

REPORT

PLANT ECOLOGY

Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands

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Soil biota influence plant performance through plant-soil feedback, but it is unclear whether the strength of such feedback depends on plant traits and whether plant-soil feedback drives local plant diversity. We grew 16 co-occurring plant species with contrasting nutrient-acquisition strategies from hyperdiverse Australian shrublands and exposed them to soil biota from under their own or other plant species. Plant responses to soil biota varied according to their nutrient-acquisition strategy, including positive feedback for ectomycorrhizal plants and negative feedback for nitrogen-fixing and nonmycorrhizal plants. Simulations revealed that such strategy-dependent feedback is sufficient to maintain the high taxonomic and functional diversity characterizing these Mediterranean-climate shrublands. Our study identifies nutrient-acquisition strategy as a key trait explaining how different plant responses to soil biota promote local plant diversity.

Evidence is mounting that interactions between plants and microbes influence the maintenance of terrestrial plant diversity (1–3). Plant roots interact closely with a wide range of soil biota, including beneficial ones that enhance nutrient acquisition (e.g., mycorrhizal fungi) and pathogens that cause root necrosis or plant death (1, 4). As such, effects of soil biota on plant survival and growth, and their role in maintaining plant diversity, should critically depend on traits such as plant nutrient-acquisition strategy (5). Previous studies have recognized the importance of plant traits in explaining feedback between plants and soil biota (6), yet the ecological importance of belowground traits remains poorly understood. For example, soil-borne pathogens can promote local plant species diversity via conspecific negative density dependence (1, 7), which might be particularly important for nonmycorrhizal plant species whose roots are less well defended (5). By contrast, arbuscular and ectomycorrhizal plants are better defended against pathogens, which could prevent pathogen-mediated negative density depen-

dence and even promote monodominance via positive plant-soil feedback (8, 9). Other belowground nutrient-acquisition strategies, such as those involving nitrogen (N)-fixing bacteria, might also have consequences for local plant diversity. A research challenge is to determine how the strength and direction of plant-soil feedback depend on traits such as nutrient-acquisition strategy (6, 10) and how such feedback contributes to the maintenance of plant diversity (1).

Mediterranean climate regions contribute to global plant diversity by supporting 20% of all plant species on only 5% of the land area (11). Local plant diversity in some sclerophyll shrublands in these regions is comparable to that of species-rich tropical rain forests (12). These shrublands are also characterized by a high diversity in belowground plant strategies to acquire nutrients, including a variety of mycorrhizal symbioses and the capacity to fix N₂ via bacterial symbioses (13, 14). A better understanding of the mechanisms, such as plant-soil feedback, that drive plant diversity in this biome is important because all five Mediterranean-climate regions are hot spots for global biodiversity conservation (15). More broadly, determining plant-soil feedback will enhance our ability to predict community and ecosystem responses to global environmental change (16).

We studied hyperdiverse Mediterranean shrublands in Southwest Australia (fig. S1) (17). The exceptional diversity of plant species and nutrient-acquisition strategies in these shrublands (12, 18) makes them ideal for exploring how plant-soil feedback depends on root strategies and how such feedback contributes to the maintenance of plant diversity. We collected soil from the root-

ing zone of 26 plant species representing five nutrient-acquisition strategies: (i) arbuscular mycorrhizal (AM), (ii) ectomycorrhizal (EcM), (iii) ericoid mycorrhizal (ErM), (iv) N-fixing (NF), and (v) nonmycorrhizal cluster-rooted (NM_{CR}), and then prepared seven inocula for each species: (1) sterilized conspecific soil, (2) conspecific soil, (3) soil from all species of the same strategy but excluding conspecific soil, and (4–7) strategy-specific soil, using all species from the other strategies. Plant species were assigned to different nutrient-acquisition strategies based on our recent studies in the area (18) and our analyses of fine roots (19). Sixteen of the 26 plant species (strategies: NF, NM_{CR}, EcM, and AM) germinated in sufficient numbers to be included in a large plant-soil feedback experiment (16 species × 7 soil inocula × 10 replicates = 1120 pots with one plant per pot). The experiment was conducted in a glasshouse for 9 months (19), after which we measured survival, growth, and root structures. We then used survival and growth data from this glasshouse experiment (19) to parameterize simulation models exploring the long-term effects that plant-soil feedback can have on plant species and functional diversity (i.e., diversity of nutrient-acquisition strategies) (19).

