1   **Title**: Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands

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22   **One Sentence Summary**: Feedback between plants of contrasting nutrient-acquisition strategies

23   and their associated soil biota contributes to the maintenance of plant species and functional

24   diversity in hyperdiverse shrublands.

25

26   **Abstract:**

27   Soil biota influence plant performance through plant–soil feedback, but it is unclear whether the

28   strength of such feedback depends on plant traits, and whether plant–soil feedback drives local

29   plant diversity. We grew 16 co-occurring plant species with contrasting nutrient-acquisition

30   strategies from hyperdiverse Australian shrublands and exposed them to soil biota from under

31   their own or other plant species. Plant responses to soil biota varied according to their nutrient-

32   acquisition strategy, including positive feedback for ectomycorrhizal plants and negative

33   feedback for nitrogen-fixing and non-mycorrhizal plants. Simulations revealed that such

34   strategy-dependent feedback is enough to maintain the high taxonomic and functional diversity

35   characterizing these Mediterranean-climate shrublands. Our study identifies nutrient-acquisition

36   strategy as a key trait explaining how different plant responses to soil biota promote local plant

37   diversity.

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Main Text:

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 significance 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 non-mycorrhizal 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 dependence 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 rainforests (*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 N_2 via bacterial

62 symbioses (*13, 14*). A better understanding of the mechanisms, such as plant–soil feedback, that

63 drive plant diversity in this biome is important because all five Mediterranean-climate regions

64 are hotspots for global biodiversity conservation (*15*). More broadly, determining plant–soil

65 feedback will enhance our ability to predict community and ecosystem responses to global

66 environmental change (*16*).

67   We studied hyperdiverse Mediterranean shrublands in Southwest Australia (Fig. S1) (*17*).

68 The exceptional diversity of plant species and nutrient-acquisition strategies in these shrublands

69 (*12, 18*) makes them ideal for exploring how plant–soil feedback depends on root strategies, and

70 how such feedback contribute to the maintenance of plant diversity. We collected soil from the

71 rooting zone of 26 plant species representing five nutrient-acquisition strategies: (i) arbuscular

72 mycorrhizal (AM), (ii) ectomycorrhizal (EcM), (iii) ericoid mycorrhizal (ErM), (iv) nitrogen-

73 fixing (NF), and (v) non-mycorrhizal cluster-rooted (NM_{CR}), and then prepared seven inocula for

74 each species: (1) sterilized conspecific soil, (2) conspecific soil, (3) soil from all species of the

75 same strategy, but excluding conspecific soil, and (4–7) strategy-specific soil, using all species

76 from the other strategies. Plant species were assigned to different nutrient-acquisition strategies

77 based on our recent studies in the area (*18*) and our analyses of fine roots (*19*). Sixteen of the 26

78 plant species (strategies: NF, NM_{CR}, EcM, and AM) germinated in sufficient numbers to be

79 included in a large plant–soil feedback experiment (16 species $\times$ 7 soil inocula $\times$ 10 replicates =

80 1120 pots with one plant per pot). The experiment was conducted in a glasshouse for nine

81 months (*19*), after which we measured survival, growth, and root structures. We then used

82 survival and growth data from this glasshouse experiment (*19*) to parameterize simulation

83 models exploring the long-term effects that plant–soil feedback can have on plant species and

84 functional diversity (i.e. diversity of nutrient-acquisition strategies) (*19*).

85   Plant survival and growth were strongly influenced by the origin of the soil inoculum,

86 and the effects varied among nutrient-acquisition strategies (Figs. 1, 2A, and S2). First, survival

87 of N-fixing and non-mycorrhizal cluster-rooted plants declined when inoculated with conspecific

88 soil, suggesting a response to soil-borne pathogens or other antagonists; by contrast, survival of

89 arbuscular and ectomycorrhizal plants was unaffected by inoculum origin (Fig. 1A). Second,

90 growth of surviving N-fixing and non-mycorrhizal plants was reduced when inoculated with

91 conspecific soil compared with soil from heterospecific plants (i.e. negative feedback), whereas

92 the growth of ectomycorrhizal plants was enhanced in conspecific soil (i.e. positive feedback)

93 (Fig. 1B). In addition, the effects of heterospecific soil inocula depended on the strategy: for

94 example, non-mycorrhizal plants grew best in soil from all three mycorrhizal types, whereas N-

95 fixing plants grew best in ectomycorrhizal soil (Fig. 1B). By contrast, ectomycorrhizal plants

96 grew worst in ericoid mycorrhizal soil (Fig. 1B). Arbuscular mycorrhizal plants had invariant

97 feedback (Fig. 1B), but the net effect of soil biota (i.e. growth with vs. without soil biota) on this

98 group was consistently positive across all soil inocula (Fig. S2). Overall, the effects of soil

99 inocula on plant growth were significant for three out of four strategies (Figs. 1B, 2A).

