

Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development

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Plant species diversity increases as soil phosphorus availability declines during long-term ecosystem development^{1,2}. The increase in plant species diversity is associated with a decline in above-ground functional diversity, because leaf traits converge on a high phosphorus-use efficiency strategy on old and infertile soils^{3,4}. In contrast, the response of below-ground traits that directly influence nutrient acquisition remains poorly understood^{3,5}; yet it might be key to understanding how soil fertility drives patterns of plant species diversity¹. Here we show a marked increase in the richness and diversity of plant nutrient-acquisition strategies with declining soil phosphorus availability during long-term ecosystem development in a global biodiversity hotspot. Almost all nutrient-acquisition strategies currently known were found in plants from the most infertile soils, despite these being some of the most phosphorus-impooverished soils on Earth. Mycorrhizal plants declined in relative abundance by >30%, although the decline was compensated by an increase in non-mycorrhizal, carboxylate-exuding species that 'mine' phosphorus from the soil using different strategies. Plant species richness within individual nutrient-acquisition strategies also increased dramatically, with the species richness of many strategies more than doubling between the youngest and oldest soils. These results reveal increasing functional diversity of below-ground traits related to nutrient acquisition during ecosystem development, suggesting that no single combination of traits, including those related to nutrient-acquisition strategies, is superior to all others at extremely low soil fertility. Furthermore, the increasing diversity of nutrient-acquisition strategies with declining soil fertility, despite functional convergence of above-ground traits^{4,6}, suggests that fundamentally different plant community assembly processes operate above- and below-ground.

The biotic composition of many ecosystems is being altered at an alarming rate⁷, so there is an urgent need to better understand the fundamental processes that shape the assembly of ecological communities and maintain their biodiversity. Soil fertility strongly influences plant community composition through plant traits related to nutrient acquisition and use^{8,9}. Functional convergence of above-ground plant traits during plant community assembly is associated with the dominance of species with 'slow' leaf economic traits (for example long-lived leaves with low nutrient concentrations) in soils of low fertility, whereas species with 'fast' leaf traits (for example short-lived leaves with high nutrient concentrations) are favoured in fertile soils^{3,8}. Much less is known, however, about the below-ground traits that directly influence nutrient acquisition.

One of the below-ground traits that is rarely considered is the plant's nutrient-acquisition strategy; yet in most nutrient-poor

systems nutrient acquisition strongly influences plant interactions and community composition¹⁰. Many nutrient-acquisition strategies exist, with mycorrhizal symbioses being the most common strategies, found in more than 80% of all vascular plant species¹¹. On the other hand, some plants are non-mycorrhizal, including those forming cluster roots that effectively 'mine' the soil for phosphorus¹⁰ by exuding large amounts of carboxylates. Yet other species employ even more specialized strategies, including parasitism and carnivory¹¹. Although it is hypothesized that the community-wide diversity and composition of nutrient-acquisition strategies varies in concert with declining soil fertility¹⁰, empirical evidence is lacking¹². Such knowledge is essential to forecast shifts in plant biodiversity following nutrient enrichment, and to determine the fundamental processes shaping plant community assembly¹³.

Soil chronosequences¹⁴ form strong soil nutrient availability gradients driven by long-term (that is tens to hundreds of thousands of years) soil development and have long been recognized as powerful 'natural experiments' for the investigation of plant-soil interactions^{2,9,15}. Here, we use a >2-million year dune chronosequence in the southwest Australian global biodiversity hotspot¹⁶ to examine the link between soil fertility and the functional diversity of plant nutrient-acquisition strategies. This dune chronosequence provides an exceptionally strong nutrient gradient consistent with expectations from long-term pedogenic changes^{14,15}. Specifically, primary productivity is limited by nitrogen availability on young soils and phosphorus availability on old soils¹⁶, and the sequence includes both the progressive and retrogressive¹⁷ stages of ecosystem development. Although plant species richness increases continually along the sequence¹, there is strong functional convergence of leaf traits toward high nutrient-use efficiency (for example low foliar nutrient concentrations, high resorption efficiencies) with increasing soil age and declining soil fertility⁶.