Plant survival and growth were strongly influenced by the origin of the soil inoculum, and the effects varied among nutrient-acquisition strategies (Figs. 1 and 2A and fig. S2). First, survival of N-fixing and nonmycorrhizal cluster-rooted plants declined when inoculated with conspecific soil, suggesting a response to soil-borne pathogens or other antagonists; by contrast, survival of arbuscular and ectomycorrhizal plants was unaffected by inoculum origin (Fig. 1A). Second, growth of surviving N-fixing and nonmycorrhizal plants was reduced when inoculated with conspecific soil compared with soil from heterospecific plants (i.e., negative feedback), whereas the growth of ectomycorrhizal plants was enhanced in conspecific soil (i.e., positive feedback) (Fig. 1B). In addition, the effects of heterospecific soil inocula depended on the strategy: For example, nonmycorrhizal plants grew best in soil from all three mycorrhizal types, whereas N-fixing plants grew best in ectomycorrhizal soil (Fig. 1B). By contrast, ectomycorrhizal plants grew worst in ericoid mycorrhizal soil (Fig. 1B). Arbuscular mycorrhizal plants had invariant feedback (Fig. 1B), but the net effect of soil biota (i.e., growth with versus without soil biota) on this group was consistently positive across all soil inocula (fig. S2). Overall, the effects of soil inocula on plant growth were significant for three out of four strategies (Figs. 1B and 2A).

Plant growth and feedback strength were partly explained by differences in the expression of nutrient-acquisition strategies, since the different inocula affected the root occupancy response (Fig. 2B and fig. S3). For example, reduced growth of arbuscular, ectomycorrhizal, and N-fixing plants in sterilized soil was associated with little root colonization by mycorrhizal fungi (Fig. 2B and fig. S4) and low root nodule mass for N-fixing plants (Fig. 2B). By contrast, the better growth

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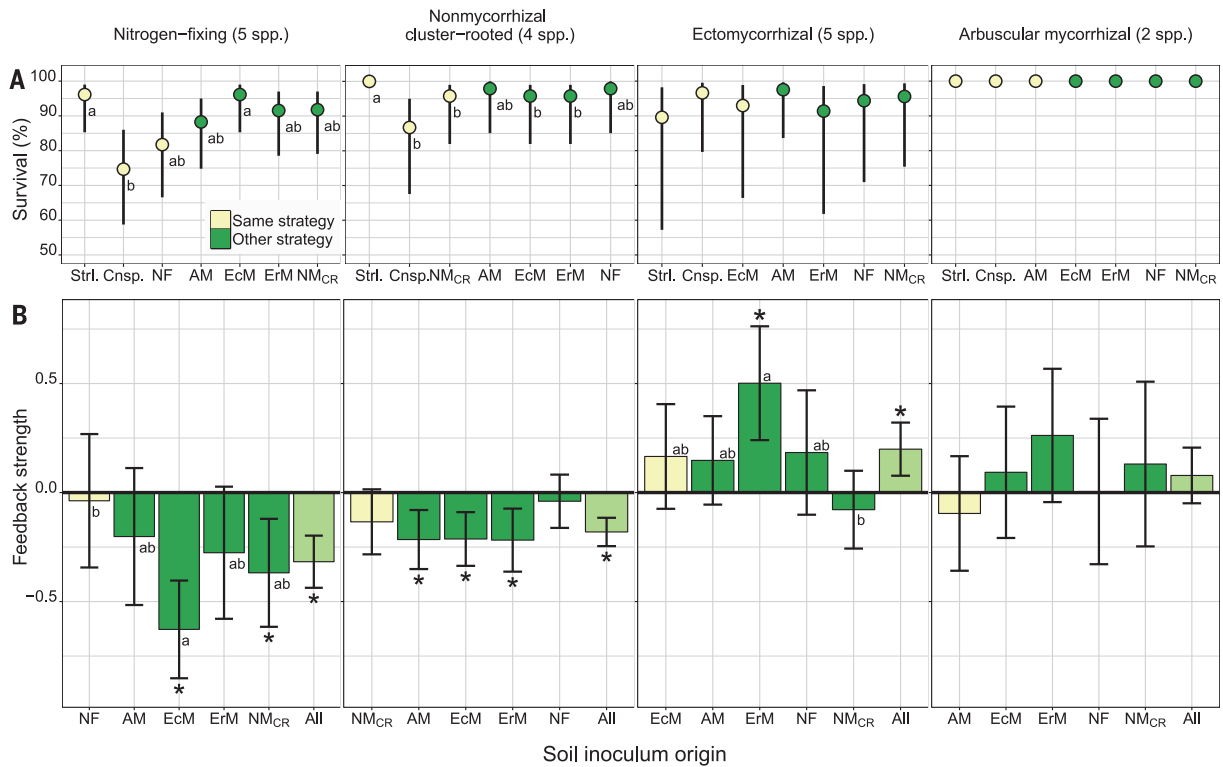


