PLANT–SOIL FEEDBACK

Water shifts the balance of coexistence

Experimentally manipulating precipitation levels in a plant–soil feedback experiment reveals changes to the interactions between plants and soil microbes that render community dynamics less predictable under wetter conditions.

Po-Ju Ke

The soil in which plants grow contains a diverse array of soil microbes that can affect plant growth[1]. Recent research has highlighted that the interactions between plants and soil microbes can vary with environmental factors, such as nutrient and water availability[2,3]. Such context dependency makes it challenging to predict the consequences of interactions between plants and soil microbes, but understanding them is of increasing importance as climate change introduces variation in environmental factors across time[4]. Writing in this issue of *Nature Ecology & Evolution*, Dudenhöffer and colleagues[5] combine greenhouse experiments, high-throughput sequencing and ecological modelling to show how the soil water content alters the community-level consequences of interactions between plants and soil microbes.

In the ecological literature, plant–soil feedback (PSF) theory[6] highlights that soil microbes can affect plant communities by generating frequency-dependent feedback loops, with overall effects on plant coexistence that can be predicted by a theory-derived pairwise PSF metric. Under the original two-species framework, negative pairwise PSF can occur when both plants condition their microbial communities to favour heterospecifics over conspecifics (Fig. 1a, left). When this happens, soil microbes drive negative frequency dependence that increases the tendency of different plant species to coexistence (Fig. 1b, left). Conversely, positive pairwise PSF can occur when plants condition microbial communities that favour conspecifics over heterospecifics (Fig. 1a, right), which destabilizes plant coexistence by favouring the initially abundant plant species (Fig. 1b, right). However, these biotic interactions do not exist in isolation, but may be modulated by abiotic context. Although previous studies have investigated the effect of soil water content on interactions between plants and soil microbes, they have not yet leveraged existing theory to make predictions regarding plant coexistence.

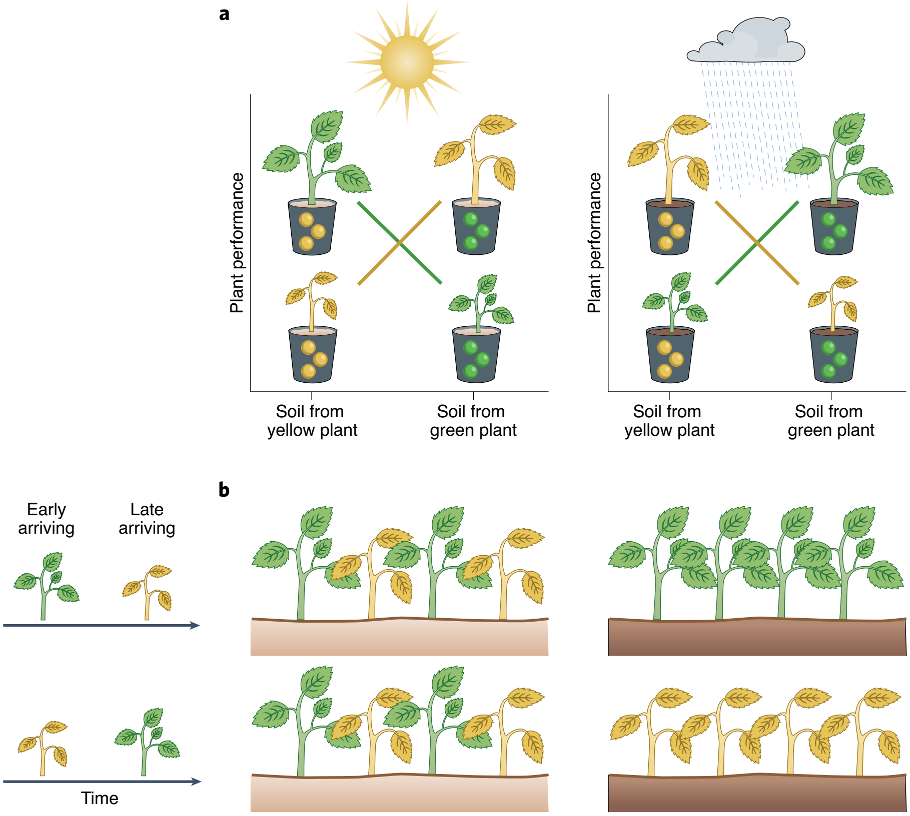

Fig. 1 | PSF under different precipitation levels. a, Quantifying pairwise PSF with a transplant experiment. Soils with a different history are prepared by allowing the yellow and green plant to condition their species-specific soil microbial community (that is, the conditioning phase), indicated by yellow and green circles, respectively. Then, seedlings of the yellow and green plants are transplanted into soils conditioned by conspecifics and heterospecifics (that is, the response phase), indicated by the match and mismatch between plant and microbe colours, respectively. The *x* axis represents soils with different conditioning history and the *y* axis represents plant performance, which is also indicated by the size of the plant icon. Negative pairwise PSF can occur when both plants condition their microbial community such that they perform worse in conspecific soils relative to the performance of the other species (left); positive pairwise PSF can occur when the opposite is true (right). **b**, Predicted plant competitive outcome under different PSF scenarios. Negative pairwise PSF increases the tendency of plant coexistence (left), whereas positive pairwise PSF increases the tendency of priority effects (that is, the competitive outcome depends on plant arrival order, which is indicated by the black arrow) (right). Dudenhöffer and colleagues[5] conducted a PSF experiment in which they subjected both the conditioning and response phase to different watering treatments, indicated here with different shadings of brown. Their results suggest a shift from negative pairwise PSF under drier conditions (left, light brown) to positive pairwise PSF under wetter conditions (right, dark brown).

