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RESEARCH ARTICLE

Under greenhouse settings, mycorrhizal responsive herbs establish better in their own soil compared to less responsive counterparts

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Abstract

Background and aims The processes that structure plant communities are understood better in forests than in herbaceous systems. Here, we test the hypothesis that mycorrhizal responsive herbaceous plant species experience favourable plant-soil feedbacks compared to less mycorrhizal responsive species.

Methods We extracted plant-soil feedback information for herbaceous species from a recent meta-analysis and collated this information with three sources of mycorrhizal responsiveness data.

Results Our results support our hypothesis that mycorrhizal responsive plants, notwithstanding if they experience positive or negative mycorrhizal responses, receive more positive plant-soil feedbacks, and were robust to most of the sensitivity tests we carried out.

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Conclusion We uncover an underappreciated mechanism that could confer spatiotemporal stability across herbaceous plant communities. Mycorrhizal responsive plant species may receive less negative plant-soil feedback but most likely experience higher interspecific competition. These effects could promote a balance of mycorrhizal responsive and less-mycorrhizal responsive species within herbaceous systems.

Keywords Baylis postulate · Negative conspecific density dependencies · Mycorrhizal responsiveness · Plant-soil feedbacks · Root architecture

Introduction

Plant-soil feedbacks (PSFs) occur when plants substantially modify the properties (abiotic) and microbiome (biotic) of the soil, which either favour or disfavour growth of conspecific individuals compared to heterospecifics (van der Putten et al. 2013). It is possible to partially predict aspects of PSFs based on characteristics (*aka* plant traits) of the plant at an individual level. For example, annuals and early successional plants show more negative PSFs than perennials and late successional plants (Kulmatiski et al. 2008), and the same (i.e. more negative PSFs) applies for tall plants with high specific leaf area and high specific root length (Xi et al. 2021).

The roots of most herbaceous plant species associate with beneficial arbuscular mycorrhizal fungi (Smith and Read 2008) alongside pathogenic fungi. The accumulation of species (or genus)—specific arbuscular mycorrhizal fungi on soil tends to promote the growth of the plant host (i.e. either species or genus; but see Bever et al. 1996 showing that the resident mycorrhizal community favors plants that have been absent in the plant community), whereas the accumulation of species (or genus) specific pathogen to suppress it. However, the overall PSFs tend to be negative (Bennett et al. 2017). Thus, we can further decompose plant-soil feedbacks into a constituent favouring overall plant growth via mutualistic relationships with mycorrhizal associations, and a constituent underpinning aggravated plant growth via the local accumulation of plant pathogens and herbivores (Liang et al. 2015). Each individual constituent of PSFs can either favour heterospecifics over conspecifics (i.e. negative PSFs), or conspecifics over heterospecifics (i.e. positive PSFs). The mycorrhizal constituent of PSFs, however, is more likely to induce positive PSFs (van der Putten et al. 2013; Cheng et al. 2024 but see Bever 2002), and often the balance between positive and negative PSFs is critical in determining overall outcomes (Semchenko et al. 2018; Jiang et al. 2024).

It is less clear how dependency on mycorrhizal fungi, reflecting the degree to which a plant host can or cannot survive without mycorrhiza, could shape PSFs. Mycorrhizal responsiveness, an expression capturing biomass gains with versus without mycorrhiza, often correlates poorly with mycorrhizal colonization in the roots and hyphal density in the soil (Frew 2025), which would indicate the likelihood that mycorrhizal dependency and PSF are unrelated. Yet, it is also likely that there is a positive relationship between these factors. The Baylis hypothesis (Baylis 1975; Fitter 2004) proposes that less well developed root systems (such as those in magnolioid plants) depend more strongly on arbuscular mycorrhiza for growth. The Baylis hypothesis, in its generalized form, makes the prediction that mycorrhizal responsiveness is higher for plant species that maintain coarser and less developed root systems (but see some non-mycorrhizal species in the Brassicaceae which maintain coarse roots and are resistant to pathogens; Hossain et al. 2015) and there is a large body of literature supports the Baylis postulate (Yang et al. 2014; Bergmann et al. 2020; but see Maherali 2014). The Baylis hypothesis implies that plant species with coarser roots might have stronger fitness gains from arbuscular mycorrhiza and so maximize the specific constituent of PSFs. At the same time, herbaceous plant species with coarser roots might be less susceptible to pathogens (Dai et al. 2023), implying that the specific subset of plant species might experience smaller fitness declines from growing on its own soil and thus maximize overall PSFs. By contrast, explaining a negative relationship between mycorrhizal responsiveness and PSFs is also possible. Lekberg et al. (2018) showed that strong competitors are more likely to induce negative PSFs. If mycorrhizal responsive plants have stronger competition coefficients than those with a lower mycorrhizal responsiveness (Veresoglou et al. 2018), then the relationship between the two variables could be negative.

