

Global patterns and drivers of plant–soil microbe interactions

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Abstract

Plant–soil feedback (PSF) is an important mechanism determining plant community dynamics and structure. Understanding the geographic patterns and drivers of PSF is essential for understanding the mechanisms underlying geographic plant diversity patterns. We compiled a large dataset containing 5969 observations of PSF from 202 studies to demonstrate the global patterns and drivers of PSF for woody and non-woody species. Overall, PSF was negative on average and was influenced by plant attributes and environmental settings. Woody species PSFs did not vary with latitude, but non-woody PSFs were more negative at higher latitudes. PSF was consistently more positive with increasing aridity for both woody and non-woody species, likely due to increased mutualistic microbes relative to soil-borne pathogens. These findings were consistent between field and greenhouse experiments, suggesting that PSF variation can be driven by soil legacies from climates. Our findings call for caution to use PSF as an explanation of the latitudinal diversity gradient and highlight that aridity can influence plant community dynamics and structure across broad scales through mediating plant–soil microbe interactions.

KEY WORDS

aridity, growth form, Janzen–Connell effect, plant–soil feedback, species coexistence

INTRODUCTION

Understanding the mechanisms underlying the maintenance of species diversity has been a central issue in ecology (Schemske et al., 2009; Wright, 2002). Recent studies have highlighted the potential importance of interactions between plants and soils (plant–soil feedback, PSF) in the maintenance of plant diversity in plant communities (Bennett et al., 2017; Teste et al., 2017). PSF is based on the process that plants influence the abiotic and biotic soil environment, which can in turn impact the performance of other subsequent conspecific and heterospecific plants (Bever, 1994; Van der Putten et al., 1993). Since the early 1990s, ecologists have conducted a large

number of experiments and found that PSF processes have significant influences on plant species abundance (Klironomos, 2002; Mangan et al., 2010, but see Heinze et al., 2020; Reinhart et al., 2021), invasion success (Callaway et al., 2004; Klironomos, 2002), community succession (Kardol et al., 2006), and species richness (Teste et al., 2017). Therefore, it is expected that PSF may contribute to plant diversity patterns on large spatial scales. Previous studies have demonstrated that PSF can range from positive to neutral and negative across different species and regions (Kulmatiski et al., 2008), yet the geographic patterns in PSF remain highly controversial, which limits our understanding of the generality of PSF effects on plant diversity patterns.

The Janzen–Connell hypothesis suggests that conspecific negative density/distance dependence tends to be stronger in tropical regions than in high latitudes, which leads to decreasing species diversity from the tropics to high latitudes (also known as the latitudinal gradient of species diversity) (Connell, 1971; Janzen, 1970). Several mechanisms and agents may lead to strong conspecific negative density/distance dependence, among which soil-borne microbes are likely important belowground agents (Augspurger, 1983; Chen et al., 2019; Liang et al., 2015). Corresponding with the expectation of the Janzen–Connell hypothesis, researchers expect that PSF tends to be more negative in the tropics and will become neutral or positive with the increase of latitude. On the other hand, the strength of PSF is a net effect of multiple soil microbial groups (mainly pathogens and mutualists), and different soil microbial groups usually show different geographic patterns. For example, although the diversity or abundance of some soil microbe groups (e.g. arbuscular mycorrhizal fungi and pathogens) decrease with latitudes (Davison et al., 2015; Delgado-Baquerizo et al., 2020; Tedersoo et al., 2014), other groups (e.g. ectomycorrhizal fungi) do not exhibit the same latitudinal patterns (Tedersoo et al., 2014). This decoupling in the biogeography between these important plant-dependent microbial groups suggests that PSF may not be strongly associated with latitude as suggested by the Janzen–Connell hypothesis. Therefore, although the variation of PSF has been evaluated well by previous meta-analyses (Crawford et al., 2019; Kulmatiski et al., 2008; Xi et al., 2021), the latitudinal gradient of PSF needs to be clarified.

Previous studies suggest that the geographic variations in the abundance and diversity of soil microbial groups that are important for PSF are influenced by climates (Hendershot et al., 2017; Serna-Chavez et al., 2013). Especially, increased drought can increase the abundance of mycorrhizal fungi but decrease that of soil-borne pathogens, which may cause a more positive PSF at drier sites (de Vries et al., 2023). Previous experimental studies also found that increased temperature could increase the abundance of soil-borne pathogens (Delgado-Baquerizo et al., 2020), which might cause a more negative PSF at warmer sites. These studies suggest that climates are likely important drivers of the geographic variations in PSF (Crawford & Hawkes, 2020; van der Putten et al., 2013). Yet, previous work has mainly limited to experimental manipulations of climate to evaluate climatic effects on PSF (Hassan et al., 2022), while the influences and relative importance of aridity and other climate factors on the geographical variation of PSF remain unclear due to limited data (Crawford et al., 2019; Hassan et al., 2022). Quantification of the climate drivers of PSF variation across space can also inform us how the interactions between plant and soil microbes response to the climate change (de Vries et al., 2023; van der Putten et al., 2013).

