

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.

38

39 **Main Text:**

40 Evidence is mounting that interactions between plants and microbes influence the maintenance  
41 of terrestrial plant diversity (1-3). Plant roots interact closely with a wide range of soil biota,  
42 including beneficial ones that enhance nutrient acquisition (e.g. mycorrhizal fungi) and  
43 pathogens that cause root necrosis or plant death (1, 4). As such, effects of soil biota on plant  
44 survival and growth, and their role in maintaining plant diversity, should critically depend on  
45 traits such as plant nutrient-acquisition strategy (5). Previous studies have recognized the  
46 importance of plant traits in explaining feedback between plants and soil biota (6), yet the  
47 ecological significance of belowground traits remains poorly understood. For example, soil-  
48 borne pathogens can promote local plant species diversity via conspecific negative density  
49 dependence (1, 7), which might be particularly important for non-mycorrhizal plant species  
50 whose roots are less well defended (5). By contrast, arbuscular and ectomycorrhizal plants are  
51 better defended against pathogens, which could prevent pathogen-mediated negative density  
52 dependence and even promote monodominance via positive plant–soil feedback (8, 9). Other  
53 belowground nutrient-acquisition strategies, such as those involving nitrogen (N)-fixing bacteria,  
54 might also have consequences for local plant diversity. A research challenge is to determine how  
55 the strength and direction of plant-soil feedback depend on traits such as nutrient-acquisition  
56 strategy (6, 10), and how such feedback contributes to the maintenance of plant diversity (1).

57 Mediterranean climate regions contribute to global plant diversity by supporting 20% of  
58 all plant species on only 5% of the land area (11). Local plant diversity in some sclerophyll  
59 shrublands in these regions is comparable to that of species-rich tropical rainforests (12). These  
60 shrublands are also characterized by a high diversity in belowground plant strategies to acquire  
61 nutrients, including a variety of mycorrhizal symbioses and the capacity to fix N<sub>2</sub> 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<sub>CR</sub>), 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<sub>CR</sub>, EcM, and AM) germinated in sufficient numbers to be  
79 included in a large plant–soil feedback experiment (16 species × 7 soil inocula × 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

108 mycorrhizal soils (Fig. 2A), which was associated with lower cluster root biomass in particular  
109 species (Fig. S3). These results provide a mechanistic basis for explaining how soil biota interact  
110 with the deployment of plant nutrient-acquisition strategy, thereby influencing plant survival and  
111 growth via plant–soil feedback.

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

125       Previous studies have shown how feedback between plants and their associated soil biota  
126 drive plant community dynamics (1, 20-24). However, until now studies have not determined  
127 whether the strength and direction of plant–soil feedback depended on belowground traits such  
128 as nutrient-acquisition strategies (6, 10), despite increasing recognition that these strategies  
129 should determine plant responses to soil mutualists (e.g. mycorrhizal fungi, N-fixing bacteria)  
130 and susceptibility to root pathogens (5, 25). Our study addresses this question by showing that