We stratified the chronosequence into six distinct stages, the first three of which represent the initial ~6500 years of soil development (Holocene), with the remainder representing development from ~120,000 to >2 million years (Pleistocene; Supplementary Fig. 1 and Supplementary Table 1). We identified 14 main plant nutrient-acquisition strategies along the chronosequence, including five mycorrhizal strategies and seven non-mycorrhizal strategies that incorporate root specializations (Supplementary Table 2). For our first analysis of nutrient-acquisition strategy diversity, we treated each unique combination of the main strategies as a distinct strategy, due to many species (between 26% and 55%, based on relative canopy cover) concurrently employing more than one strategy (Supplementary Fig. 2). The mean number (that is richness) of distinct nutrient-acquisition strategies doubled along the chronosequence

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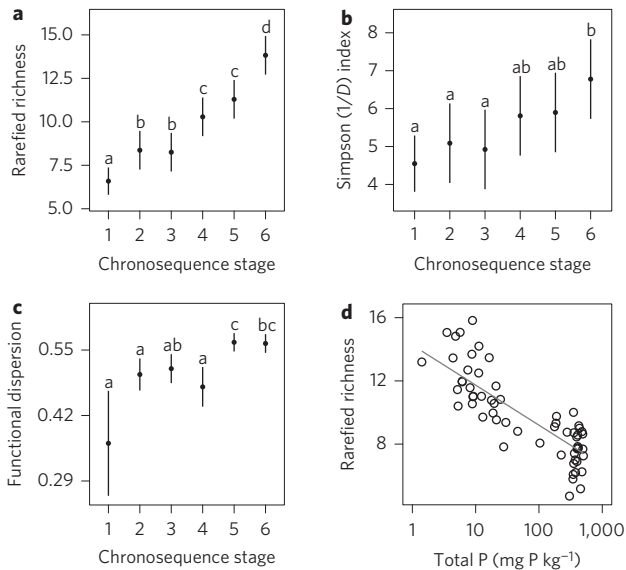


Figure 1 | Nutrient-acquisition strategy richness and diversity increase along the chronosequence. **a–d**, Richness and diversity of strategies increase along the chronosequence and decrease in response to soil total phosphorus (P) concentration. **a**, Mean rarefied strategy richness. **b**, Simpson's inverse diversity index ($1/D$). **c**, Functional dispersion. **d**, Rarefied strategy richness as a function of the plot total soil P concentration ($R^2 = 0.80$, $P = 0.0003$). For the richness and diversity measures (**a,b,d**) each unique combination of the main strategy types was classified as a distinct strategy. Error bars represent the 95% confidence intervals; letters above each mean represent Tukey honest significant difference (HSD) groupings ($P \leq 0.05$).

(Fig. 1a). These values were based on rarefied estimates¹⁸, which account for the influence of differential sampling effort or plant density. However, we found a similar pattern in non-rarefied data (Supplementary Fig. 3a). We also quantified the diversity of the distinct nutrient-acquisition strategies using several diversity indices that take into account species relative abundances (here, relative canopy cover): Simpson's reciprocal index ($1/D$) increased by 42% along the chronosequence (Fig. 1b) and the Shannon index increased by 30% (Supplementary Fig. 3c,d). To account for the fact that many species possessed more than one unique main strategy, we also used distance-based metrics of functional dispersion (based on the Jaccard dissimilarity among species) taking into account relative abundances, while being *a priori* independent of species richness^{4,19}: the functional dispersion¹⁹ of the nutrient-acquisition strategies increased by 46% (Fig. 1c) and Rao's quadratic entropy²⁰ increased by 76% (Supplementary Fig. 3e,f). The increase in functional diversity was not simply due to an increase in plant species richness, because the functional dispersion was generally greater than expected given the plant species richness (Supplementary Fig. 3g).

Our results clearly showed an increase in the diversity of plant nutrient-acquisition strategies along the chronosequence. However,

as phosphorus is the limiting nutrient in the oldest chronosequence stages^{6,16}, and as those stages contain some of the lowest total phosphorus concentrations ever reported (Table 1), we investigated the relationship between the diversity of strategies and total soil phosphorus. Indeed, linear mixed-effect models also revealed a strong increase in rarefied strategy richness with declining (log-transformed) soil total phosphorus ($R = 0.80$, $P = 0.0003$) (Fig. 1d).

Our second set of analyses assessed the changes in plant species richness within individual nutrient-acquisition strategies. Most of these strategies increased in their species richness to some degree; none, apart from species lacking specializations for nutrient acquisition, decreased significantly (Fig. 2 and Supplementary Fig. 4). Richness of species using the four most-abundant strategies—arbuscular mycorrhizal (AM), cluster roots, sand-binding roots and ectomycorrhizal—increased substantially (AM richness doubled, sand-binding richness increased fourfold and species with cluster roots were almost absent in the first three stages), although ectomycorrhizal species richness did not change significantly (Fig. 2a). Interestingly, the richness of nitrogen-fixing species increased by 67% between the youngest and oldest chronosequence stages (Supplementary Fig. 4), despite plant growth in the youngest stage being nitrogen limited^{6,16}. Richness of other non-mycorrhizal strategies—carnivorous plants and non-mycorrhizal plants with dauciform or capillaroid roots—also increased. These less-abundant strategies were absent in the first chronosequence stage, but were most diverse in the oldest stage (Supplementary Fig. 4).