Woody and non-woody species usually have contrasting traits and vary differently along latitudinal and climatic gradients and thus may show different geographic and climatic gradients in PSFs (Diaz et al., 2016; Reich & Oleksyn, 2004; Soudzilovskaia et al., 2020). For example, woody species can be associated with multiple mycorrhizal fungi groups, but non-woody species are mainly associated with arbuscular mycorrhizal fungi (Soudzilovskaia et al., 2020). A decline in the diversity of arbuscular mycorrhizal fungi at higher latitudes may lead to less positive PSF for non-woody species at high latitudes compared to woody species (Davison et al., 2015; Tedersoo et al., 2014), which can also be associated with ectomycorrhizal fungi that are common at high latitudes (Tedersoo et al., 2014). Further, experimental environments may also influence the changes in PSF along latitudinal and climatic gradients (Casper et al., 2008; Forero et al., 2019). If there is a soil legacy effect from climates (i.e. the influences of prior climates on current soil microbial communities) (Pugnaire et al., 2019), relationships between climates and PSFs can be found in both field and greenhouse experiments. In contrast, if there is not a soil legacy from climates, the relationships between climates and PSFs may not be found in greenhouse experiments due to the lack of a direct climate effect on plant–soil microbe interactions. Therefore, distinguishing the effects of plant life forms and experimental environments on PSF will improve our understanding about the geographic patterns and climatic drivers of PSF.

Several meta-analyses have been previously conducted and revealed important patterns on how PSF was associated with experimental settings and plant growth forms (Beals et al., 2020; Forero et al., 2019; Hassan et al., 2022; Kulmatiski et al., 2008), plant invasion (Suding et al., 2013), plant functional traits and phylogenetic distances (Mehrabi & Tuck, 2015; Xi et al., 2021), climate change (Hassan et al., 2022), species coexistence (Crawford et al., 2019; Lekberg et al., 2018; Yan et al., 2022), and species abundance (Reinhart et al., 2021). However, to date, the geographic patterns and climate drivers of PSF strength remain to be demonstrated (Gundale & Kardol, 2021). Furthermore, previous meta-analyses on specific PSF drivers included limited sets of publications and observations ranging from 14 studies with 182 observations (Hassan et al., 2022), to 69 studies with 1038 observations (Crawford et al., 2019). The limitation of sample size may impede the distinguishing of climate drivers on PSF [e.g. non-significant effect of precipitation on PSF found by (Crawford et al., 2019)]. Based on this knowledge, we provide a much larger dataset of PSF that included 5969 experimental observations compiled from 202 studies to explore the geographic patterns and climate drivers of PSF strength for both woody and non-woody growth forms. Because previous studies have found that plant species attributes (e.g. native vs. non-native species) and experimental settings may also influence the strength of PSF

(Kulmatiski et al., 2008), we first evaluated how multiple plant attributes and experimental settings influenced the variation of PSF. Then, we evaluated whether PSF values were more negative at lower latitudes as suggested by the Janzen–Connell hypothesis. Third, we explored how climate factors, especially aridity, affected the geographic patterns of PSF. Finally, we compared the differences in geographic patterns and climate drivers of PSF across different growth forms (woody vs. non-woody species) and across different experimental environments (field vs. greenhouse experiments).

METHOD AND MATERIALS

Study selection

On 2 November 2021, we searched the Web of Science using the term *plant AND soil AND feedback*, which resulted in a total of 4155 papers. We initially filtered this list to exclude those unrelated to PSF and then filtered these papers by checking the title and abstract, which left 547 papers. From these papers, we only included studies that met our criteria below: (1) the study contrasted growth between a species grown in soil conditioned by conspecific individuals with soil conditioned by heterospecific individuals or sterilized soil, (2) the study evaluated the effect of total microbes rather than specific groups (e.g. fungi), (3) the study provided the mean biomass, its standard deviation or standard error, and the sample size for each observation, and (4) we excluded studies conducted in agricultural ecosystems (e.g. crop species). Finally, 179 studies from the Web of Science met these criteria. To maximize the data we could use, we included studies that measured plant biomass as either aboveground biomass or total biomass. We also contacted the authors if these data were not provided in the original study. We also searched additional studies in Google Scholar using the term *plant and soil feedback*, the China National Knowledge Internet using the term *plant and soil feedback* in Chinese, and other papers included by three previous meta-analyses on PSF and their citations (Crawford et al., 2019; Kulmatiski et al., 2008; Xi et al., 2021), which brought our final total number to 202 papers and 5969 observations of 669 species. These species belonged to 364 genera and 85 families across 367 locations (unique latitude by longitude, Figure 1a). Of these, 72.4% used aboveground biomass as the response variable, with the remainder using total biomass.

Plant attributes and plant–soil feedback experiments

From these studies, we compiled data on 14 moderators that reflected plant attributes, environmental settings and climate that might influence PSF. For plant

attributes, we included species life form (woody or non-woody species) and species origin (native or non-native species) (Table S1). For the experimental settings, we included the approach used (comparison of biomass between conspecific live soil and sterilized soil (self-sterilized) or between conspecific live soil and heterospecific live soil (self-other)) and how biomass was measured (aboveground or total biomass). Relating to the conditioning phase, we included the experimental environment (field or greenhouse), plant community context (mixture or monoculture) and duration of conditioning. Relating to the response phase, we included the experimental environment (field or greenhouse), soil type (feedback soil from inoculum or whole soil), plant community (plant grown in feedback soil alone or with other plants) and duration. If species origins were absent in the original literature, we determined whether this species was native or non-native at the study site by searching in the Plants of the World Online (<https://powo.science.kew.org/>). Besides the information above, we also recorded the latitude, mean annual temperature (MAT) and mean annual precipitation (MAP) data from each study. If the climate variables were not provided, we used the location information provided by the study to obtain MAT and MAP in WorldClim version 2.0 using a 30s resolution (<https://www.worldclim.org/data/worldclim21.html>) (Fick & Hijmans, 2017). To evaluate how the geographic variation in PSF was influenced by aridity, we obtained the aridity data from the Global Aridity Index (ver. 3) (Zomer et al., 2022).

