediate or low N:P niches. This aligns with recent work (Scheifes et al. 2024) showing that species adapted to P-limitation are not necessarily more associated with arbuscular mycorrhiza but may instead be associated with non-mycorrhizal traits such as cluster roots (Neumann and Martinoia 2002). As a result, a stronger expression of 'do-it-yourself' traits under P-limitation in high N:P species does not necessarily lead to more positive PSFs mediated by PSF. In addition to the effects of mutualistic interactions, we had expected pathogen pressure to increase for plants growing out of their natural stoichiometric niche, as plant nutritional status can lower disease resistance (Martín-Cardoso and San Segundo 2025). However, pathogen infection success is influenced by both N and P availability (Lacroix et al. 2017), and since pathogens have their own stoichiometric niches (Frenken et al. 2021), their success depends on the nutrient stoichiometry of the host. This suggests that plants may experience reduced infection – and thus more positive PSFs – when shifts in soil nutrient stoichiometry push plant tissue stoichiometry outside the optimal range for pathogen success, a mechanism supported in algal and phytoplankton systems (Clasen and Elser 2007, Frost et al. 2008, Maat and Brussaard 2016), but not yet demonstrated in plants.

Despite the absence of generalizable effects of nutrient availability on PSF, the distinct species-specific responses observed in this study open avenues for future research. Integrating soil nutrient stoichiometry with PSF mechanisms may enhance our understanding of ecological processes, such as exotic plant invasions. Exotic invasive species often experience more positive PSF due to pathogen release in their new range, which can facilitate their establishment (De Long et al. 2023). High nutrient availability may further promote invasion success by increasing the relative dominance of invasive species (Heckman et al. 2017). Similarly, most invasive species thrive under low N:P ratios, i.e. N-limitation (Lannes et al. 2012, Zhang et al. 2017, Wan et al. 2018). Given our findings on the relationship between nutrients and PSF, it is plausible that these factors interact in shaping invasion dynamics. Future research should explore whether variations in PSF, driven by soil stoichiometry, contribute to species invasions.

The dependency of PSF on nutrient availability may have implications for plant community composition. Theoretical models suggest that negative species-specific PSFs can promote species coexistence, provided they are not outweighed by interspecific competition (Bonanomi et al. 2005, Revilla et al. 2013, Ke and Wan 2020). This is supported by experimental studies on grassland communities (Bonanomi et al. 2005, Kulmatiski et al. 2008), showing that pathogen presence disproportionately affects dominant species, indirectly benefiting less competitive species by reducing competition (Goossens et al. 2023). Thus, if anthropogenic changes in the soil nutrient status cause a shift towards more positive feedbacks in a plant community, this could have cascading effects on biodiversity by destabilizing species coexistence. Our results demonstrate that nutrient availability and stoichiometry fundamentally shape PSF in a species-specific manner, demonstrating that PSF outcomes cannot be generalized across species or nutrient environments. Recognizing this complexity is crucial, not only for predicting plant community dynamics, but also for anticipating how global changes in nutrient deposition may disrupt coexistence mechanisms and drive shifts in biodiversity.

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Author contributions

Elias Goossens: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (lead); Supervision (equal); Visualization (equal); Writing – original draft (lead). **Jeremias Uyttenbroeck**: Data curation (equal); Formal analysis (equal); Investigation (equal); Visualization (equal); Writing – original draft (equal). **Harry Olde Venterink**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://datadryad.org/dataset/doi:10.5061/dryad.98sf7m0x7 (Goossens et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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