Belowground drivers of plant diversity

Feedbacks between soil microbes and plants affect the diversity of plant communities

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long before Ernst Haeckel coined the term “ecology” in 1866, nature explorers, such as Alexander von Humboldt, observed that vegetation composition changes with climate. However, it still remains unclear what determines the local composition and species richness of vegetation. Understanding the roles of belowground invertebrates and microbes is particularly challenging. On pages 173 and 181 of this issue, respectively, Teste et al. and Bennett et al. report field studies that elucidate the role of soil microorganisms as drivers of plant community composition.

Plant roots are exposed to an enormous amount of soil biodiversity; a handful of soil can contain more than 5000 species that together operate like a gigantic symphony orchestra. Groups of players can be classified according to their instruments, but the overall tune can be understood only when listening to all musicians together. Ecologists measure a soil’s tune, or plant-soil feedback, by comparing plant performance in soil previously exposed to the same or other plant species. This approach may yield results that range from reduced (negative plant-soil feedback) to enhanced performance (positive plant-soil feedback). Teste et al. apply this approach to hyperdiverse Mediterranean shrublands in Southwest Australia; Bennett et al. do the same in temperate forests in the United States (see the photos).

Teste et al. first classify shrubland plant species into five different groups according to how they acquire nutrients from the nutrient-poor soils in which they grow. Three groups use different types of mycorrhizal fungi, which take up resources from the soil and exchange those with plants against carbohydrates and sugars. The fourth group uses rhizobium bacteria, which bind atmospheric nitrogen and provide it to plants in return for assimilates. The fifth uses cluster roots, closely spaced short lateral rootlets that enable phosphorus uptake without a need for mycorrhizal fungi.

The authors performed a plant-soil feedback experiment under controlled conditions and used simulation modeling to relate plant-soil responses in the greenhouse to vegetation patterns in the field. They collected field soil, which had been conditioned by mature plants, and added 7% of that to a pasteurized bulk soil. They then grew the plants in several different soils: soil from their own species, sterilized soil, soil from all other four nutrient uptake types, and a mixture of those four types. After 9 months, they measured the survival, shoot mass, and root mass and used these data for simulation modeling.

Model runs without soil organisms were based on plant performances in sterilized soil and produced unnaturally species-poor vegetation. When the authors added more realistic soil biotic conditions and their feedback effects, the simulated plant communities started to resemble those in the hyperdiverse Australian vegetation. Previous plant-soil feedback models have indeed predicted that adding negative or positive feedback components will influence the species diversity of vegetation (5–7); however, stepwise addition of plant nutrient acquisition strategies, as done in the present study, shows that a variety of positive and negative feedback effects led to greater diversity in the vegetation, rather than negative feedback effects alone.

The vast majority of plant-soil feedback studies have been carried out under greenhouse conditions; very few studies have assessed the role of plant-soil feedback in the field (8). To address this shortcoming, Bennett et al. studied two types of tree species in real forest settings. The first type is associated with ectomycorrhizal fungi, which form a dense network of fungal hyphae around plant roots but do not penetrate root cell walls. The second type is associ-
ated with arbuscular mycorrhizal fungi, which penetrate cortical cells of plant roots. The authors placed tree seedlings with or without mycorrhizal fungi in the forest and recorded their performances. In addition, they used forest inventory data to determine which tree species produce established seedlings under mature trees from each of the two mycorrhizal types. They show that fewer offspring are recruited under the parent arbuscular mycorrhizal trees than when the trees are ectomycorrhizal. There were more seedlings from other tree species under arbuscular mycorrhizal trees than under ectomycorrhizal trees. Thus, arbuscular mycorrhizal trees promote forest diversity because these symbionts protect tree offspring less well against pathogen effects than do ectomycorrhizal fungi. This finding provides a novel dimension to the Janzen-Connell hypothesis, which explains diversity in natural ecosystems by the need of species to establish outside the control of their parents’ enemies (9). Bennett et al. show that Janzen-Connell effects are more profound under arbuscular mycorrhizal than under ectomycorrhizal trees.

Both research studies show that ectomycorrhizal fungi generally enhance plant performance (1, 2). This is in line with expectations based on previous studies. However, Bennett et al. find that trees associated with arbuscular mycorrhizal fungi negatively affected their own offspring, whereas Teste et al. report that in the Australian shrublands, plant-soil feedback effects of arbuscular mycorrhizal plant species were neutral. Moreover, plants that acquire nutrients via ericoid mycorrhizal fungi, rhizobia, and cluster roots had mainly negative plant-soil feedback (1).

Determining what causes these observations would require testing Koch’s postulates, which involves excluding all possible factors one by one and adding them back again one by one. But this is impossible considering the many possible interactions. Both studies circumvent this approach by quantifying root infection by the symbionts; Bennett et al. also scored root lesions as disease symptoms caused by soil pathogens. Plants with more mycorrhizal colonization had fewer lesions and grew better. Arbuscular mycorrhizal trees also had more root lesions than ectomycorrhizal trees. This strongly suggests that the symbiotic fungi were protecting the plants from soil pathogens, with ectomycorrhizal fungi doing so better than arbuscular mycorrhizal fungi.

Teste et al. also were able to relate plant performance, at least in part, to the coverage of the roots with the symbiotic fungi and rhizobia. However, they did not quantify pathogen abundance. Their model simulations show that only adding negative plant-soil feedback did not result in as much vegetation diversity as when positive feedback was added as well. The mechanisms underlying soil effects on plants can vary from pathogen effects to partial or complete pathogen suppression by symbionts or other growth-promoting microbes. Further examination of these mechanisms requires a microbiome community approach (10).

What role do the symbiotic soil microbes play in the soil symphony orchestra? Do they play the first violin, or are they led by the soil pathogens? Bennett et al. report that the coverage of the American tree roots by mycorrhizal fungi in the feedback experiments was negatively related to the number of pathogen lesions on the roots, and arbuscular trees had more lesions than did ectomycorrhizal trees. This suggests that ectomycorrhizal fungi protect plant roots better against pathogens than do arbuscular mycorrhizal fungi. The fact that arbuscular plants in the Australian system had a more neutral plant-soil feedback than that of the arbuscular trees in North America suggests that the effects are context-dependent. Further field studies will be crucial for understanding context dependence and inclusion of plant-soil feedback effects in predictions of ecosystem responses to global changes (11).

The two studies (1, 2) open up new avenues toward searching for plant traits that may predict plant-soil feedback effects (12, 13). They support the view that ectomycorrhizal fungi provide positive plant-soil feedback under a wider range of environmental conditions and suggest that the role of arbuscular mycorrhizal fungi depends on environmental context. My colleagues and I have recently reported that root thickness and the percentage of roots infected by arbuscular mycorrhizal fungi correlate positively with plant-soil feedback (13), and this suggests that various plant-soil feedback outcomes are possible in this nutrient acquisition type.

In the soil symphony orchestra, arbuscular mycorrhizal fungi may thus play the first violin, leading to positive plant-soil feedback. An alternative view is that the pathogens play the first violin and that the mycorrhizal fungi, more or less successfully, overrule the pathogens’ sound. Future studies should elucidate the underlying mechanisms and trait and context dependencies and should incorporate these insights into mainstream ecological-evolutionary theories. If this is done successfully, it has the potential to further improve ecosystem management and diversity conservation.

REFERENCES
Editor's Summary

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