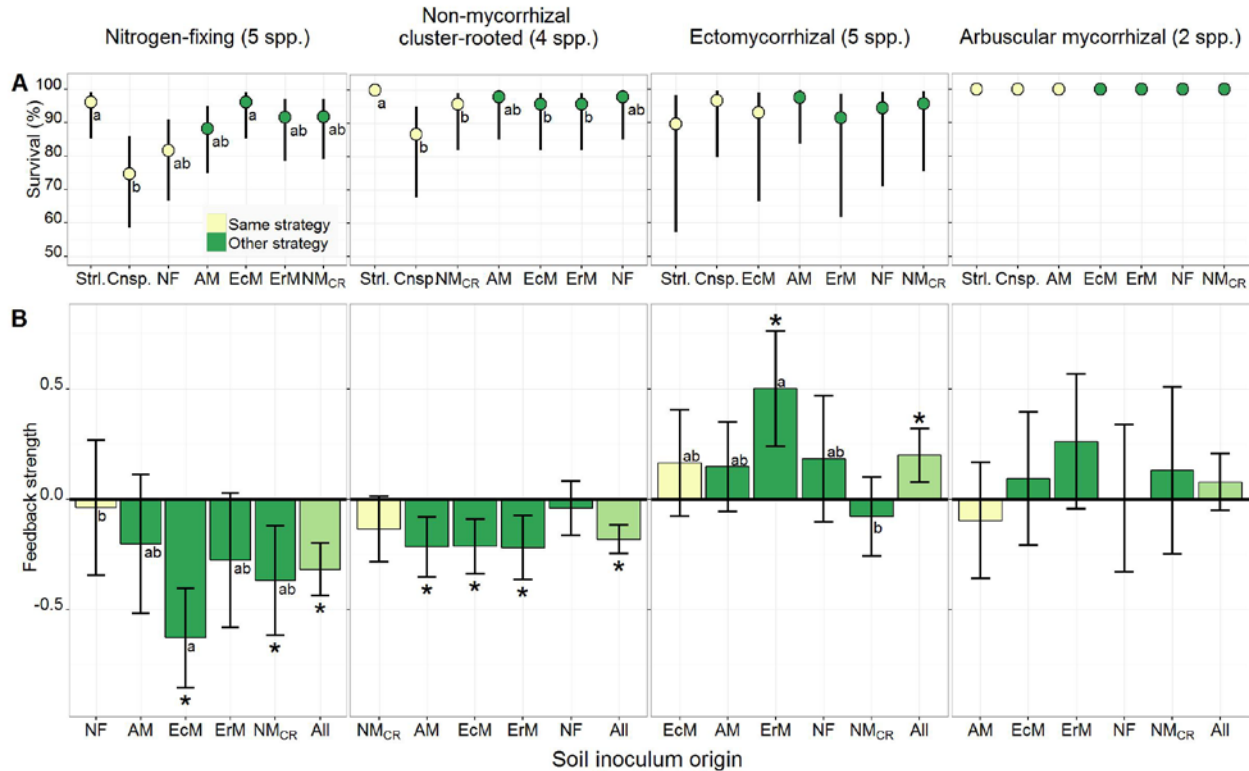
131 feedback between plants and their associated soil biota critically depends on nutrient-acquisition  
132 strategy. As such, this could be a useful trait to generalise and predict plant responses to soil  
133 biota in natural, mixed-species communities.

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-impooverished 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).





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162 **Fig. 1. Plant survival (A) and plant-soil feedback strength (B) in relation to plant nutrient-**

163 **acquisition strategy.** Feedback strength is shown as  $\log_{10}$ -response ratios of plant biomass in

164 conspecific soil compared to heterospecific soils (19, 29). For (A) and (B), each panel represents

165 the average responses of species belonging to each strategy. Panel (A) shows survival means

166 with 95% confidence intervals (CIs) (19). In (B), error bars are 95% CIs and are indicated by an

167 asterisk if they do not include zero. In each panel, different letters indicate statistically significant

168 differences ( $P \leq 0.05$ ) according to Tukey HSD tests for (B) or Dunnett tests and non-

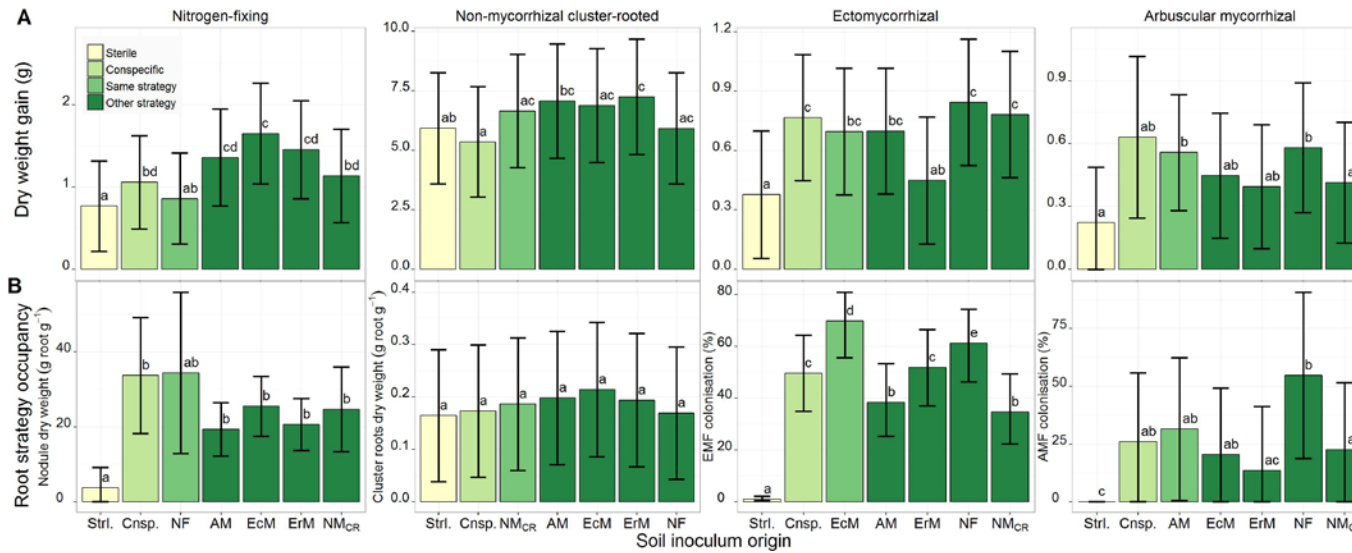
169 overlapping CIs for (A)(19). Strl: sterile conspecific, Cnsp.: conspecific, AM: arbuscular