Effect size

Two PSF indices are commonly used: (1) individual PSF that represents biomass comparison of one species grown in conspecific and heterospecific soils; and (2) pairwise PSF that represents biomass comparison of two species grown in conspecific and another species' soils (Bever, 1999), which is thought to better represent the effects of PSF on coexistence and is calculated as the effect that PSF has on the fitness differences between a pair of coexisting species (but see Yan et al., 2022). Among previous meta-analysis studies, Crawford and colleagues evaluated the broad-scale pattern of pairwise PSF and did not find a significant variation for PSF across gradients of both latitude and precipitation (Crawford et al., 2019). In contrast to pairwise PSF, a continental-scale experiment examining individual PSF in temperate trees across North America found that individual PSF observed in greenhouse experiments was significantly associated with conspecific negative density dependence quantified through forest inventory data and precipitation (Bennett et al., 2017; Bennett & Klironomos, 2018), which is a mechanism to influence species diversity suggested by Janzen–Connell hypothesis (Lebrija-Trejos et al., 2023). Therefore, we calculated individual PSF

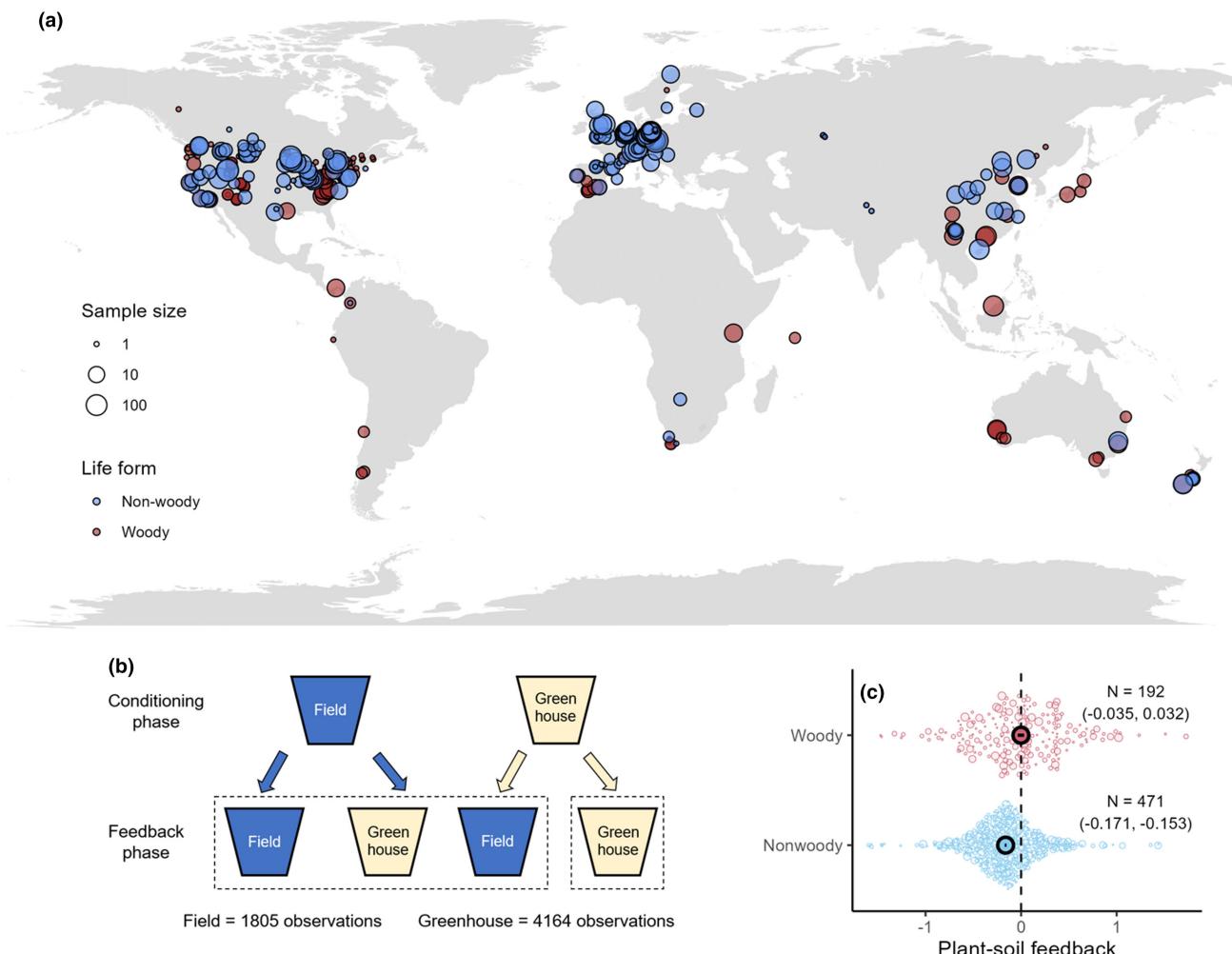


FIGURE 1 Panel (a) shows the distribution of sample locations (latitude by longitude) for woody (brown points) and non-woody (blue points) species. The point size is proportional to the observation number at each study site. Panel (b) shows the division of experimental environments and sample size. Panel (c) shows the plant–soil feedback (confidence interval of effect size) for woody and non-woody species. Six outliers with absolute values larger than 1.8 are removed in panel (c) to show the point distribution better. Point size was negatively related to the variance of plant–soil feedback.

as a log response ratio (Hedges et al., 1999) following (Kulmatiski et al., 2008). The effect size of PSF is calculated as follows:

$$\text{Effect size} = \ln\left(\frac{X_{con}}{X_{other}}\right),$$

where X_{con} is the plant species biomass in live soil conditioned by the conspecific, and X_{other} is the plant species biomass in live soil conditioned by the heterospecific or sterilized soil.