We build on the abovementioned ideas to propose the hypothesis that plant species that experience on average high average mycorrhizal responsiveness tend to receive more positive PSFs than plant species showing low average mycorrhizal responsiveness. We specifically test whether there is relationship between mycorrhizal responsiveness and PSFs across common herbaceous plant species and genera.

Materials and methods

Sources of data

We used plant-soil feedback data from Jiang et al. (2024). We worked exclusively on the subset of greenhouse experiments with herbaceous individuals and calculated means of PSFs at a species (i.e. means of all species for which we had data). We subsequently extracted mycorrhizal responsiveness data from three sources: Wilson and Hartnett (1998), Reinhart et al. (2017) and Anacker et al. (2014), representing the largest existing sets of plant mycorrhizal responsiveness values, assessed under identical settings. Mycorrhizal responsiveness in Wilson and Hartnett (1998) was calculated as the difference in biomass of mycorrhizal versus non mycorrhizal individuals standardized by the weight of non-mycorrhizal plants and multiplied by 100 to yield a percentage. Mycorrhizal responsiveness in Reinhart et al. (2012) was calculated as the log response ratio of mycorrhizal over non-mycorrhizal biomass. Anacker et al. (2014) calculated mycorrhizal responsiveness as -ln(1-(biomass with mycorrhiza—biomass without mycorrhiza)/100). We did not combine data from diverse studies for mycorrhizal responsiveness because the mycorrhizal responsiveness values can be extremely context dependent (i.e. most plants will have negative responses if grown in fertile soil, whereas a large fraction of those plants will have positive responses at moderately low P fertility) and existing databases do not contain sufficient studies to make means comparable: as an example there are only 14 plant species with data from over nine studies in MycoDB v4.0 (Chaudhary et al. 2016), and the vast majority of these are crop species. To reconstruct the phylogeny of angiosperms, we used the megatree GBOTB.extended in the library V.phylomaker (Jin and Qian 2019) on R v4.2.2 (R Core Team 2024).

Analysis one: mycorrhizal responsiveness as a continuous variable

We used Pearson correlation tests with the common species per mycorrhizal responsiveness dataset and the plant-soil feedback data from Jiang et al. (2024). Overall, we matched mycorrhizal responsiveness information for 109 plant species with plant-soil feedback data from Jiang et al. (2024; Fig. S1). There were 42, 38 and 57 matches in the datasets from Wilson and Hartnett (1998), Reinhart et al. (2012) and Anacker et al. (2014), respectively (Fig. S1). We used the responsiveness data in two ways: untransformed responsiveness data, quantifying the degree to which the plant hosts benefited from mycorrhiza, and absolute values of those responsiveness data, capturing the degree to which their biomass was dependent on mycorrhiza. We assessed phylogenetic signal via the Blomberg K statistic (which in neither case presented evidence for phylogenetic signal). We nonetheless carried out, in the form of a sensitivity test, a phylogenetic generalised least squares analysis. To fit phylogenetic generalized least squares models, we used the command pgls of the R library caper. To fit the model, we used maximum likelihood estimators for the parameters lambda and kappa.

Analysis two: working with mycorrhizal responsiveness classes

We divided the mycorrhizal responsiveness data across the studies of Wilson and Hartnett (1998), Reinhart et al. (2017) and Anacker et al. (2014) for which we had matches in Jiang et al. (2024) into those above the median (i.e. “high”) and those below the median (i.e. “low”). We did this with both untransformed data and after we had extracted their absolute values. We used *t*-tests to assess whether mycorrhizal responsiveness modified plant-soil feedbacks at this crude level and how. To address likely phylogenetic dependencies, we used phylogenetic generalized least squares models, as for analysis one.

