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RESEARCH ARTICLE

A cool spot in a biodiversity hotspot: why do tall *Eucalyptus* forests in Southwest Australia exhibit low diversity?

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Abstract

Background and aims Southwest Australia is a biodiversity hotspot, with greatest plant species diversity on the most severely phosphorus (P)-impoverished soils. Here, non-mycorrhizal species with highly-effective carboxylate-releasing P-acquisition strategies coexist with mycorrhizal species that are less effective at accessing P on these soils. Non-mycorrhizal carboxylate-releasing species facilitate P acquisition of mycorrhizal neighbours that are better defended against pathogens. In the Southwest Australian Biodiversity Hotspot, there are also 'cool spots' of low-diversity tall mycorrhizal *Eucalyptus* communities on P-impoverished soils. These *Eucalyptus* trees obviously do not require facilitation of their P acquisition by carboxylate-releasing neighbours, because these are only a minor component of the low-diversity communities. We hypothesised that in low-diversity tall *Eucalyptus* forests, mycorrhizal species release carboxylates to acquire P. Thus, they would not depend on facilitation, and must be strong competitors. However, because they would not depend on external mycorrhizal hyphae to acquire P, they would also not be able to access soil organic nitrogen (N), for which they would need external hyphae.

Methods Since carboxylates not only mobilise P, but also manganese (Mn), we used leaf Mn concentrations ([Mn]) in the natural habitat to proxy rhizosphere carboxylates. To verify this proxy, we also measured carboxylate exudation of targeted species with high leaf [Mn] using seedlings grown in low-P nutrient solutions.

Results Using these complementary approaches, we confirmed our hypothesis that dominant *Eucalyptus* species in 'cool spots' release carboxylates. Since mineralisation of organic N is associated with fractionation of N, enriching organic N with ^{15}N while nitrate is depleted in ^{15}N, we measured the stable N isotope composition of leaf material. The results

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show that dominant *Eucalyptus* species did not access organic N, despite being ectomycorrhizal.

Conclusions The low diversity of tall *Eucalyptus* forests in southwest Australia can be explained by dominant mycorrhizal species exhibiting a carboxylate-releasing strategy. The tall eucalypts are therefore strong competitors that do not require facilitation, but also do not access organic N.

Keywords Biodiversity hotspot · Carboxylate exudation · Determinants of plant community diversity and structure · *Eucalyptus diversicolor* · *Eucalyptus patens* · Leaf manganese concentration · Mycorrhizas · Phosphorus · *Tremandra diffusa*

Introduction

Southwest Australia is a global biodiversity hotspot (Myers et al. 2000), one of only 36 in the world (Habel et al. 2019), with the greatest biodiversity associated with the most nutrient-depauperate soils that exhibit a very low availability of phosphorus (P) (Lambers 2014; Lambers et al. 2010). This trend of increasing plant diversity with decreasing soil P availability is not restricted to this biodiversity hotspot; it is a trend that is found globally (Huston 1994; Wardle et al. 2004; Zemunik et al. 2016).

A relatively large proportion of all plant species in severely P-impoverished habitats are non-mycorrhizal (Brundrett 2017; Zemunik et al. 2018; Zemunik et al. 2015). These non-mycorrhizal species use a range of carboxylate-releasing strategies to acquire P when the availability of soil P is extremely low (Lambers 2022). These non-mycorrhizal species co-occur with many mycorrhizal species, even though mycorrhizas are less effective than carboxylate-releasing roots when the availability of soil P is extremely low (Lambers et al. 2015a; Parfitt 1979; Treseder 2004). Yet, many mycorrhizal species are still present on the poorest soils (Lambers et al. 2008; Zemunik et al. 2018; Zemunik et al. 2015). This conundrum has been resolved by recent findings: Proteaceae that are most effective at acquiring P, based on a carboxylate-releasing P-mobilising strategy, are more sensitive to oomycete pathogens than co-occurring mycorrhizal species (Albornoz et al. 2017; Laliberté et al. 2015). However, mycorrhizal plants, while less effective at mobilising P from severely P-impoverished soils (Parfitt 1979; Treseder and Allen 2002), are protected against oomycete pathogens by their mycorrhizal partners (Albornoz et al. 2021b; Jung et al. 2012; Laliberté et al. 2015; Lambers et al. 2018). This protective role of mycorrhizal fungi in ecosystem functioning has been known for quite some time (Azcón-Aguilar and Barea 1997; Marx 1972; Wehner et al. 2010), and is increasingly acknowledged (Berdeni et al. 2018; Boutaj et al. 2020; Frew et al. 2021; Gonthier et al. 2019). Protection against oomycetes is also well documented (Cordier et al. 1998; Jung et al. 2012; Pozo et al. 2002; Veresoglou and Rillig 2012). The dominant species in *Eucalyptus* forests with a low plant diversity, *E. patens* and *E. diversicolor*, are both mycorrhizal species, being both arbuscular and ectomycorrhizal (Table 1).