We also calculated the variance of the effect size to weight the effect sizes when we performed the meta-analysis. The variance of the effect size is calculated as follows (Xi et al., 2021):

$$Var_{\text{effect size}} = \frac{(SD_{con})^2}{n_{con}(X_{con})^2} + \frac{(SD_{other})^2}{n_{other}(X_{other})^2},$$

where SD_{con} , SD_{other} , n_{con} and n_{other} are standard deviations and sample sizes of plant biomass in conspecific live soil and heterospecific live or sterilized soils, respectively.

Statistical analysis

We first evaluated whether the strength of PSF varied with species attributes and experimental settings to provide information on the effects of these moderators and a comparison with previous studies (Kulmatiski et al., 2008). To compare the difference in PSF between woody and non-woody species, we first calculated species-level mean PSF values using a meta-regression with species identity as the lone predictor (no intercept) and study source as a random effect. Then, we obtained the species-level effect size and variance (i.e. the square of standard deviation) and performed the univariate meta-regression with species growth form (woody or

non-woody species) as the predictor. Different from the analysis above, for species origin (native or non-native species) and each experimental setting variable that varied within species across experiments, we used observation-level effect size and variance (i.e. raw data) to perform univariate meta-regressions using each moderator separately. For all these models, species identities nested in the study source were included as random effects. Because the results about the effects of plant attributes and experimental settings on PSF were similar between univariate and multiple meta-regressions, we only reported the results from the univariate meta-regression in the main text and included those based on multiple meta-regressions in the supplementary materials.

We used multiple meta-regressions to evaluate the relationships between the global patterns in PSF of woody and non-woody species and latitude/climates. Especially, we only considered the PSF variation with latitude as an important geographic pattern (Schemske et al., 2009), rather than a driver. Here, we considered all observations that had the same location (latitude by longitude), experimental settings, species identity, species origin and study sources as a unique 'site'. Therefore, we averaged PSFs across some replicated observations (e.g. if the same plant species was used in multiple experiments with the same experimental settings at the same location). We then obtained the mean and variance of PSF values using meta-analysis with the site (a categorical variable) as a predictor and the study source as random effect. To evaluate whether the latitudinal and climatic gradients of PSF depended on experimental environments, we divided all observations into two groups: (1) field experiments that were conducted in the field at least in one of the conditioning and feedback phases and (2) greenhouse experiments that were conducted in the greenhouse in both phases (Figure 1b). To evaluate the differences in geographic patterns and drivers of PSF across growth forms and experimental environments, we performed meta-regression models separately for woody and non-woody, and for field and greenhouse experiments, respectively. Therefore, we had 15 meta-regression models with combinations of [2 growth forms (woody and non-woody) \times 2 experimental environments (field and greenhouse) + 1 pooled data] \times 3 predictors (latitude, aridity and both temperature and precipitation). Aridity index was included in an individual model because it is associated with precipitation (Figure S1). In these models, we included the species origin and experimental setting variables to control for their influences (Crawford et al., 2019). Model formulas are shown in Table S2. The duration in the conditioning phase was included as a moderator for only greenhouse experiments as this is not typically known for naturally occurring plants (Table S1). We used a funnel plot to evaluate the publication bias and the *regtest* function

to test the funnel plot asymmetry. All meta-regression analyses were performed using the *rma.mv* function in the *metafor* R package (R Core Team, 2020; Viechtbauer, 2010).