Fig. 1. Plant survival and plant-soil feedback strength in relation to plant nutrient-acquisition strategy. Feedback strength is shown as \log_{10} -response ratios of plant biomass in conspecific soil compared with hetero-specific soils (19, 29). (A) Plant survival. (B) Plant-soil feedback strength. Each panel represents the average responses of species belonging to each strategy. (A) shows survival means with 95% confidence intervals (CIs) (19). In (B), error bars are 95% CIs and are indicated by an asterisk if they do not include zero. In

each panel, different letters indicate statistically significant differences ($P \leq 0.05$) according to Tukey HSD tests for (B) or Dunnett tests and nonoverlapping CIs for (A) (19). Strl, sterile conspecific; Cnsp., conspecific; AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; ErM, ericoid mycorrhizal; NF, nitrogen-fixing; NM_{CR}, nonmycorrhizal cluster rooted; All, overall feedback across all heterospecific soil inocula. Feedback strength for each plant species is provided in fig. S5 and across all plant species in fig. S6.

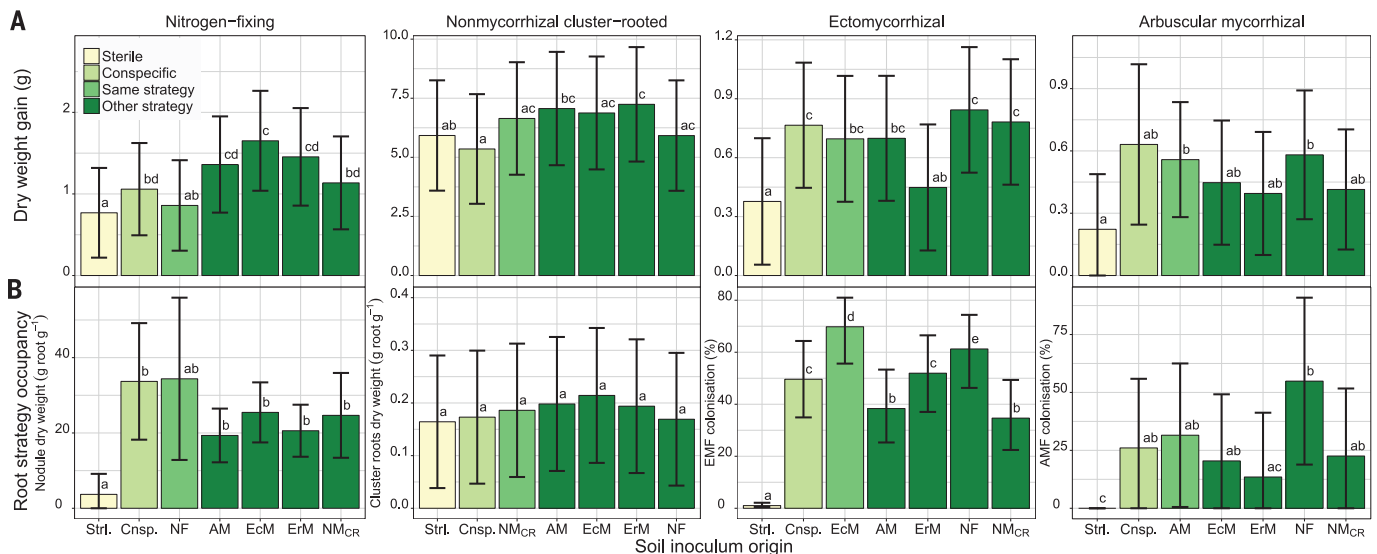


Fig. 2. Dry weight gain and root strategy occupancy of plants inoculated with soil of different nutrient-acquisition strategies or with sterilized soil. (A) Dry weight gain. (B) Root strategy occupancy. In (A), bars represent mean plant dry weight gain of surviving plants with 95% CIs. In (B), bars represent mean nodule dry weight and cluster roots dry weight standardized on a total root