100   Plant growth and feedback strength were partly explained by differences in the

101 expression of nutrient-acquisition strategies, since the different inocula affected the root

102 occupancy response (Figs. 2B, S3). For example, reduced growth of arbuscular, ectomycorrhizal,

103 and N-fixing plants in sterilized soil was associated with little root colonization by mycorrhizal

104 fungi (Figs. 2B, S4) and low root nodule mass for N-fixing plants (Fig. 2B). By contrast, the

105 better growth of N-fixing plants in ectomycorrhizal soil relative to conspecific soil was

106 associated with greater ectomycorrhizal root colonisation (Fig. S4). Finally, the non-mycorrhizal

107 cluster-rooted plants had reduced growth in conspecific soils compared to 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 (Figs. 3, 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

drive 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

131   feedback between plants and their associated soil biota critically depends on nutrient-acquisition

132   strategy. As such, this could be a useful trait to generalise and predict plant responses to soil

133   biota in natural, mixed-species communities.

134   Soil biota, particularly soil-borne pathogens, have been suggested as key drivers of plant

135   diversity (*1*). For example, theory suggests that the role of pathogens on plant diversity can arise

136   through the build-up of host-specific pathogens when a given plant species increases in

137   abundance (*1, 5, 7*), or when generalist pathogens have more detrimental effects on dominant

138   plants than on subordinates (*1*). While such theory emphasises conspecific negative plant–soil

139   feedback as an important mechanism driving plant diversity (*1*), our simulations that included

140   only soil biota effects from conspecific plants actually showed a decline in plant species and

141   functional diversity. Indeed, it is only when we integrated all effects of conspecific and

142   heterospecific soil inocula in our simulation models that plant species and functional diversity

143   were maintained at realistically high levels. As such, our results suggest that the maintenance of

144   plant diversity by soil biota cannot be explained solely by negative effects (e.g. pathogens)

145   conditioned by conspecific individuals, but also by positive effects of soil biota conditioned by

146   heterospecific individuals with contrasting nutrient-acquisition strategies. Although our

147   experiment cannot identify the actual mechanisms underlying these positive effects, possibilities

148   include facilitation of subordinate plants (*3*) or suppression of pathogens by mycorrhizal fungi

149   (*5*).

150   Our study provides clear evidence that plant–soil feedback is an important driver of local

151   plant diversity in species-rich plant communities, mediated by interactions between plants of

152   different nutrient-acquisition strategies and their associated soil biota. The importance of

153   complementary resource use among plants with different resource-acquisition strategies for

154   promoting plant diversity has conventionally been linked with partitioning of soil resources such

155   as nutrients and water (*26, 27*), yet local competition for soil resources cannot explain the high

156   plant diversity found in these nutrient-impoverished shrublands (*17*). Our study empirically

157   supports theoretical work on plant–soil feedback suggesting that it can contribute to species

158   coexistence (*28*). Studying interactions between plants and soil biota should enhance our

159   understanding of mechanisms underlying the maintenance of plant diversity at local scales, and