Carboxylates released by roots not only mobilise P, but also manganese (Mn); since Mn uptake in roots is poorly controlled (Baxter et al. 2008), leaf Mn concentration ([Mn]) is a proxy for rhizosphere carboxylates (Lambers et al. 2021; Lambers et al. 2015b; Pang et al. 2018). Poaceae tend not to release large amounts of carboxylates, but typically release phytosiderophores (Ma 2005), which potentially also mobilise P (Zanin et al. 2017). In contrast, arbuscular and ectomycorrhizal hyphae intercept Mn (Bethlenfalvay and Franson 1989; Canton et al. 2016), so low leaf [Mn] indicates an effective mycorrhizal symbiosis. Since leaf [Mn] also depends on a range of other environmental factors (Lambers et al. 2021), either community-weighted average leaf [Mn] need to be known (Lambers et al. 2021), or appropriate reference species need to be included (Zhong et al. 2021). Positive reference species are those that are known to release large amounts of carboxylates, e.g., *Banksia* species (Proteaceae) (Lambers 2022; Zhong et al. 2021). Negative reference species comprise those that do not depend on carboxylates for their P acquisition, e.g., *Xanthorrhoea* species (Xanthorrhoeceae) (Zhong et al. 2021). In the event that no suitable negative reference species are available, young leaves may be used as an alternative, because Mn typically accumulates only in old leaves (Lambers et al. 2021; Shane and Lambers 2005b).

Within the Southwest Australian Biodiversity Hotspot, tall eucalypt forests form 'cool spots', characterised by low diversity of vascular plants at the community level and limited diversity of growth forms. For example, tall karri forests dominated by *E.*

Table 1 Species sampled from southwest Australia and their putative nutrient-acquisition strategies. Putative strategies were assigned based on observations of symbiotic structures or cluster roots in the cited references, but we do not imply that being mycorrhizal actually demonstrates that the assessed plants relied on these symbiotic partners for their nutrient acquisition (Albornoz et al. 2021a). When we did not find information on mycorrhizal status for a particular species, but did have information for the genus, we included "very likely"; when we did not find information on mycorrhizal status for a particular genus, but did have information for the family, we included "likely". All specimens were identified by reference to material held at the WA Herbarium PERTH and with checking for *Hibbertia* by a relevant expert in this field. As these species are common and very widespread, no vouchers were retained

Plant species	Common name	Family	Putative nutrient-acquisition strategy	References
***Eucalyptus patens* site at Cypress Form, Waroona**				
Acacia drummondii Lindl.	Drummond's wattle	Fabaceae	N_2-fixing nodules; AM, EM	Brundrett and Abbott (1991)
Agrostocrinum hirsutum Keighery	–	Hemerocallidaceae	Likely AM	Wang & Qiu (2006)
Banksia grandis Willd.	Bull banksia	Proteaceae	CR, NM	Shane and Lambers (2005a)
Bossiaea aquifolium Benth.	Water bush	Fabaceae	N_2-fixing nodules; AM	Brundrett & Abbott (1991)
Clematis pubescens Endl.	Common clematis	Ranunculaceae	Very likely AM	Wang and Qiu (2006)
Corymbia calophylla Hill & Johnson	Marri	Myrtaceae	AM, EM	Brundrett & Abbott (1991)
Diplolaena drummondii Ostenf.	–	Rutaceae	Likely AM	Wang and Qiu (2006)
Eucalyptus marginata Sm.	Jarrah, Swan river mahogany	Myrtaceae	AM, EM	Brundrett and Abbott (1991)
E. patens Benth.	Yarri, (Swan river) blackbutt	Myrtaceae	AM, EM	Brundrett and Abbott (1991)
Hibbertia silvestris Diels		Dilleniaceae	Very likely AM	Brundrett & Abbott (1991)
Lasiopetalum floribundum Benth.	Free flowering lasiopetalum	Malvaceae	AM	Gardner and Malajczuk (1988)
Leucopogon verticillatus R.Br.	Tassel flower	Ericaceae	EM	Brundrett & Abbott (1991)
Lepidosperma tetraquetrum Nees	–	Cyperaceae	NM	Brundrett (2009)
Macrozamia riedlei Gardner	Zamia	Zamiaceae	N_2-fixing coralloid roots; AM	Halliday and Pate (1976); Brundrett & Abbott (1991)
Mirbelia dilatata R.Br.	Holly-leaved mirbelia	Fabaceae	N_2-fixing nodules; AM, EM	Brundrett & Abbott (1991)
Microlaena stipoides R.Br.	Weeping grass	Poaceae	Likely AM	Wang and Qiu (2006)
Pteridium esculentum Cockayne	Bracken	Dennstaedtiaceae	Likely AM or NM	Wang & Qiu (2006)
Tremandra diffusa DC.	–	Elaeocarpaceae	Likely AM	Wang & Qiu (2006)
Trymalium odoratissimum Lindl.	Karri hazel	Rhamnaceae	AM, EM	Brundrett and Abbott (1991)
Xanthorrhoea preissii Endl.	Balga, grasstree	Xanthorrhoeaceae	Very likely AM	Brundrett and Abbott (1991)
Xanthorrhoea gracilis Endl.	Graceful grasstree	Xanthorrhoeaceae	Very likely AM	Brundrett and Abbott (1991)