weight basis, ectomycorrhizal fungal (EMF), or arbuscular mycorrhizal fungal (AMF) root colonization with 95% CIs. Different letters indicate statistically significant differences [Tukey HSD (honest significant difference) tests with $P \leq 0.05$]. Abbreviations as in Fig. 1. Dry weight gain and root strategy occupancy per plant species are provided in fig. S3 and for secondary strategies in fig. S4.

of N-fixing plants in ectomycorrhizal soil relative to conspecific soil was associated with greater ectomycorrhizal root colonization (fig. S4). Finally, the nonmycorrhizal cluster-rooted plants had reduced growth in conspecific soils compared with arbuscular and ericoid mycorrhizal soils (Fig. 2A), which was associated with lower cluster-root biomass in particular species (fig. S3). These results provide a mechanistic basis for explaining how soil biota interact with the deployment of plant nutrient-acquisition strategy, thereby influencing plant survival and growth via plant-soil feedback.

Spatially explicit simulations using our experimental data showed that the complex feedback between plants of contrasting nutrient-acquisition strategies and their associated soil biota can contribute strongly to the maintenance of the high plant species and functional diversity in these hyperdiverse shrublands (Fig. 3). In simulations where soil biota were absent (i.e., using only survival and growth data from sterilized soil), plant species and functional diversity declined rapidly to unrealistically low levels (Fig. 3). Similarly, diversity also declined rapidly when only conspecific (and not heterospecific) effects of soil biota were considered in the simulations (Fig. 3). By contrast, when all measured effects of soil biota from conspecific and heterospecific plants were included, plant species diversity and functional diversity were maintained at considerably higher levels. Moreover, such high levels were much closer to those characteristically observed for these hyperdiverse Mediterranean shrublands (Fig. 3 and fig. S4). These positive effects of soil biota on diversity were partly explained by a more even abundance distribution among faster-growing mycorrhizal plant species (fig. S6).

Previous studies have shown how feedback between plants and their associated soil biota drives plant community dynamics (1, 20–24). However, until now, studies have not determined whether the strength and direction of plant-soil feedback depended on belowground traits such as nutrient-acquisition strategies (6, 10), despite increasing recognition that these strategies should determine plant responses to soil mutualists (e.g., mycorrhizal fungi, N-fixing bacteria) and susceptibility to root pathogens (5, 25). Our study addresses this question by showing that feedback between plants and their associated soil biota critically depends on nutrient-acquisition strategy. As such, this could be a useful trait to generalize and predict plant responses to soil biota in natural, mixed-species communities.

Soil biota, particularly soil-borne pathogens, have been suggested as key drivers of plant diversity (1). For example, theory suggests that the role of pathogens in plant diversity can arise through the buildup of host-specific pathogens when a given plant species increases in abundance (1, 5, 7) or when generalist pathogens have more detrimental effects on dominant plants than on subordinates (1). Although such theory emphasizes conspecific negative plant-soil feedback as an important mechanism driving plant