We then assessed the abundance of the main nutrient-acquisition strategies (Supplementary Table 2) by the relative canopy cover of plant species using those strategies (Fig. 2b). The arbuscular mycorrhizal strategy was the most abundant in the chronosequence, consistent with the observation that most plant species worldwide form arbuscular mycorrhizal symbioses¹¹. However, the relative cover of plants with arbuscular mycorrhizal associations declined by 42% from the youngest to the oldest soils (Fig. 2b). Plants with ectomycorrhizal symbioses, the second most-abundant mycorrhizal strategy in the system, also decreased in relative cover with increasing soil age. By contrast, plants employing several non-mycorrhizal strategies (Supplementary Fig. 5), most notably cluster roots (Fig. 2b), increased in relative cover.

Combining the nutrient-acquisition strategies into broad mycorrhizal and non-mycorrhizal classes resulted in a clear overall trend: species richness of both nutrient-acquisition classes (that is mycorrhizal and non-mycorrhizal) increased dramatically along the chronosequence, with mycorrhizal species more than doubling in richness and non-mycorrhizal species richness more than quadrupling (Supplementary Fig. 6a). Mycorrhizal species richness was, nonetheless, always greater than non-mycorrhizal species richness, with richness of mycorrhizal species being 50% greater than non-mycorrhizal species in the oldest chronosequence stage. The decrease in cover of mycorrhizal species was linked to declining the soil total phosphorus concentration (Fig. 3c; $R^2 = 0.43$, $P = 0.003$; Supplementary Fig. 6b).

Because long-term soil development is associated with a decline in soil pH in addition to a decline in soil phosphorus concentrations^{9,15},

Table 1 | Selected soil chemical properties of the six chronosequence stages.

Stage	pH	Resin P (mg P kg ⁻¹)	Total P (mg P kg ⁻¹)	Total N (g kg ⁻¹)	Carbonate (%)
1	8.2 [8.1, 8.2]	1.4 [1.1, 1.7]	370 [338, 403]	0.51 [0.46, 0.56]	75.8 [71.5, 80.2]
2	7.8 [7.8, 7.9]	2.1 [1.0, 3.1]	436 [409, 463]	1.2 [1.0, 1.3]	78.0 [73.7, 82.2]
3	7.8 [7.7, 7.8]	1.2 [1.0, 1.5]	288 [191, 384]	0.96 [0.61, 1.31]	43.1 [23.4, 62.8]
4	5.9 [5.6, 6.1]	1.1 [0.9, 1.3]	24.3 [18.0, 30.6]	0.28 [0.18, 0.38]	BDL
5	5.4 [5.2, 5.6]	0.43 [0.32, 0.54]	9.09 [7.23, 11.0]	0.14 [0.10, 0.18]	BDL
6	4.8 [4.6, 5.0]	0.47 [0.40, 0.53]	5.98 [3.98, 7.97]	0.25 [0.19, 0.31]	BDL

BDL, below detection limit. All values are means with associated 95% confidence intervals in square brackets. The pH was measured in 10 mM CaCl₂ in a 1:2 soil/solution ratio.