170 mycorrhizal, EcM: ectomycorrhizal, ErM: ericoid mycorrhizal, NF: nitrogen-fixing, NM<sub>CR</sub>: non-

171 mycorrhizal cluster rooted, All: overall feedback across all heterospecific soil inocula. Feedback

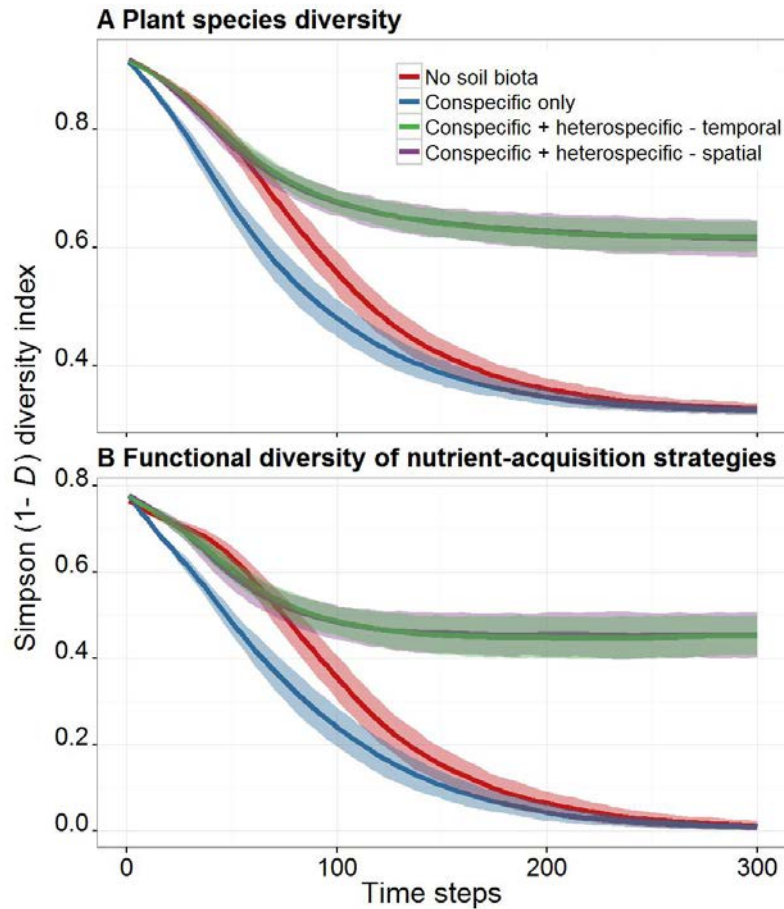
172 strength for each plant species is provided in Fig. S5 and across all plant species in Fig. S6.

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175 **Fig. 2. Dry weight gain (A) and root strategy occupancy (B) of plants inoculated with soil of different nutrient-acquisition**  
 176 **strategies or with sterilized soil.** In (A), bars represent mean plant dry weight gain of surviving plants with 95% CIs. In (B), bars  
 177 represent mean nodule dry weight and cluster roots dry weight standardized on a total root weight basis, ectomycorrhizal fungal  
 178 (EMF), or arbuscular mycorrhizal fungal (AMF) root colonization with 95% CIs. Different letters indicate statistically significant  
 179 differences (Tukey HSD tests with  $P \leq 0.05$ ). See Fig. 1 for complete figure legends. Dry weight gain and root strategy occupancy per  
 180 plant species are provided in Fig. S3 and for secondary strategies in Fig. S4.



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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

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