All analyses were carried out on R v4.2.2 (R Core Team 2024). To manipulate phylogenetic trees, we used the libraries picante and ape (Paradis and Schliep 2019). To match species to families we used the library taxize (Chamberlain and Szocs 2013). To plot our figures, we used ggplot2 (Wickham 2016).

Results

Analysis one: mycorrhizal responsiveness as a continuous variable

With the Wilson and Hartnett (1998) datasets there were relationship notwithstanding whether we used absolute or untransformed values of mycorrhizal responsiveness (untransformed: r = 0.31, $P = 0.048$; absolute: r = 0.33, $P = 0.035$; Fig. 1a; Notes S1). We observed no relationships with the Reinhart dataset (untransformed: r = 0.14, $P = 0.42$; absolute: r = 0.07, $P = 0.68$; Fig. 1b; Notes S1). With the Anacker dataset there were only relationships when we used the absolute values (untransformed: r = 0.09, $P = 0.52$; absolute: r = 0.32, $P = 0.017$; Fig. 1c; Notes S1). There was weak, non-significant phylogenetic signal for both variables across all three datasets (i.e. in all cases $K \approx 0.02$, $P > 0.05$). Upon correcting for phylogenetic signal with the absolute value of mycorrhizal responsiveness the relationships with the dataset from Wilson and Hartnett (1998) became marginally non-significant (F = 3.39, $P = 0.059$; Table 1), whereas the relationship with the dataset from Anacker et al. (2014) remained significant (F = 10.2, $P = 0.002$; Table 1). Overall, mycorrhizal responsive plant species experienced more positive plant soil feedbacks than less mycorrhizal responsive plants.

Analysis two: working with mycorrhizal responsiveness classes

There were relationships with the two mycorrhizal classes in all three datasets and these were of a consistent sign. In Wilson and Hartnett (1998), plants with a "high" mycorrhizal responsiveness experienced more positive plant soil feedbacks (untransformed: t = 2.37, $P = 0.023$; absolute: t = 2.37, $P = 0.023$; Fig. 2; Notes S1). In Reinhart et al. (2017) we observed significance only in the untransformed mycorrhizal responsiveness data (untransformed: t = 2.09, $P = 0.044$; absolute: t = 0.94, $P = 0.35$; Fig. 2; Notes S1). With Anacker et al. (2014) both relationships were significant with the test using the absolute values of mycorrhizal responsiveness showing stronger results (untransformed: t = 2.24, $P = 0.035$; absolute: t = 2.98, $P = 0.004$; Fig. 2; Notes S1). We again fitted phylogenetic generalized least squares