Table 1 (continued)

Plant species	Common name	Family	Putative nutrient-acquisition strategy	References
Torndirrup National Park, Albany				
Adenanthos obovatus Labill.	Basket flower	Proteaceae	CR, presumably NM	Shane & Lambers (2005a)
Banksia grandis Willd.	Bull banksia	Proteaceae	CR, NM	Shane and Lambers (2005a)
Eucalyptus diversicolor F.Muell.	Karri	Myrtaceae	AM, EM	Bougher et al. (1990)
Porongurup National Park. Albany				
E. diversicolor F.Muell.	Karri	Myrtaceae	AM, EM	Bougher et al. (1990)

Abbreviations: AM – Arbuscular mycorrhizal, EM – Ectomycorrhizal, CR – Cluster roots, NM – Non-mycorrhizal

diversicolor, occupy a substantial area (190,000 ha) (Bradshaw 2015), whereas yarri (Swan River blackbutt) forests, dominated by *E. patens*, cover a somewhat smaller area and are far less studied (https://florabase.dpaw.wa.gov.au/browse/profile/5739). Both *E. diversicolor* and *E. patens* forests occur in recharge zones in high-rainfall areas with extraordinarily low soil P availability. *Eucalyptus diversicolor* occurs as tall (up to ~90 m) open forests in the high-rainfall region (> 900 mm annual rainfall) (Grove 1988; Hingston et al. 1979). *Eucalyptus diversicolor* forest soils contain "negligible concentrations of labile-P, low concentrations of total P and more P in organic forms than inorganic" (Adams 1992). *Eucalyptus patens* forests occur in recharge regions with >1100 mm rainfall (Macfarlane et al. 2010), with soils even less fertile than *E. diversicolor* forest soils.

Our main aim was to reveal why *E. patens* and *E. diversicolor* forests exhibit remarkably low plant diversity, compared with many other habitats in the Southwest Australian Biodiversity Hotspot (Gioia and Hopper 2017; Hopper and Gioia 2004; Lambers 2014). We showed previously that the mycorrhizal *E. patens* releases carboxylates (Lambers et al. 2021). Building on this, we hypothesised that some co-occurring species and *E. diversicolor*, whilst being protected against pathogens by their mycorrhizal partners, also release P-mobilising carboxylates. This would allow them to function like Proteaceae, which are well known to release P-mobilising carboxylates (Shane and Lambers 2005a) and not require facilitation by P-mobilising neighbours (Lambers et al. 2019). A second aim was to acquire more information on the nitrogen (N) nutrition of *E. patens* forest species including the understorey community. Ectomycorrhizal species would be expected to access organic N (Högberg 1990), but if they depend on carboxylates to acquire P, rather than on ectomycorrhizal symbioses, the ectomycorrhizal hyphae might not function to acquire organic N. We also aimed to assess the contribution of N fixation by Fabaceae and a cycad, *Macrozamia riedlei* to their N nutrition. Whilst N is not the key limiting nutrient in these P-impoverished habitats, N does need to be fixed, to compensate for losses of N due to denitrification, leaching and fire.

We tested our main hypothesis, first, by measuring leaf [Mn] of *E. patens, E. diversicolor* and co-occurring species, using leaf [Mn] as a proxy for rhizosphere carboxylate concentrations. Second, following this field study, we grew seedlings of a range of species for which we had acquired leaf [Mn] data in their natural habitat in low-P nutrient solutions in a glasshouse to measure their carboxylate release. To address our second aim, we measured leaf [N] and $\delta^{15}N$ of *E. patens* forest species to disclose the contribution of N fixation by species of Fabaceae and a cycad, *M. riedlei*, as well as their dependence on organic N (Högberg 1990).