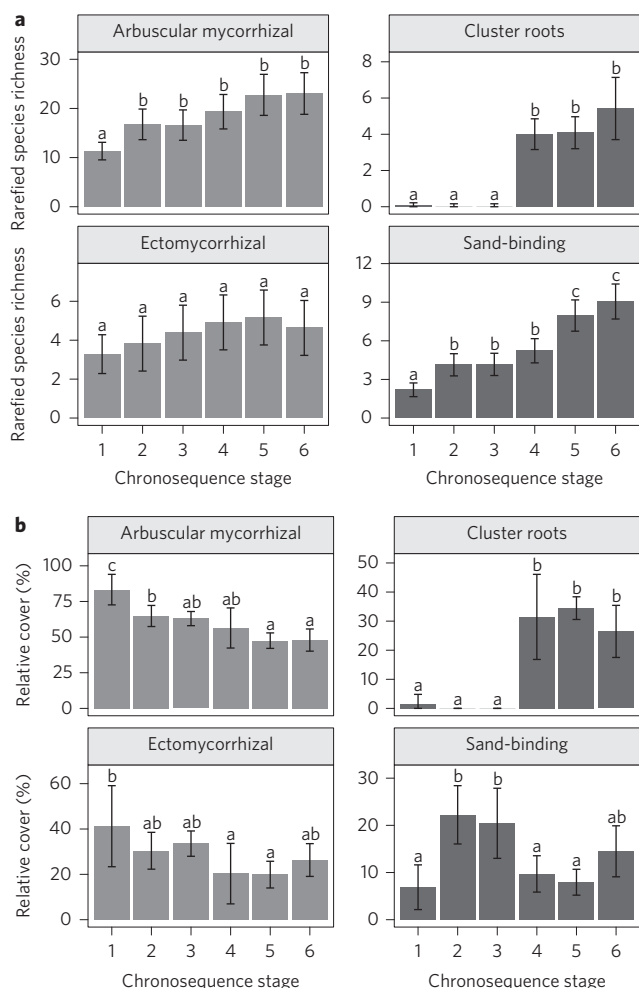


Figure 2 | Rarefied richness and canopy cover of the four most-abundant individual strategies along the chronosequence. **a**, Rarefied richness increases consistently for arbuscular mycorrhizal species and species with sand-binding roots, whilst cluster-rooted species were mainly confined to the three oldest stages. **b**, Relative cover declines for arbuscular mycorrhizal and ectomycorrhizal species, but increases for cluster-rooted species. In (**a,b**) each of the four most-abundant strategies were treated in isolation from all other strategies; hence, total relative cover can sum to more than 100%. Mycorrhizal strategies are shaded with lighter grey bars, and non-mycorrhizal strategies with darker bars. Error bars represent the 95% confidence intervals; letters above each mean represent Tukey HSD groupings ($P \leq 0.05$).

we also tested models that included soil pH and its interaction with phosphorus concentration. Changes in the richness of nutrient-acquisition strategies (Fig. 1d), as well as the relative cover of mycorrhizal species (Fig. 3c,d), were equally well explained by either soil total phosphorus concentration or pH, reflecting the strong correlation between the two soil properties ($R^2 = 0.94$, $P < 0.0001$; log-transformed total phosphorus concentration).

The diversity of some mycorrhizal symbioses, such as arbuscular mycorrhizal, can respond strongly to soil pH¹², while non-mycorrhizal cluster-root species tend to be naturally adapted to acidic soils^{10,21}. However, in the older stages of the chronosequence, where both soil phosphorus concentrations and pH are at their lowest, we interpret changes in the diversity of nutrient-acquisition strategies as being driven by low soil phosphorus concentrations rather than low pH. In these extremely phosphorus-impoorished soils, arbuscular mycorrhizal fungi may be less efficient at acquiring phosphorus,

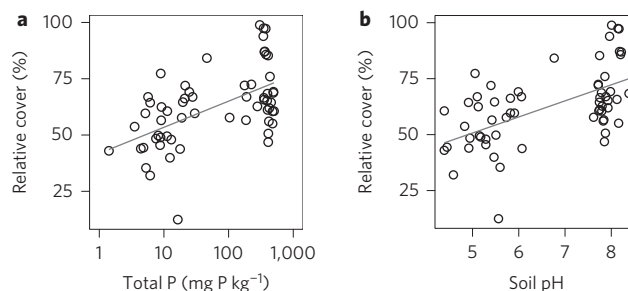


Figure 3 | Relative cover of mycorrhizal species increases with increasing soil phosphorus concentration and soil pH. **a**, Relative cover of mycorrhizal species increases logarithmically with soil total P concentration ($R^2 = 0.43$, $P = 0.004$). **b**, Relative cover of mycorrhizal species increases linearly with soil pH (measured in 10 mM CaCl₂) ($R^2 = 0.43$, $P = 0.003$).

either because phosphate concentrations are too low or because a larger fraction of the phosphorus occurs in organic or insoluble inorganic forms that are unavailable to arbuscular mycorrhizal fungi²².

Microscopic examination revealed that the roots of many species were colonized by fungi that lacked all the features of mycorrhizal colonization^{11,23}. We therefore classified these fungi as endophytic (Supplementary Fig. 7 and Supplementary Table 3). Further investigation may reveal that some of these fungi contribute to nutrient acquisition, thus increasing the diversity of strategies in this chronosequence. For species with multiple strategies, we did not determine the degree of mycorrhizal colonization or the contribution of each strategy to nutrient acquisition, but we would expect to find changes in these proportions along the chronosequence. Such shifts would add to the observed complexity.