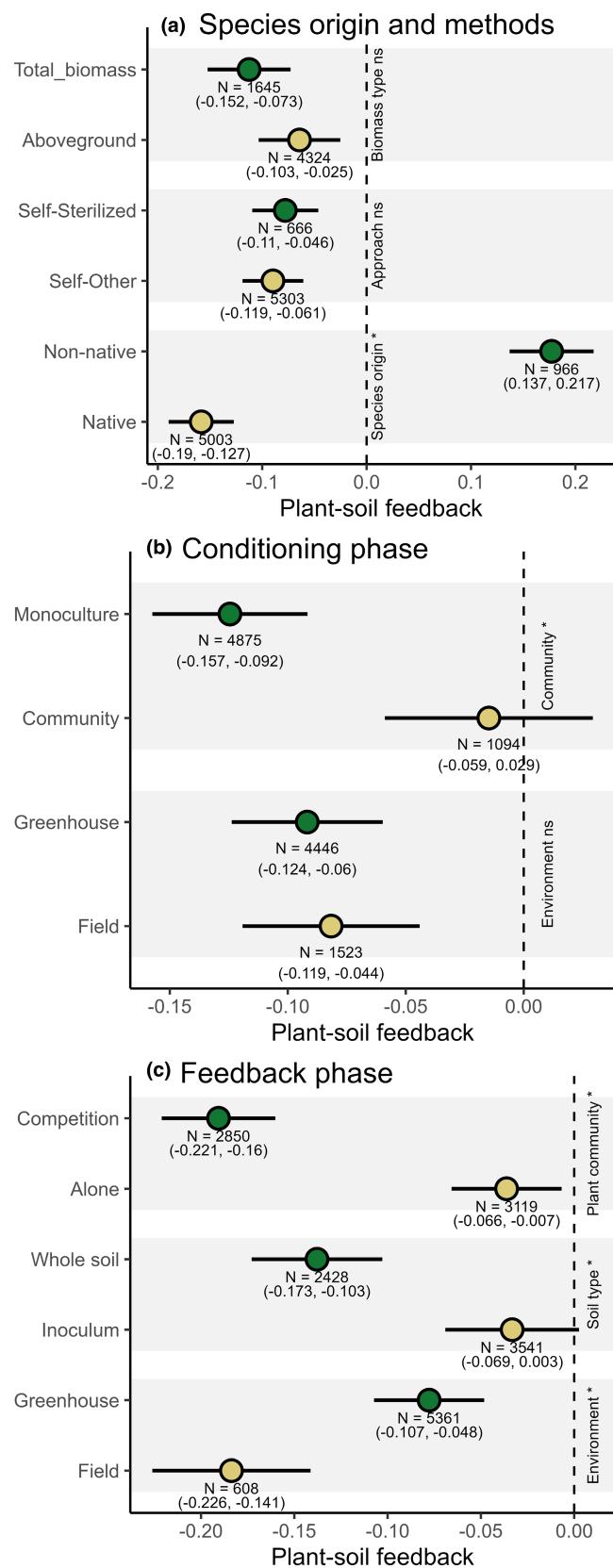
RESULTS

Data summary

In our dataset, we had 1805 observations in field experiments and 4164 observations in greenhouse experiments (Figure 1b). The latitude of the studied sites ranged from -45.16° S to 68.35° N with the lowest absolute latitude at 3.33° . The aridity index of the studied sites ranged from 0.05 (arid) to 4.57 (humid). The MAT ranged from -5.29° C to 26.49° C and MAP ranged from 50 to 3753 mm. Our dataset included data for 669 species. Specifically, for woody species, the dataset included 192 species from 828 observations where 82% and 18% of observations were field and greenhouse experiments, respectively. For non-woody species, the dataset included 477 species from 5141 observations where 22% and 78% of sites are field and greenhouse experiments, respectively. At the species level, woody species had neutral PSF while non-woody species had significantly negative PSF (Figure 1c). The regression test indicated that the funnel plot was symmetrical ($z = -1.3249$, $p = 0.1852$), suggesting that there was no systematic publication bias (Figure S2).

The influences of plant attributes and experimental settings on plant–soil feedback

We found that plant attributes and experimental settings significantly affected the strength of PSF (Figure 2; Figure S3). Species with different origins showed contrasting PSF, in which PSF for non-native species was significantly positive and for native species significantly negative (Figure 2a). Multiple experimental attributes had no significant effect on PSF. Especially, there were no significant differences between PSF values estimated as conspecific live and sterilized soil (self-sterilized approach) versus conspecific and heterospecific live soil (self-other approach), between PSFs calculated using total versus aboveground biomass (Figure 2a), or between PSFs estimated using field-conditioned or greenhouse-conditioned soils during the conditioning phase (Figure 2b). Other experimental settings did have significant effects on PSF. Soil conditioned by monocultures exhibited stronger negative PSF than those conditioned by a plant community (Figure 2b). In the feedback phase, plants in the field had more negative PSF than those in the greenhouse (Figure 2c). Plants grown in whole soil showed stronger negative PSF than those grown in soil as an inoculum (Figure 2c). PSF was also more negative when plants were



grown with competitors (Figure 2c). Finally, duration of the conditioning phase had a negative effect on PSF, whereas the duration of the feedback phase had no significant influence on PSF (Figure S3).

FIGURE 2 Effects of plant attributes and experimental settings on plant–soil feedback. Panel (a) shows the effects of species origin and methods used in the plant–soil feedback experiments, Panel (b) shows the effects of experimental choices imposed during the conditioning phase of plant–soil feedback experiments and Panel (c) shows the effects of experimental choices imposed during the feedback phase of plant–soil feedback experiments. Significance in difference between two levels within variables is shown: * significant ($p < 0.05$); ns, non-significant. Sample size and confidence interval of each level are shown below the error bar. Results are obtained by meta-regression without intercept.

Latitudinal patterns and climate drivers of plant–soil feedback

For pooled data, we did not find a significant latitudinal pattern for PSF (Figure 3a; Figure S4a). However, PSF strength was more negative with increasing latitude for non-woody species but did not significantly change for woody species, regardless of field or greenhouse experiments (Figure 3a–c; Table S3). PSF was consistently more positive with increasing aridity (Figure 3d–f; Table S4). Unexpectedly, temperature was not significantly correlated with the geographic variation of PSF (Figure S5; Table S5). Similar to aridity, the strength of PSF was more negative with increasing precipitation (Figure S5; Table S5). These relationships between climates and PSF were consistent whether we conducted analysis using all data pooled together, or separately for different growth forms or different experimental environments. The uneven sampling sizes across biogeographical regions (e.g. more samples in temperate sites) did not systematically influence the significant relationships between PSF and the latitude and climates (Appendix 2).