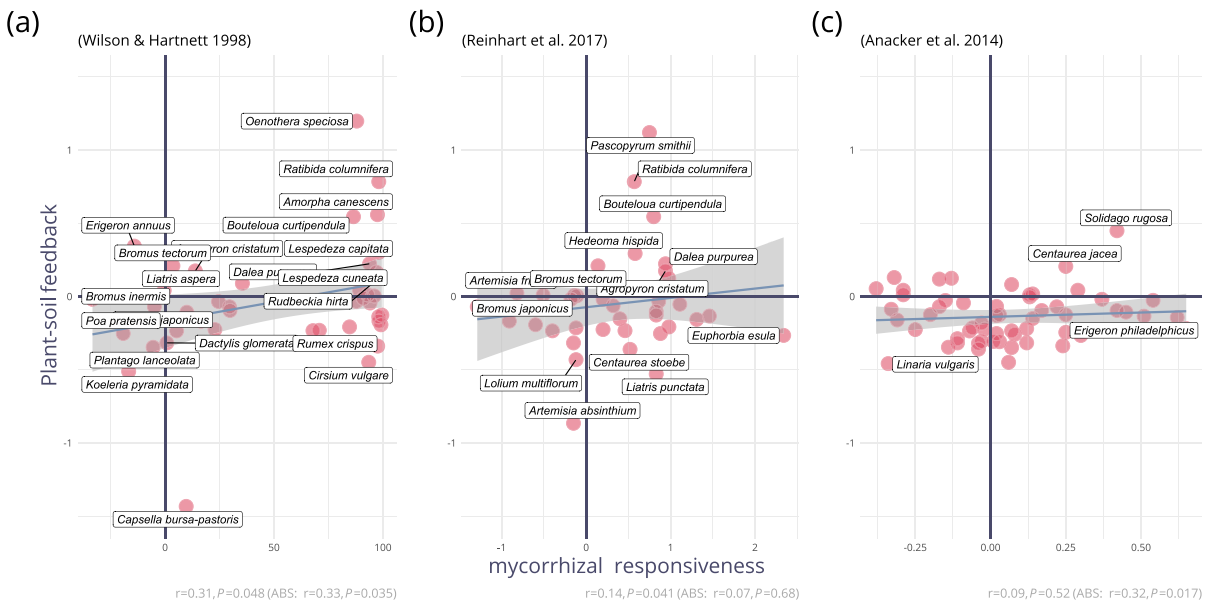

Fig. 1 Relationships between plant soil feedback data (*y* axis) from Jiang et al. (2024) and mycorrhizal responsiveness (*x* axis) from (**a**) Wilson and Hartnett (1998); (**b**) Reihart et al. (2017); (**c**) Anacker et al. (2014). We report on statistics with either the untransformed mycorrhizal responsiveness data or their absolute values (i.e. "ABS"). We report on associated test statistics in the legends of each panel. The take home message is that mycorrhizal responsive plant species experienced more positive plant soil feedbacks than less mycorrhizal responsive plants

Table 1 Summary statistics on phylogenetic comparative methods addressing how responsiveness (predictor) related to the plant soil feedback statistics (response variable) after correcting (PGLS) for phylogenetic relatedness

	Wilson and Hartnett 1997		Reinhard et al. 2017		Anacker et al. 2014	
	continuous	categorical	continuous	categorical	continuous	categorical
k	1.36	1.94	0.53	0.53	0	0
λ	0	0	0	0	0	0
$\mathbf{F_{(responsiveness)}}$	**3.39**	**2.1**	0	0.04	**3.01**	**14.7**
P	**0.07**	**0.042**	0.99	0.85	**0.004**	**< 0.001**