160   of how plant diversity will respond to global environmental changes (*4, 16*).
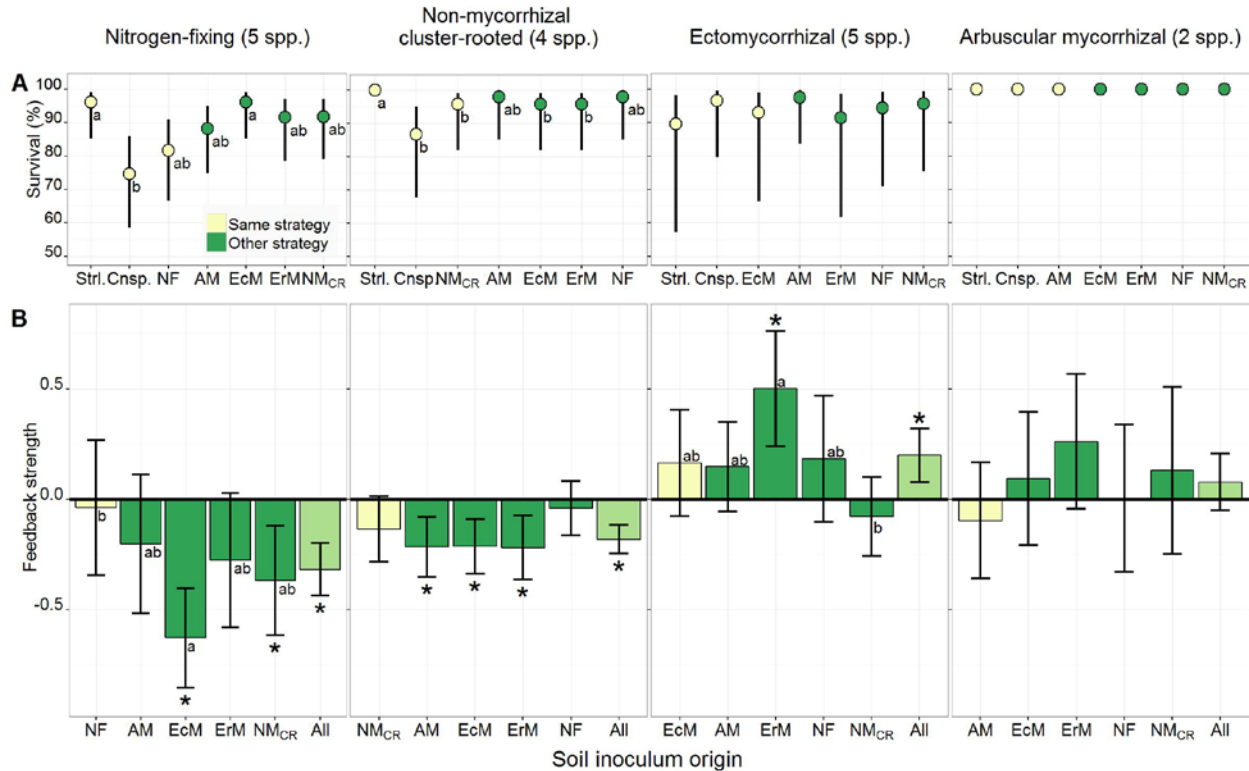
Fig. 1. **Plant survival (A) and plant–soil feedback strength (B) in relation to plant nutrient-acquisition strategy.** Feedback strength is shown as $\log_{10}$-response ratios of plant biomass in conspecific soil compared to heterospecific soils (*19, 29*). For (**A**) and (**B**), each panel represents the average responses of species belonging to each strategy. Panel (**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 non-overlapping CIs for (**A**)(*19*). Strl: sterile conspecific, Cnsp.: conspecific, AM: arbuscular mycorrhizal, EcM: ectomycorrhizal, ErM: ericoid mycorrhizal, NF: nitrogen-fixing, NM_{CR}: non-mycorrhizal cluster rooted, All: overa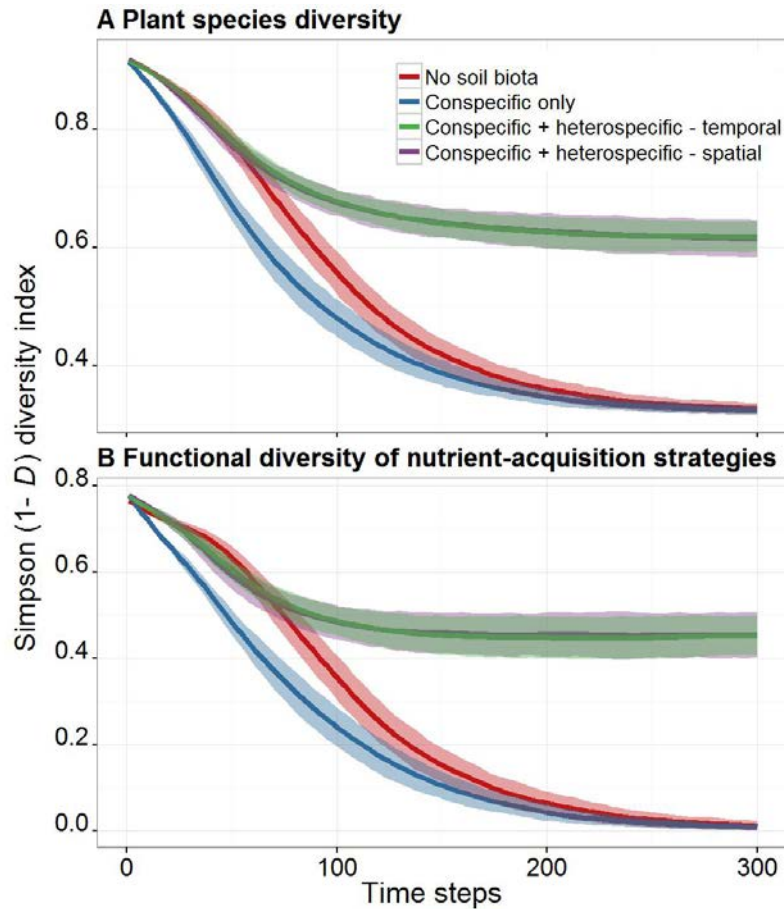ll feedback across all heterospecific soil inocula. Feedback strength for each plant species is provided in Fig. S5 and across all plant species in Fig. S6.