DISCUSSION

Using a newly compiled large database that contained nearly 6000 experimental observations, we explored the geographic patterns of PSF and their climate drivers. We found that PSF strength was influenced by species attributes and experimental settings. After controlling for these effects, we found that the geographic patterns of PSF differed between woody and non-woody growth forms. Woody species PSFs did not exhibit a significant variation across the latitudinal gradient, whereas non-woody species PSF was more negative at higher latitudes. The geographic patterns of PSF were significantly associated with aridity where PSF was more positive at drier sites for both woody and non-woody species, as well as for field and greenhouse experiments. Our results suggest that PSF is not generally more negative at lower latitudes, which do not support the expectation of the Janzen–Connell hypothesis. The latitudinal gradient of PSF was even reversed for non-woody species, being more negative at higher latitudes. The more negative PSF at wetter than

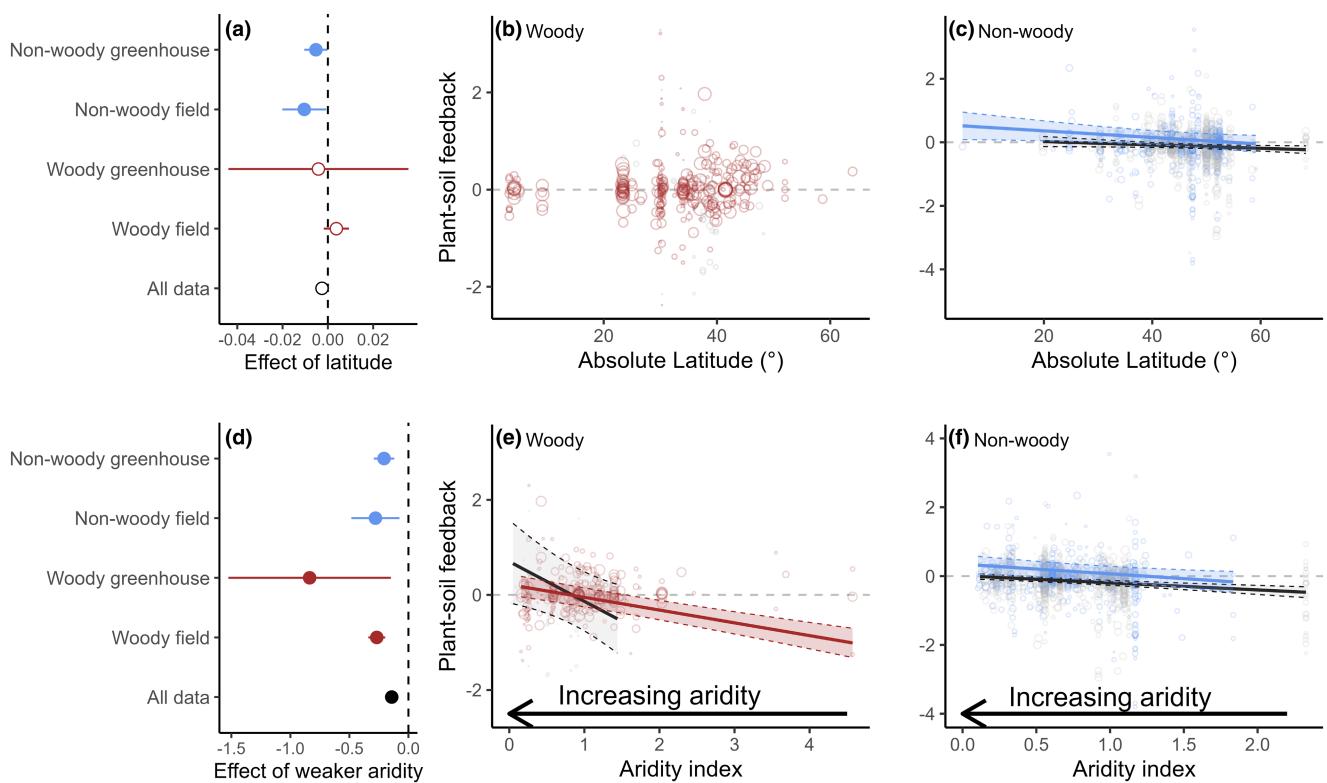


FIGURE 3 Relationships between absolute latitude, aridity index, and plant–soil feedback in five separate datasets (i.e. pooled data, $N=2064$; woody field, $N=400$; woody greenhouse, $N=64$; non-woody field, $N=376$; and non-woody greenhouse, $N=1224$). Panels (a) and (d) shows the slopes (\pm confidence interval) of each multiple meta-regression model, and open and solid circles represent non-significant and significant effects by $p<0.05$. Panels (b), (c), (e), and (f) shows the relationships between plant–soil feedback and absolute latitude and aridity index, and only significant relationships are shown. Points are raw data and the point size was negatively related to the variance of plant–soil feedback.

drier sites are likely because water drives the change of soil microbial compositions that are related to PSF (i.e. more pathogens and fewer beneficiais). Change in aridity may influence the dynamics and diversity of plant communities by mediating the interactions between plants and soil microbes (Bever et al., 2015).