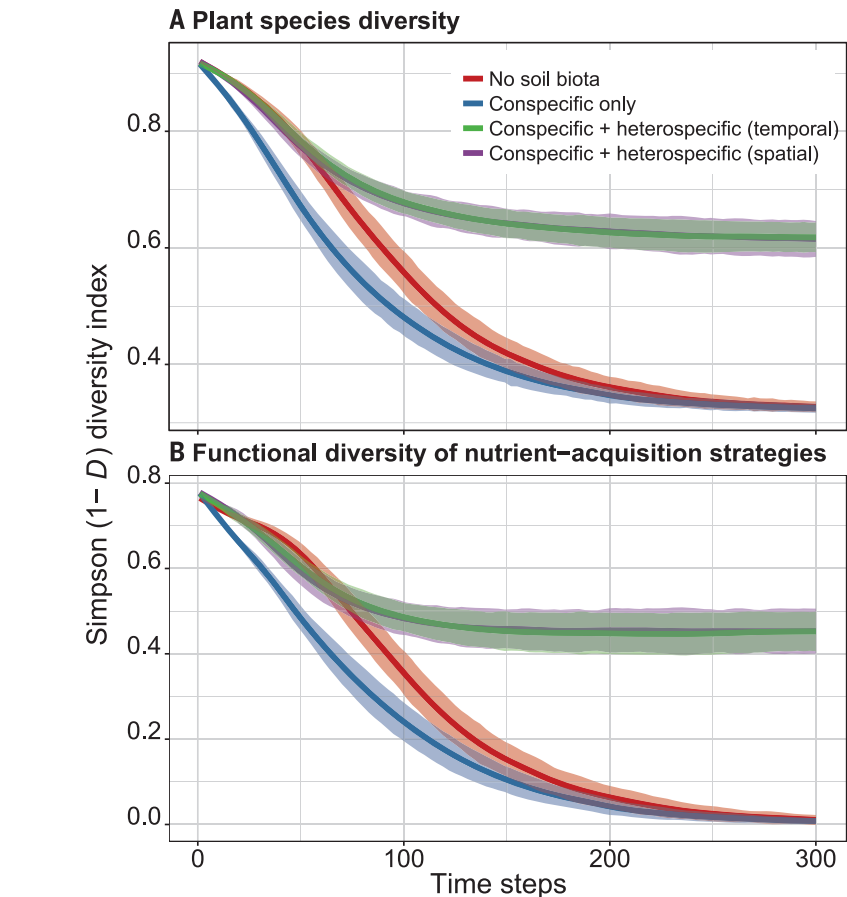


Fig. 3. Model simulations based on experimental data showing that feedback between plants of contrasting nutrient-acquisition strategies maintains plant species diversity and functional diversity. (A) Plant species diversity. (B) Functional diversity. Simulation models were parameterized from survival and relative growth rates from our glasshouse experiment under four different scenarios (19). Curves were generated with generalized additive models, and shown here are the means (thin dark curves) and associated standard deviations (lighter and wider curves) from the raw data for 100 simulation runs per time step per scenario. Figure S9 shows results of simulations exploring effects of survival and growth separately, which revealed that patterns were mainly driven by growth rather than by survival.

diversity (1), our simulations that included only soil biota effects from conspecific plants actually showed a decline in plant species and functional diversity. Indeed, it is only when we integrated all effects of conspecific and heterospecific soil inocula in our simulation models that plant species and functional diversity were maintained at realistically high levels. As such, our results suggest that the maintenance of plant diversity by soil biota cannot be explained solely by negative effects (e.g., pathogens) conditioned by conspecific individuals but also by positive effects of soil biota conditioned by heterospecific individuals with contrasting nutrient-acquisition strategies. Although our experiment cannot identify the actual mechanisms underlying these positive effects, possibilities include facilitation of subordinate plants (3) or suppression of pathogens by mycorrhizal fungi (5).

Our study provides clear evidence that plant-soil feedback is an important driver of local plant diversity in species-rich plant communities, mediated by interactions between plants with dif-

ferent nutrient-acquisition strategies and their associated soil biota. The importance of complementary resource use among plants with different resource-acquisition strategies for promoting plant diversity has conventionally been linked with partitioning of soil resources such as nutrients and water (26, 27), yet local competition for soil resources cannot explain the high plant diversity found in these nutrient-impooverished shrublands (17). Our study empirically supports theoretical work on plant-soil feedback, suggesting that it can contribute to species coexistence (28). Studying interactions between plants and soil biota should enhance our understanding of mechanisms underlying the maintenance of plant diversity at local scales and of how plant diversity will respond to global environmental changes (4, 16).

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S12

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Editor's Summary

Soil biota and plant diversity

Soil biota, including symbionts such as mycorrhizal fungi and nitrogen-fixing bacteria, as well as fungal and bacterial pathogens, affect terrestrial plant diversity and growth patterns (see the Perspective by van der Putten). Teste *et al.* monitored growth and survival in Australian shrubland plant species paired with soil biota from plants of the same species and from other plants that use different nutrient acquisition strategies. Plant-soil feedbacks appear to drive local plant diversity through interactions between the different types of plants and their associated soil biota. Bennett *et al.* studied plant-soil feedbacks in soil and seeds from 550 populations of 55 species of North American trees. Feedbacks ranged from positive to negative, depending on the type of mycorrhizal association, and were related to how densely the same species occurred in natural populations.

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