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

Teste, F. P., Kardol, P., Turner, B. L., Wardle, D. A., Zemunik, G., Renton, M., & Laliberté, E. (2017). Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science*, 355(6321), 173-176. DOI: 10.1126/science.aai8291

Published in:
Science

DOI:
[10.1126/science.aai8291](https://doi.org/10.1126/science.aai8291)

Document Version
Peer reviewed version

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DOI:10.1126/science.aai8291

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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 N₂ 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 × 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).

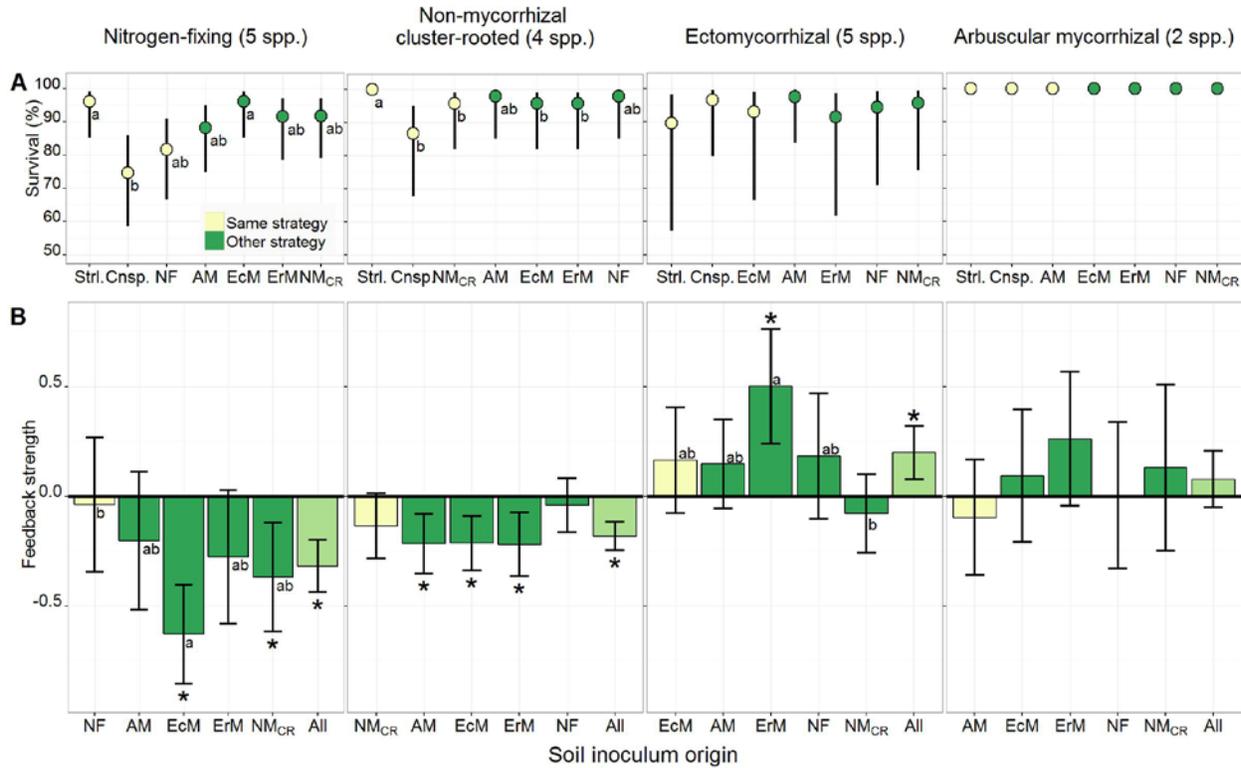
125 Previous studies have shown how feedback between plants and their associated soil biota
126 drive plant community dynamics (1, 20-24). However, until now studies have not determined
127 whether the strength and direction of plant–soil feedback depended on belowground traits such
128 as nutrient-acquisition 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).



161

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-

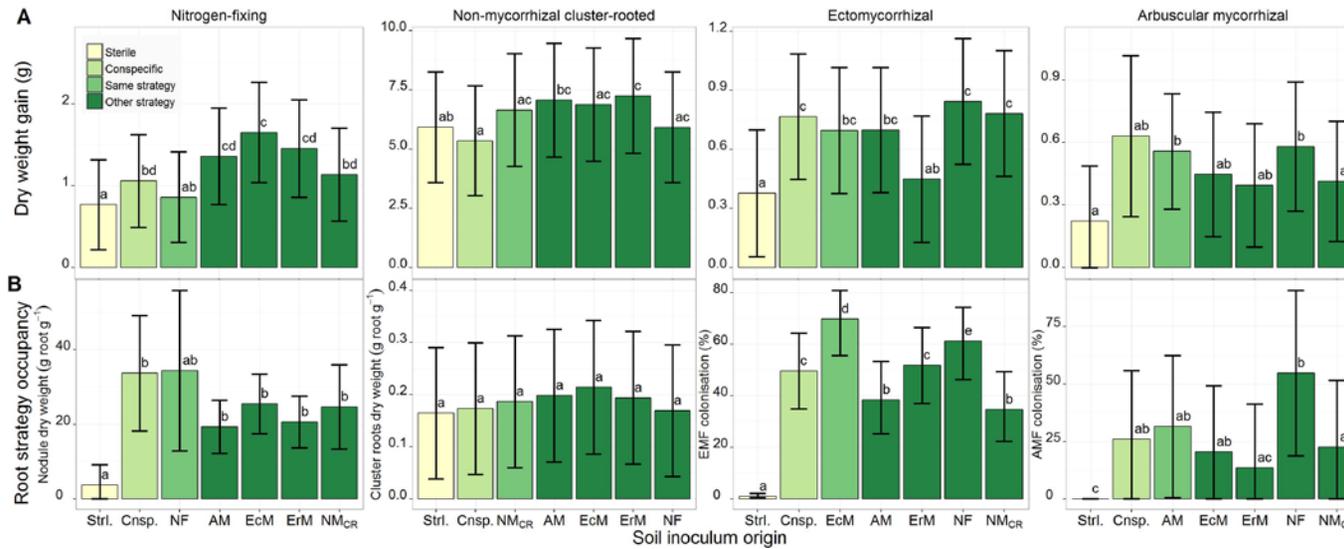
169 overlapping CIs for (A)(19). Strl: sterile conspecific, Cnsp.: conspecific, AM: arbuscular