Plant attributes and experimental settings are important sources of plant–soil feedback variation

Both growth form and species origin were important drivers of PSF strength. Consistent with a previous meta-analysis (Kulmatiski et al., 2008), we found that non-woody species had more negative PSFs than woody species, which likely reflects their differences in functional traits (Xi et al., 2021). Compared with non-woody species, woody species usually have larger height and seed size, thicker roots, lower specific root length, and higher root tissue density (Diaz et al., 2016; Freschet et al., 2017). These differences in functional traits can make woody plants less susceptible to pathogens (Xi et al., 2021). Compared to the herbaceous species that mostly interact with arbuscular mycorrhizal fungi (Soudzilovskaia et al., 2020), some woody species are

also associated with ectomycorrhizal fungi, which can provide physical protection for plant roots and hence result in more positive PSF (Bennett et al., 2017).

In addition to the growth form of species, the origin of species (i.e. native vs. non-native) is also important in determining PSF. Compared to native species, non-native species grow better in conspecific soils than other soils, which supports the enemy release hypothesis and enhanced mutualism hypothesis that has been found in many PSF experiments (Agrawal et al., 2005; Callaway et al., 2004; Reinhart et al., 2003; Reinhart & Callaway, 2004). Using this large dataset, we suggest that the lack of accumulated antagonistic and species-specific soil microbes from their non-native ranges may be one important mechanism enhancing the success of invasive plants worldwide.

Our results indicated that PSF was weaker in soils conditioned by plant community than in soils conditioned by monoculture, which was also found in pairwise PSFs (Crawford et al., 2019). This finding supports the pathogen dilution hypothesis that soil pathogens decreased with the increase in plant diversity (Bennett et al., 2020; Kulmatiski et al., 2012). For example, many field studies have found that seedling survival in forests can be improved when seedlings were surrounded by more heterospecific trees rather than conspecific trees

(Comita et al., 2010; Jiang et al., 2020). This could also explain why PSF was less negative in inoculated than in whole soils which might have a higher abundance of soil pathogens. In addition, more negative PSFs in whole soils could also be caused by nutrient declines in whole soils that are avoided when using inoculated soils (Bennett & Klironomos, 2019).

The stronger negative PSF for plants grown in the field compared to those grown in greenhouse in the feedback phase was likely due to the differences in both biotic and abiotic environments between field and greenhouse experiments (Forero et al., 2019; Heinze et al., 2016). Compared to the greenhouse, some natural enemies such as herbivores in the field might also strengthen the negative feedback by reducing the plant's ability to defend itself from pathogens (Heinze et al., 2020 but see Bennett et al., 2020). Consistent with previous meta-analyses (Kulmatiski et al., 2008; Lekberg et al., 2018), we found that the presence of a competitor in the feedback phase had more negative PSF likely due to the lower resource allocation to plant defences when competition presents in experiments (Lekberg et al., 2018).

Strengthening of negative PSF with the duration of the conditioning phase was consistent with expectation, likely due to the increase in soil microbial abundance with time. Unexpectedly, the durations of feedback phases did not influence PSFs, which is in contrast to earlier studies (Diez et al., 2010; Hawkes et al., 2012; Kardol et al., 2013). This might be because many studies measured PSFs in short-term experiments and thus long-term effects of PSFs might have been overlooked (Dostál, 2021). However, it is also possible that the process of PSF is more important for the growth of very young plants (i.e. seedlings) so that the effects of duration can be captured in very short times (Fenner, 2008). Overall, our study indicates that plant attributes and experimental settings have important impacts on PSF so it is necessary to control for these influences before comparing PSFs across experiments.

Latitudinal patterns of plant–soil feedback

For woody species, the strength of PSF did not show a significant latitudinal gradient, which does not support the expectation of the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970) and the hypothesis that biotic interactions were stronger at lower latitudes (Schemske et al., 2009). This result also suggests that soil microbes (e.g. pathogens), as an important agent for the Janzen–Connell effect, do not have a more negative effect on plant performance at lower latitudes. Similarly, previous studies found that conspecific negative density dependence (Lambers et al., 2002; Song et al., 2020) and PSF (Crawford et al., 2019) did not show significant latitudinal gradients. Although continental- and

global-scale studies have found that conspecific negative density dependence varied with latitude (Johnson et al., 2012; LaManna et al., 2017), these results were recently questioned due to the method used to estimate conspecific negative density dependence suggested to be biased (Dettman et al., 2019). The lack of a latitudinal gradient in PSF for woody species may be caused by the contrasting latitudinal patterns in the diversity or abundance of different soil microbial groups that are important for PSF. The diversity or abundance of some harmful soil microbes, such as fungal pathogens (Delgado-Baquerizo et al., 2020; Tedersoo et al., 2014) and parasites (Oliverio et al., 2020), decrease with latitude and is lower at higher latitudes. Conversely, the diversity or abundance of other harmful soil microbes, such as the nematodes, increase with latitude (van den Hoogen et al., 2019). Similarly, the diversity or abundance of the mutualistic soil microbes, arbuscular mycorrhizal fungi (Davison et al., 2015), decreases with latitude, but those of ectomycorrhizal fungi (Tedersoo et al., 2012, 2014) increase. Therefore, the net effects of important harmful and mutualistic soil microbial groups in driving PSF may have not a systematic variation along with latitudinal gradient, which may cause a lack of latitudinal gradient in PSF.