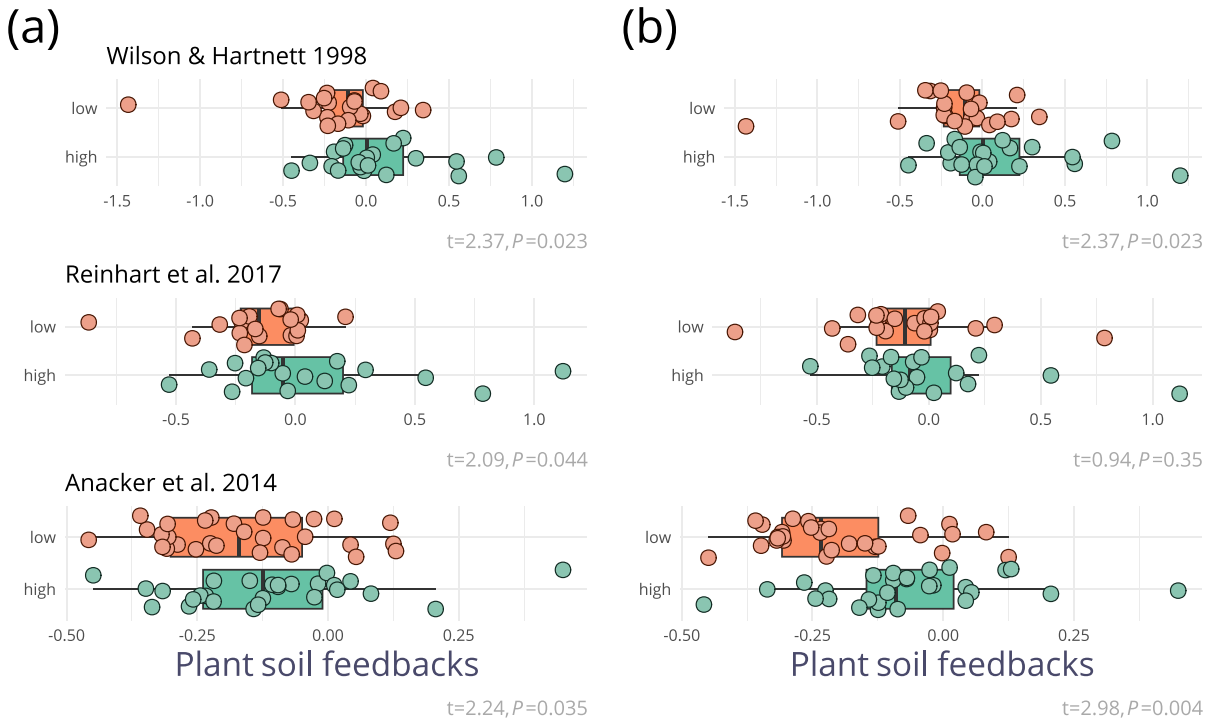

Fig. 2 Relationships between plant soil feedback data (*y* axis) from Jiang et al. (2024) and mycorrhizal responsiveness data clustered into above median – "high" and below median – "low" untransformed values (panel a) or above median – "high" and below median – "low" absolute responsiveness values (panel b). The three contrasts per panel represent the analysis with the responsiveness data from (**a**) Wilson and Hartnett (1998); (**b**) Reihart et al. (2017); (**c**) Anacker et al. (2014), respectively. Even though all tests with the untransformed values were significant, the respective tests with the absolute values performed on average better

with the absolute values of the mycorrhizal responsiveness data being used to classify mycorrhizal responsiveness into the classes "high" and "low". In Wilson and Hartnett (1998) the differences between the two classes remained significant ($F=4.41$, $P=0.042$; Table 1). In Reinhart et al. (2017) there were no relationships $F=0.08$, $P=0.77$; Table 1). In Anacker et al. (2014) the relationship was strongly significant ($F=12.8$, $P<0.001$; Table 1). Even though all tests with the untransformed values were significant, the respective tests with the absolute values performed on average better.

Discussion

We present here a synthesis of two properties of plant-soil interactions that are rarely considered together: mycorrhizal responsiveness and plant – soil feedbacks. To address the constraints that arise from the degree to which mycorrhizal responsiveness depends on growth settings, we combined the plant – soil feedback dataset from Jiang et al. (2024) with three independent datasets on mycorrhizal responsiveness of plants growing under "similar" growth settings. Our analyses with continuous responsiveness data were idiosyncratic but at the same hinted that the absolute values of mycorrhizal responsiveness estimates work better than their untransformed equivalents. The respective analysis with crudely clustered mycorrhizal responsiveness data into "high" vs "low" was more conclusive and supported the idea that plants that invest into mycorrhizal interactions tend to experience more positive plant – soil feedbacks.

In agreement with our hypothesis, we observed that mycorrhizal responsive species and genera, presented in the dataset from Jiang et al. (2024), had more positive PSFs than herbaceous plants with weaker mycorrhizal responsiveness. We used a subset of PSFs that were assessed under greenhouse settings to overcome the confounding biogeographical factors, such as latitude (Jiang et al. 2024). To draw our conclusions, we combined three unrelated sources of mycorrhizal responsiveness data, which minimized the chances that we integrated forms of conscious or unconscious biases when compiling the literature. Mycorrhizal responsiveness at a species level explained about 10% of variance in PSF (i.e. $r = 0.31$), which is a substantial fraction given the different contexts of the assays. Mycorrhizal responsiveness data from diverse studies are often integrated into large syntheses (e.g. Hoeksema et al. 2010; Veresoglou and Begum 2024) but there have been concerns that mycorrhizal responses are too context dependent to be compared across studies (Hoeksema et al. 2010; Wang et al. 2023), and ideally growth responses should be assessed in plants under identical growth settings. To address the concern, we used interchangeably data originating from three different studies (Wilson and Harnett 1998; Reinhart et al. 2012; Anacker et al. 2014): even though in some cases our statistics were non-significant, the overarching patterns indicate a trend, addressing future research.