Our results highlight a fundamental difference in the patterns of functional diversity of above-ground and below-ground plant traits with declining soil fertility. In contrast to the strong functional convergence of foliar traits towards high nutrient-use efficiency along chronosequences^{6,7}, our study shows an increase in the functional diversity of nutrient-acquisition strategies with decreasing soil phosphorus availability. The high functional diversity in nutrient-acquisition strategies could favour resource partitioning for soil phosphorus²⁴, facilitation among co-occurring plant species²⁵, or reflect a trade-off between efficient phosphorus acquisition and defence²⁶, thus reducing interspecific competition and promoting local plant species coexistence on phosphorus-impoorished soils. Although the nutrient-acquisition strategy is not the only trait relevant to nutrient acquisition, our results suggest that variation in above- and belowground traits along soil fertility gradients are not necessarily coordinated, as had been proposed^{3,4,27}.

Within the framework of community assembly theory, our results suggest that plant competitive interactions may limit the functional similarity of co-occurring plant species, with respect to their nutrient-acquisition strategy. Our results are consistent with the view that different community assembly processes (that is environmental filtering versus limiting similarity⁶) can operate simultaneously to shape plant community assembly, yet act on different axes of functional variation²⁸. Importantly, however, our results do not support the view that environmental filtering is the dominant community-assembly process operating at very low soil fertility⁴. Rather, filtering of the regional pool due to high soil pH on younger soils appears to be the most important factor shaping local plant species diversity along this sequence²¹.

We conclude that the diversity of below-ground strategies plays a critical role in plant community assembly, especially in phosphorus-impoorished soils. Plants with a highly efficient 'phosphorus-mining' root physiology are well adapted to such phosphorus-poor soils¹⁰, although the high diversity of strategies

present on the oldest soils of this chronosequence suggests that either many alternative strategies are equally successful or that such high efficiency is traded off against other desirable traits (for example defence against pathogens)²⁶. However, given that many of these strategies, such as arbuscular mycorrhizas, are not as efficient as those of 'phosphorus-mining' species at accessing all forms of phosphorus in impoverished soils²², we surmise that synergies between plants and soil microorganisms also play an important role. For example, enhanced nutrient uptake due to neighbouring plants with differing strategies²⁵, or bacterial activity (for example mineralization) and symbioses (for example mycorrhizal helper bacteria)²⁹, might contribute to the coexistence of plants in extremely infertile soils. The observed, fundamentally contrasting patterns in below-ground functional diversity, relative to aboveground functional diversity, emphasize the importance of incorporating below-ground traits into trait-based community ecology frameworks³.

Methods

The study was conducted on the Jurien Bay dune chronosequence¹⁶, which harbours exceptional floral diversity and where soil development extends from the Early Pleistocene through to the present¹⁶. The region experiences a Mediterranean climate, with a pronounced winter wet season (June–August) and an extended seasonal summer drought. The six chronosequence stages spanned ~45 km north to south and ~15 km west to east, and were delineated using a randomized stratified design. Each stage contained ten plots (10 × 10 m), each of which contained seven randomly positioned 2 × 2 m subplots. All vascular plant species within the subplots were identified, individuals per species counted, and canopy cover estimated visually. Relative cover was subsequently calculated by normalizing the absolute cover against the total cover. Nutrient-acquisition strategies were initially assigned based on the literature and online resources¹¹; species that had substantial relative cover within a plot (>4%), but whose strategies were unknown, were subsequently analysed for mycorrhizal colonization using root samples taken in the field during the rainy season. In total, 62 plant species (out of 349 species in total), representing 27 families, were examined for their nutrient-acquisition strategies (Supplementary Table 3). Seven soil samples per 10 × 10 m plot (that is one in the middle of each of the seven 2 × 2 m subplots) were taken from the top 20 cm and were analysed for a range of total and available nutrients, and properties. Data and statistical analyses were performed using the R software platform³⁰. We used generalized least squares models for the modelling of nutrient-acquisition strategy richness, diversity and cover, and mixed-effect linear models, with the chronosequence stage as the random effect, in the regression analyses. For the models using phosphorus concentration and pH as the independent variables, backward selection was used to eliminate variables producing no significant improvements to the model. Total phosphorus was used in the models, rather than resin phosphorus, as it is likely to better encompass the capacity of plants to access many different forms of phosphorus via root exudates. The data set for the study is now online in a repository (<http://aekos.org.au/home>) and has a DOI: 10.4227/05/551A3DDE8BAF8.

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Author contributions

G.Z. designed the study with assistance from E.L. and H.L. G.Z. collected the vegetation and mycorrhizal data, and performed the statistical analyses. E.L. and B.T. collected the soil data and B.T. analysed the soil samples. G.Z. wrote the manuscript and all authors contributed to revisions.

Additional information

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Competing interests

The authors declare no competing financial interests.