170 mycorrhizal, EcM: ectomycorrhizal, ErM: ericoid mycorrhizal, NF: nitrogen-fixing, NM_{CR}: non-

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

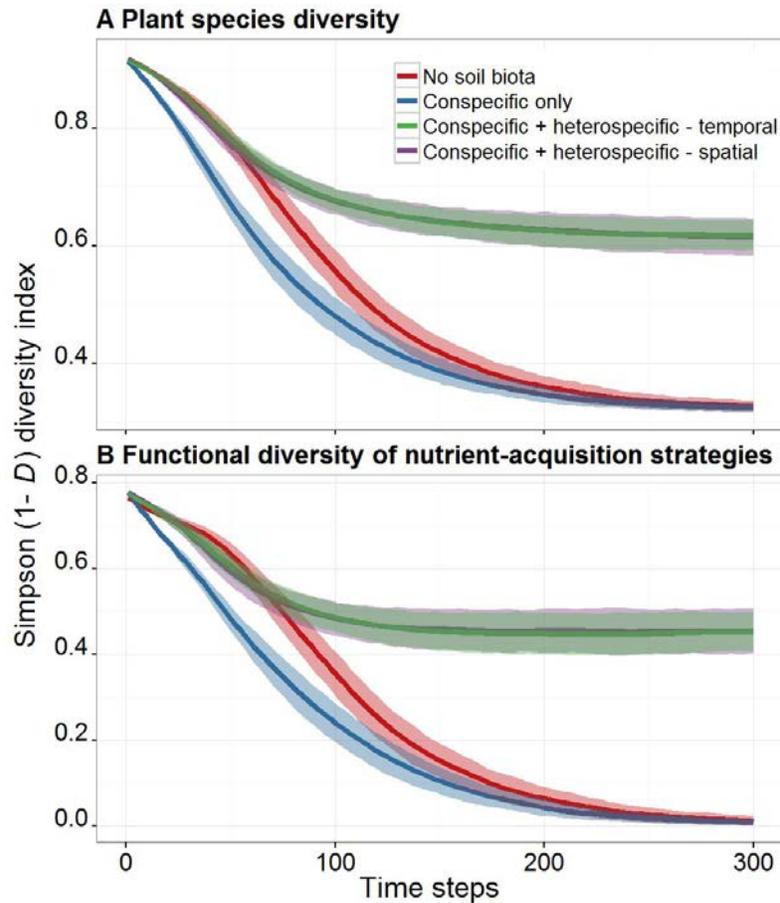
172 strength for each plant species is provided in Fig. S5 and across all plant species in Fig. S6.

173



174

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.



181

182 **Fig. 3. Model simulations based on experimental data showing that feedback between**

183 **plants of contrasting nutrient-acquisition strategies maintains (A) plant species diversity**

184 **and (B) functional diversity.** Simulation models were parameterized from survival and relative

185 growth rates from our glasshouse experiment under four different scenarios (19). Curves were

186 generated with generalized additive models and shown here are the means (thin dark curves) and

187 associated standard deviations (lighter and wider curves) from the raw data for 100 simulation

188 runs per time step per scenario. Figure S9 shows results of simulations exploring effects of

189 survival and growth separately, which revealed that patterns were mainly driven by growth rather

190 than by survival.

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343 **Acknowledgments:**

344 We thank the Western Australian Department of Parks and Wildlife for providing access to field
345 sites. Y. Khentry, G. Abbas, K. Kariman, B. Desmond, B. Jupp, and A. Lane helped with the
346 field and glasshouse work. D. Merrit kindly provided advice on seed germination. We thank staff
347 from UWA Plant Growth Facilities for logistical support. The plant survival and growth data are
348 available on Dryad (www.datadryad.org). F.P.T., E.L., P.K., and D.A.W. designed the
349 experiment; F.P.T., E.L. and G.Z. collected the field data; F.P.T. performed the experiments and
350 root analyses and B.L.T. performed the soil laboratory analyses; M.R., E.L. and F.P.T. developed
351 the models. F.P.T. analyzed the data; F.P.T., E.L., P.K., B.L.T., D.A.W., G.Z., and M.R. wrote
352 the manuscript. Funding was provided by the Australian Research Council (ARC DP130100016)
353 to E.L. and F.P.T. and a Hermon Slade Foundation (HSF 13/3) grant to E.L. The contribution of
354 D.A.W. was supported by a Wallenberg Scholars award.

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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)