When comparing growth in conspecific over heterospecific soil, grassland species experience strong PSFs which, according to some estimates, can scale up to over 25% biomass (Petermann et al. 2008). Bever (2002) experimented with grassland species to show that the partner preferences of the plant host and the mycorrhizal fungi under controlled settings are sufficiently strong to induce negative PSFs. Species that have high mycorrhizal responsiveness also engage into stronger competition with other mycorrhizal responsive species, whereas less mycorrhizal responsive species do no compete so strongly with each other (Veresoglou et al. 2018; Wagg and McKenzie-Gopsill 2023). We thus propose that mycorrhizal responsiveness could be an underappreciated driver conferring spatiotemporal stability across grassland communities: mycorrhizal responsive species preferentially establish on their own soil but face stronger competition upon establishment. Such a mechanism could favour mycorrhizal responsive herbaceous species when they occur at low relative abundances but disfavour them whenever they increase in relative abundance.

How does the relationship between mycorrhizal responsiveness and PSFs scale with other known drivers of PSFs? It has been found, for example, that plant height in herbaceous populations can lower PSFs (Xi et al. 2021), but the relationship is weak (the R-squared value was 0.025 in a meta-analysis by Kutáková et al. 2018). Native plants also experience more positive drought-induced PSFs, but the relationship was again weak (Hassan et al. 2022). One of the most prevalent determinants of PSFs is the longevity of the plant species, with annuals showing the most negative PSFs (Kulmatiski et al. 2008). In comparison, the relationship we uncover from our analysis shows intermediate effect sizes (in Fig. 1a, $r = 0.31$ which corresponds to an R-squared value of about 0.1). Clearly, mycorrhizal responsiveness shapes to a considerable extent PSFs and this could in some cases have implications for a range of land use scenarios, such as restoration. *Amorpha*, as an example, represents a genus of mycorrhizal responsive legumes (e.g. Fisher and Jayachandran 2002) that is often used in restoration (Bi et al. 2023). Amorpha species present strong, robust, deep rooting systems, high branching ratio forming an extensive network, with a high concentration of fine roots in the upper soil layers (Zhou et al. 2023). At the same time the engagement of

amorpha species into a tripartite symbiosis with mycorrhiza and rhizobia explains their high mycorrhizal responsiveness. Experimental evidence suggests that *Amorpha* species usually experience less negative, or even positive PSFs than other grassland plants (e.g. Wang et al. 2019; Forero et al. 2022). There is a worry that the combined high mycorrhizal responsiveness and positive PSFs in *Amorpha* can facilitate invasions when used for restoration (Edwards et al. 2024).

Relationships with plant soil feedbacks tended to be stronger when we used the absolute values of mycorrhizal responsiveness data. This was particularly the case with the Anacker et al. (2014) mycorrhizal responsiveness dataset, whereas the differences were considerably smaller in relation to the Wilson and Hartnett (1998) dataset. The vast majority of mycorrhizal responsiveness values in Wilson and Hartnett (1998) were positive, which might explain why the respective analyses were less sensitive to the consideration of absolute values. We think that the better performance of absolute values tentatively reveals an underlying mechanism on how plant—soil feedbacks scale with mycorrhiza. Mycorrhizal strategies across hosts can be quantified in terms of dependency (i.e. quantifying the inability of a plant host to grow without mycorrhiza) and responsiveness (i.e. the biomass benefits of a plant host when it grows with mycorrhiza). Unintuitively, these two parameters are not identical to each other (e.g. Janos 2007). While mycorrhizal responsiveness is straightforward to assay, there exist no standardized tests for mycorrhizal dependency. In our case, the use of absolute values of mycorrhizal responsiveness introduced a component of mycorrhizal dependency: how variable was the plant host biomass to the addition of mycorrhizal fungi. This may not be a perfect proxy of mycorrhizal dependency but we have good reasons to think that plant—soil feedbacks scale with mycorrhizal dependency and not mycorrhizal responsiveness. Going back to the Baylis hypothesis in the introduction, Magnoliids and other plants with a poorly formed mycorrhizal system depend more strongly on mycorrhiza. We thus expect these plant species to be the ones that are favored by plant—soil feedbacks the most.

