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# Editorial: The Next Step: Disentangling the Role of Plant-Soil Feedbacks in Plant Performance and Species Coexistence Under Natural Conditions

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## Editorial on the Research Topic

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## The Next Step: Disentangling the Role of Plant-Soil Feedbacks in Plant Performance and Species Coexistence Under Natural Conditions

Effects of plant-induced changes in soil properties, which impact subsequent plant growth, have received increasing attention in plant ecology (e.g., Smith-Ramesh and Reynolds, 2017). These plant-soil feedbacks (PSFs) are considered to be important for plant performance and plant-community composition in many terrestrial ecosystems (e.g., Van der Putten et al., 2013). However, so far most conclusions on the importance of PSFs in natural systems have been drawn from experiments performed under highly controlled and artificial conditions. Under natural conditions, the growth and development of plants as well as that of soil organisms is influenced by many more abiotic and biotic interactions than in the greenhouse. Hence, there is an urgent need to investigate PSFs under more natural conditions and to better understand the interactions between PSFs and environmental drivers (DeLong et al., 2019). This Research Topic comprises 14 articles—ranging from Original research articles, meta-analytical Reviews and Perspectives—that aim to advance our understanding of the contribution of PSFs to plant growth and plant community composition in different environmental contexts.

## BASELINE

Forero et al. provide an overview of why many PSF studies have been performed under controlled conditions and show that field-based PSF studies are generally scarce. They furthermore present additional empirical evidence that PSFs differ between greenhouse and field conditions, thus highlighting the need to consider effects of environmental conditions in PSF research (see e.g., Heinze et al., 2016; Van der Putten et al., 2016).

## ENVIRONMENTAL CONDITIONS AND PSFs IN GREENHOUSE STUDIES

Although greenhouse conditions typically shelter plants from being exposed to many of the abiotic effects and biotic interactions that occur outdoors (Heinze et al., 2016), they are ideal to test effects of environmental factors on PSFs in isolation. For instance, using field-collected soil in a greenhouse study McCarthy-Neumann and Kobe observed that nutrient and light conditions impact the magnitude and direction of PSFs of tree species. These altered PSF effects could explain species abundance in the field. Furthermore, comparing effects of ambient and elevated temperatures in the conditioning and the feedback phase, the study of Duell et al. revealed that year-to-year variation in temperature reversed negative PSF effects especially for non-native grass species. This might enhance competitive strength compared to native grass species. Several studies have shown that PSFs can influence competition between native and non-native plant species (e.g., Van Grunsven et al., 2007; Callaway et al., 2013). In this context, Bennett et al. investigated an important biotic factor—aboveground herbivory—that was reported to affect PSFs (e.g., Bezemer et al., 2013; Heinze and Joshi, 2018; Heinze et al., 2019). Under greenhouse conditions, they found that simulated aboveground herbivory changed PSFs in native and non-native plants when grown in a competitive mixture. This suggests that interactions between PSFs and herbivory might influence invasion processes.

Interactions between different plant species that are mediated by PSFs are also impacted by differences in soil biota *per-se*. In a nature restoration context Wubs et al. show that inoculating nutrient-rich soil collected from a former arable field, with soils from grassland and heathland suppressed positive PSFs for early successional ruderal plant species. This enhanced the competitive success of more late-successional species.

These greenhouse studies show that PSFs are driven and affected by abiotic and biotic environmental factors (Bennett and Klironomos, 2019; DeLong et al., 2019) as well as by the composition of soil microbial communities. They suggest that PSFs might be an important factor influencing plant-community dynamics in the field.

## LINKING GREENHOUSE AND FIELD STUDIES

Kostenko and Bezemer link plant performance in greenhouse experiments with tests in the field. Under controlled conditions they investigated the response of a focal species to abiotic and biotic soil legacy effects that were created in field plots with different levels of plant diversity. They compared these results to the performance of individuals of this focal species when planted in the field plots. The authors found that plant diversity had a weak impact on soil legacy effects. However, these effects could not be explained by differences in soil community composition

because responses of the plant in the greenhouse and field considerably differed.

## FIELD STUDIES AND APPLIED ASPECTS

Under natural conditions abiotic and biotic factors act together in driving PSFs (Bennett and Klironomos, 2019; DeLong et al., 2019) and several studies have indicated that such PSF effects can be relevant for plant-community dynamics in the field. For instance, in their observational study Vukicevich et al. report that management practices in vineyards influence ground-cover vegetation and that these differences in ground-cover vegetation affect soil fungal communities involved in PSFs. Kulmatiski performed a classical two-phase experiment directly within a long-term field experiment and showed that PSFs are critical for species abundance in plant communities. Lance et al. tested PSF effects of 10 different tree species native for eastern North America with field-collected conspecific and heterospecific soil as inoculum in a field experiment. They report that PSF effects impact soil fungal communities, but that these effects play a rather minor role for tree growth in the field.

Similar results were obtained by Kirchoff et al. in an PSF experiment in grasslands. Their experiment investigated intraspecific variation in plant responses to soil biota and how these responses are shaped by aboveground insect herbivory. They found that the PSFs mediated by soil biota alone play a minor role in influencing plant performance. However, their results support the theory that interactions between plants and soil biota can be mediated through aboveground-herbivores and the responses they induce in plants.

That effects of PSFs are modulated by environmental factors under field conditions was also observed by Dietterich et al.. In a grassland-to-forest transition experiment they planted tree seedlings into tree or grass dominated plots and manipulated levels of competition between experimental plants and neighboring vegetation. Their study shows that most PSF effects are overpowered by biotic interactions such as competition and herbivory and by abiotic soil factors. Using similar field manipulations, Collins et al. investigated competition and PSF effects of a range-expanding species on two resident plant species. Although the soil of the range-expanding species negatively affected growth of the resident species, facilitation effects of the range-expanding species ameliorated the negative PSFs. This indicates that PSFs have the potential to influence plant community composition but must be examined within the context of other ecological processes.

## GENERAL FINDINGS AND FUTURE ASPECTS

In a meta-analysis Beals et al. address how environmental context (competition, stress, disturbance) impact the direction and strength of PSFs. By analyzing data from 76 studies they provide broad evidence that environmental context can change PSF effects.

Furthermore, to enhance our understanding of PSFs effects, researchers should also consider plant-litter feedbacks, as pointed out in the perspectives article by Veen et al..

## CONCLUSION

The papers in this Research Topic indicate that PSF effects are shaped, but mostly overwhelmed in the field, by environmental factors. Therefore, PSFs need to be investigated in combination with environmental factors—preferably directly in the field. This is particularly important when the goal of PSF research is to understand its contribution to plant growth under field conditions. How PSFs are influenced by environmental factors in a changing world will improve our understanding of the importance of PSFs for plant growth and plant community composition in the future.

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## AUTHOR CONTRIBUTIONS

JH, TB, and JJ co-edited the Research Topic. All authors wrote, edited, and approved the final version of the Editorial.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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