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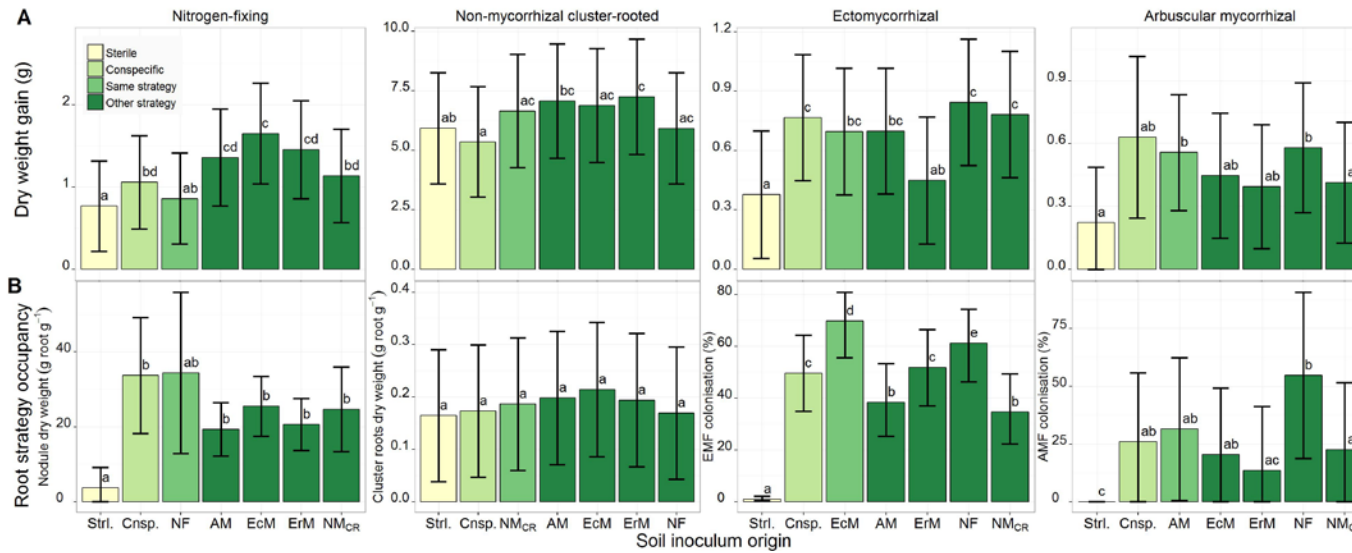
Fig. 2. Dry weight gain (A) and root strategy occupancy (B) of plants inoculated with soil of different nutrient-acquisition strategies or with sterilized soil. In (**A**), bars represent mean plant dry weight gain of surviving plants with 95% CIs. In (**B**), bars represent mean nodule dry weight and 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 tests with $P \leq 0.05$). See Fig. 1 for complete figure legends. Dry weight gain and root strategy occupancy per plant species are provided in Fig. S3 and for secondary strategies in Fig. S4.

A Plant species diversity

Legend:
- No soil biota
- Conspecific only
- Conspecific + heterospecific – temporal
- Conspecific + heterospecific – spatial

y-axis: Simpson ($1 - D$) diversity index

B Functional diversity of nutrient-acquisition strategies

x-axis: Time steps

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Fig. 3. Model simulations based on experimental data showing that feedback between plants of contrasting nutrient-acquisition strategies maintains (A) plant species diversity and (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.

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356   **Supplementary Materials**
357   Materials and Methods
358   Figures S1-S12
359   Tables S1-S6
360   References and Notes (30 – 62)