A potential concern over our analysis was the frequent mismatches between species represented in the datasets for mycorrhizal responsiveness and the species that had been tested for PSFs. We thus had to filter out a large proportion of the entries in all three datasets and reduce statistical power. To address this issue, we also used mean data at a genus level. Existing evidence supports that mycorrhizal relationships are subject to strong phylogenetic constraints with phylogenetically related plant species being more likely to show comparable mycorrhizal responsiveness (i.e. phylogenetic conservatism: Powell et al. 2009). We carried out this additional analysis in the form of a sensitivity test for the results at a species level and observed comparable, or even stronger, patterns. We have, nonetheless, worked with meta-analytical data, which implies that our results are only generalizable over the range of typical experimental conditions reported. These typical experimental conditions, in our case, both for the plant-soil feedbacks and mycorrhizal responsiveness metrics, cover herbaceous plants grown under greenhouse settings. It remains unclear how well our conclusions can be generalized for field-grown plants, because field grown plants often integrate themselves to existing mycelial fungal networks which can lower considerably the costs of the mycorrhizal symbiosis for the plant hosts and subsequent estimates of their mycorrhizal responsiveness.

In this study, we rely on compiled datasets and meta-analytical approaches, which offer unique opportunities through the large combined sample size but inevitably introduce heterogeneity in experimental methodologies, species selection, and the quantification of both mycorrhizal responsiveness and plant-soil feedbacks (PSF). Consequently, our results establish robust correlative patterns rather than unequivocal causal relationships, and the proposed mechanisms underlying the MR–PSF association beget direct experimental validation. To advance this field, future investigations should explicitly account for potential confounding ecological variables, including root morphological traits (e.g., specific root length and root tissue density), plant life-history strategies (e.g., annual versus perennial habit, relative growth rate), and functional nutrient-acquisition syndromes, all of which are likely to modulate the strength and direction of both MR and PSF. Incorporating these traits into standardized, multi-species experimental designs will be essential to disentangle the direct effects of mycorrhizal associations from indirect trait-mediated feedbacks and to rigorously test the causal hypotheses generated by our synthesis.

Mycorrhizal responsiveness is an easily assayed plant trait that unfortunately remains underexplored compared to other less plastic traits such as specific leaf area, seed mass and mycorrhizal association type. Notwithstanding the exact reasons of the small number of syntheses integrating mycorrhizal responsiveness estimates, we highlight the importance of this trait for the structuring of plant communities via PSFs, and thus anticipate an increase in comparable studies in the future.

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Author contributions Conceived the study and carried out the data analysis: Veresoglou Stavros D; Drafted the manuscript Veresoglou Stavros D and Johnson David with the help of Liu Yang, Bai jie, Bao Hanzhi, Bao Peipei, Cai Bolun, Cai Liqun, Cao Jiawei, Chen Chen, Chen Genrun, Chen Hongqiao, Chen Jiarong, Chen Zhenghong, Chen Zhenzhen, Chen Zhijian, Duan Zhaoqi, Fan Minhong, Feng kaize, Feng Qiushi, Fu Hanyang, Geng Jialin, Gu Yunyi, Huang Xiaofang, Jia Hanwen, Jia Youxin, Li Boxin, Li Jia'an, Li Wenjie, Liang Jiayong, Liang Zhijian, Liu Changning, Liu Jiaxuan, Liu Jinhui, Liu Xi, Lu Yiming, Luo Minxian, Zhao Meiqi, Meng Zhe, Ou Jingmin, Pan Fei, Peng Danying, Qin Renzhi, Shao Jiayou, Shi Dongxin, Song Hanming, Tan Jiahao, Wang Haojie, Wang Haoyu, Wang Jie, Wang Kexin, Wang Liyuan, Wang Mengxue, Wang Qiyu, Wang Xueying, Wang Zihua, Xin Ying, Xu Jingyan, Xu Tao, Xu Wanying, Xu Yuxiao, Yang Bokui, Yang Shan, Yang Wenyuan, Yang Yankun, Yao Yanting, Yu Jie, Yue Xuyang, Zeng Xiaohui, Zeng Yingzhi, Zhang He, Zhang Youwen, Zhang Zhuo, Zhao Jiaying, Zhao Yuanyuan, Zhong Xinyi, Zhou Mingrui, Zhou Yiqian and Zhu Lizhi. The manuscript has undergone multiple iterations of comments and everybody approved the final version.

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Data availability The data presented here are all in the public domain. We attach some data in the form of supplementary material.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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