Similar to PSF, the evidence for latitudinal gradients of plant defence was mixed, and plant defence abilities in plant traits usually are not necessarily stronger at lower latitudes (Moles et al., 2011; Moles et al., 2011). However, leaf herbivory rates were found to be higher at lower latitudes (Baskett & Schemske, 2018; Lim et al., 2015; Tang et al., 2023). These findings imply that different agents of the Janzen–Connell effect and biotic interactions may show different latitudinal gradients (Schemske et al., 2009). Therefore, our study suggests that we can neither conclude that the plant–soil microbe interactions are stronger at lower latitudes nor use PSF as a potential mechanism underlying the latitudinal diversity gradients. However, the observed positive but non-significant relationship between PSF and latitude for woody species may be strengthened if more experiments are included, especially in tropical forests and the southern hemisphere (Figure 1a).

The more negative PSF of non-woody species with increasing latitude was possibly due to decreased arbuscular mycorrhizal fungi with latitude (Davison et al., 2015) and their low benefits from ectomycorrhizal fungi at high latitudes relative to woody species. In addition, non-woody species have more nutrient-rich plant tissues (e.g. higher nitrogen content) at higher latitudes compared to woody species (Reich & Oleksyn, 2004). Higher nutrient content in plant tissues may cause less biomass to be allocated to plant structural defence and, thus, make plants more susceptible to pathogens and herbivores (Kitajima & Poorter, 2010). The contrasting global patterns in the strength of PSFs between woody and non-woody

species may explain why Crawford and colleagues did not find a significant relationship between the strength of pairwise PSF and latitude (Crawford et al., 2019), and why Comita and colleagues did not find a latitudinal gradient of density/distance dependence using the pooled dataset (Comita et al., 2014). Therefore, we suggest that caution is needed in inferring a general effect of plant–microbe interactions on latitudinal diversity gradients and that the importance of this mechanism is likely to vary among plant growth forms.

Plant–soil feedback was more positive with increasing aridity

We found that PSF is more positive with increasing aridity (Figure 3). This finding was also supported by the negative effect of precipitation on PSF (Figure S5). These results were consistent with our expectations but were inconsistent with a recent meta-analysis finding that drought treatment could cause a more negative PSF than ambient conditions (Hassan et al., 2022). This difference between our findings and Hassan et al. (2022) might be due to the different effects of climatic aridity and short-term drought events on soil microbial composition. The effect of aridity on PSF can be caused by increased abundance of soil pathogenetic fungi compared to mutualistic fungi in wetter conditions (Averill et al., 2016; Kardol et al., 2010). In addition, the more positive PSF with increasing aridity was found when soils were cultured in both field and greenhouse experiments, which suggests that prior aridity conditions in the study site showed a persistent influence (i.e. legacy effects) on soil microbial compositions.

In contrast to the significant effects of aridity and precipitation on PSF, temperature did not significantly influence the strength of PSF. Together, these findings suggest that aridity may have a stronger impact than temperature on the geographic variation of soil microbial composition across space. In support of this hypothesis, previous studies have found that water may show a stronger effect on the composition or richness of soil nematodes (Kardol et al., 2010) and total soil microbes (Fierer & Jackson, 2006) than temperature.

Similar to our findings, previous field and experimental studies have also highlighted the importance of water in mediating plant–soil interactions and the Janzen–Connell effects in comparison with temperature. For example, using a systematic experiment based on North American trees, Bennett and Klironomos (2018) found that water played a more important role in PSF than temperature. Studies on density/distance dependence, which quantify the net effects of aboveground and belowground enemies on the Janzen–Connell effect, also found similar results. For example, a previous meta-analysis found stronger plant distance and density dependence at wetter conditions

(Comita et al., 2014). Field observations found that conspecific density dependence was more negative in wet than in dry Hawaiian forests (Inman-Narahari et al., 2016). Analysis from 20-year seedling survival data in a tropical forest also found that negative conspecific density dependence was stronger in wetter years than in drier years (Lebrija-Trejos et al., 2023). Therefore, our findings together with previous studies suggest that water-driven plant–soil microbe interactions and other biotic interactions related to the Janzen–Connell effect are likely widespread within and across ecosystems. In addition, these findings inform us that the geographic variation of PSF across space may provide a potential mechanism to explain the relationship between species diversity and precipitation (Liang et al., 2022). Under the context of aridity and precipitation change, the change in PSF can also influence community dynamics and diversity at either short-term or long-term temporal scales (Lebrija-Trejos et al., 2023; Lundell et al., 2022).

CONCLUSION

Using a newly compiled large dataset on PSF, we evaluated the global patterns and drivers of PSFs for woody and non-woody species. We did not find a significant latitudinal gradient in PSF for woody species, which implies that we should be cautious to consider PSF, which represents an important agent of the Janzen–Connell effect, as an explanation of the widely known latitudinal diversity gradient. We also call for more experiments, especially in tropical forests and the southern hemisphere, to make a more robust evaluation of the latitudinal gradients in PSF. Aridity was the stronger driver of the geographic variation in PSF than temperature, which suggests that water plays a more important role to influence soil microbe compositions. Our findings further suggest that change in aridity or precipitation can influence species coexistence and dynamics of plant communities via mediating plant–soil microbe interactions.

AUTHOR CONTRIBUTIONS

FJ and ZHW conceived the study. FJ compiled the data, performed the meta-analysis and wrote the first draft of the manuscript. All authors contributed substantially to the revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The original data that support the findings of this paper are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.n2z34tn35> (Jiang et al., 2023).

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SUPPORTING INFORMATION

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

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