Dudenhöffer and colleagues now fill this gap by conducting a multispecies water-manipulation experiment using PSF theory. Their impressive full factorial experiment used eight coastal prairie plant species: each species was grown in sterile soil inoculated with 'conditioned' soil from either the same species or a different species to transplant their respective microbial community and measure subsequent plant performance in the 'response' phase. All 64 combinations of plant species × soil type were then grown under 3 watering treatments that corresponded to extremely high, extremely low or average local conditions. To provide a holistic prediction of PSF under conditions of climate change, the authors imposed the watering treatment onto both the conditioning and the response phase of the experiment. They found compelling evidence of a shift from coexistence-stabilizing negative pairwise PSF under drier conditions to coexistence-destabilizing positive pairwise PSF under wetter conditions (Fig. 1).

Dudenhöffer and colleagues[5] develop a novel approach to integrate seedling survival into the calculation of pairwise PSF. Previous studies have mostly calculated the pairwise PSF metric on the basis of plant biomass production in different soils[7]. However, soil microbes can affect various aspects of plant performance throughout the lifespan of a plant[8]. Although studies may also monitor seedling survival, the results are often presented as an additional microbial effect independent of biomass production. In this study, plant mortality and biomass production of the surviving plants were fitted to different statistical distributions and the model coefficients used to estimate the average performance of a plant species in different soils. The pairwise PSF metric calculated from these estimates compounds the effect of microbes on plant survival and biomass production, thereby unifying multiple microbial effects when predicting the context dependency of PSF.

To further explore the likely long-term consequences of climate change-induced alterations to precipitation regimes, Dudenhöffer and colleagues[5] then parameterize a spatially explicit model with their experimental data. These simulations predict that plant communities retain lower diversity and become less predictable under wetter conditions, as positive pairwise PSF becomes more prevalent. The latter is an important signature of positive pairwise PSF that is often overlooked: diversity is lost under such scenarios not because soil microbes confer a competitive advantage to a specific plant[9], but because they drive priority effects (that is, small random differences in initial species abundances would be amplified). Interestingly, further explorations revealed that the context dependency of PSF can have complicated consequences on plant community assembly, with patterns depending on plant mortality, the spatial scale of PSF and the number of plant species directly favoured by positive microbial effects[9].

However, attributing the observed changes in PSF to specific shifts in microbial community composition remains a nontrivial task. Common approaches usually involve searching for statistical relationships between differences in microbial composition and PSF strength, and assigning probable functional guides to the metabarcoding data[10]. However, precisely due to context dependency, the same microbial community may have different effects on plant performance in different soil-watering treatments. Although challenging, future studies can use approaches such as metatranscriptomics to obtain further functional information, as well as using single taxa or synthetic community bioassay to cement causal relationships.

In the near future, we expect to see changes not only in mean precipitation magnitude but also in its temporal variability under climate change. Moving forward requires knowledge on how the temporal aspects of PSF (for example, the rate of soil conditioning and the rate at which plant responsiveness varies with ontogeny) interact with the frequency of wet–dry fluctuations and extreme events[11,12]. For example, a change in the timing of drought may perturb the microbial succession trajectory at various stages and lead to distinct microbial legacies. Changes in the frequency of precipitation fluctuations may also influence how plants respond to soil microbes depending on the water availability during different plant ontogenetic stages. To this end, greenhouse experiments subjecting only the conditioning or response phase of PSF to varying environmental contexts can provide valuable mechanistic insight. Here, Dudenhöffer and colleagues[5] have provided a solid baseline prediction upon which more complicated manipulations can be performed. Together with latest development in PSF theory[9], we are advancing towards robust prediction of how soil microbes affect plant community diversity, stability and productivity in a changing world. ❐

Po-Ju Ke ✉

Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan.

✉*e-mail: pojuke@ntu.edu.tw*

Published online: 28 March 2022

https://doi.org/10.1038/s41559-022-01725-y

References

1. van der Putten, W. H. et al. *J. Ecol.* **101**, 265–276 (2013).
2. Smith-Ramesh, L. M. & Reynolds, H. L. *J. Veg. Sci.* **28**, 484–494 (2017).
3. De Long, J. R., Fry, E. L., Veen, G. & Kardol, P. *Funct. Ecol.* **33**, 118–128 (2019).
4. Pugnaire, F. I. et al. *Sci. Adv.* **5**, eaaz1834 (2019).
5. Dudenhöffer, J.-H., Luecke, N. C. & Crawford, K. M. *Nat. Ecol. Evol.* https://doi.org/10.1038/s41559-022-01700-7 (2022).
6. Bever, J. D., Westover, K. M. & Antonovics, J. *J. Ecol.* **85**, 561–573 (1997).
7. Crawford, K. M. et al. *Ecol. Lett.* **22**, 1274–1284 (2019).
8. Dudenhöffer, J., Ebeling, A., Klein, A., Wagg, C. & Farrer, E. *J. Ecol.* **106**, 230–241 (2018).
9. Kandlikar, G. S., Johnson, C. A., Yan, X., Kraft, N. J. B. & Levine, J. M. *Ecol. Lett.* **22**, 1178–1191 (2019).
10. Nguyen, N. H. et al. *Fungal Ecol.* **20**, 241–248 (2016).
11. Rudgers, J. A. et al. *Annu. Rev. Ecol. Evol. Syst.* **51**, 561–586 (2020).
12. Ke, P.-J., Zee, P. C. & Fukami, T. *New Phytol.* **231**, 1546–1558 (2021).

Competing interests

The author declares no competing interests.