Materials and methods

Site descriptions

The three study sites comprise evergreen tall forests in southwest Australia, a region characterised by a Mediterranean climate, with hot dry summers (December to February) and cool wet winters (June to August). The *E. patens* site is located at Cypress Form, Waroona (32°47′35"S, 116°0′46″E), ~100 km

south of Perth, with a mean annual rainfall of 992 mm (1990–2015), mean annual temperature of 21.9 °C, and mean monthly maxima from 15.1 °C (July) to 29.7 °C (January/ February) (Australian Bureau of Meteorology, http://www.bom.gov.au/climate/data/). This is where we sampled the vast majority of all vascular plant species present at the site. The two *E. diversicolor* sites occur on different soil types, in Torndirrup National Park (35°06′12"S, 117°53′57"E) and Porongurup National Park (34°41′28"S, 117°54′22"E), ~400 km south of Perth. The sites have a mean annual rainfall of 925 mm (1990–2015) and mean annual temperature of 19.5 °C and mean monthly maxima from 15.8 °C (July) to 22.9 °C (February) (Australian Bureau of Meteorology, http://www.bom.gov.au/climate/data/). These sites were included to allow a comparison of dominant *Eucalyptus* species in tall eucalypt forest in southwest Australia. At these sites we only sampled the focal species, and reference species where possible.

Soil samples

Moist surface soil was collected from five locations within each site (four samples combined at each location). Soil was sampled using an auger (diameter = 100 mm, depth = 150 mm). Samples were sieved (<2 mm), air-dried, and stored in zip-lock bags at 25 °C before chemical analyses. Soil pH was measured (in deionised water (DI) and 0.01 M $CaCl_2$ in a 1:5 soil-to-solution ratio) using a pH and electrical conductivity (EC) probe (Orion 720a, Beverly, MA, USA) (Rayment and Lyons 2011). Total N was measured by the combustion method using a Leco analyser (FP628, St. Joseph, MI, USA). 'Plant-available' soil P was measured as resin-P using anion-exchange membranes (AEM) (Rayment and Lyons 2011), with soil samples shaken for 16 h in 30 ml deionised water and four anionic form AEM strips (10 × 40 mm; manufactured by BDH, Poole, UK). Phosphate was recovered by shaking strips with 30 ml 0.5 M HCl for 1 h. Soil organic P was determined by the ignition method (550 °C, for 1 h) and extraction in 1 M HCl (16 h, 1:50 soil to solution ratio) (Saunders and Williams 1955). The organic P concentration was calculated by subtracting the 1 M HCl-extracted P without ignition from the 1 M HCl-extracted P after ignition. Phosphate concentrations in extracts were determined by the malachite-green method (Rao et al. 1997), using a UV–VIS spectrophotometer (UV160A Shimadzu, Kyoto, Japan). Elements in soil were extracted with aqua regia (3:1 mixture of HNO_3: HCl) digestion (1 h at 130 °C) and then determined by inductively coupled plasma optical emission spectrometry (ICP-OES; Model 5300DV spectrometer, Perkin Elmer, Shelton, CT, USA) (Rayment and Lyons 2011).

Selection of species

We collected 21 species at the *E. patens* site in October and November 2020, including a positive reference species (*Banksia grandis*) and a negative reference species (*Xanthorrhoea preissii*) (Fig. 1, Table 1). This comprised most species at the site, except for some understorey orchids, sundews, and sedges. We used *X. preissii* as a negative reference, because *Xanthorrhoea* species are mycorrhizal and do not release carboxylates; they invariably have a low leaf [Mn] (Hayes et al. 2014; Zhong et al. 2021).

We also sampled species at the two *E. diversicolor* sites in December 2020 (Fig.1, Table 1). In Torndirrup National Park, there were Proteaceae (*B. grandis* and *Adenanthos obovatus*) located at somewhat greater distance of over 300 m from *E. diversicolor*, but there were no *Xanthorrhoea* species as negative reference. Therefore, we used young expanding leaves of *Adenanthos obovatus* as a negative reference, because young leaves tend to exhibit consistently low [Mn] while those in old leaves vary (Shane and Lambers 2005b).

In Porongurup National Park, *E. diversicolor* was the only Myrtaceae species, whereas no Proteaceae for a positive reference or any species for a negative reference were found within at least 1000 m. Thus, we selected young expanding leaves of *E. diversicolor* as possible reference material.

Leaf samples

Mature leaf total P and Mn concentrations were analysed from five to 10 plants per species. Oven-dried leaf samples (70 °C for two days) were ground in a ball-mill grinder (Geno/Grinder 2010, Spex SamplePrep, Metuchen, NJ, USA) using plastic vials and yttria-stabilised zirconia ceramic beads. Samples were then digested with hot concentrated HNO_3:$HClO_4$ (3:1) and analysed using ICP-OES (Model 5300DV, Perkin Elmer, Shelton, CT, USA).

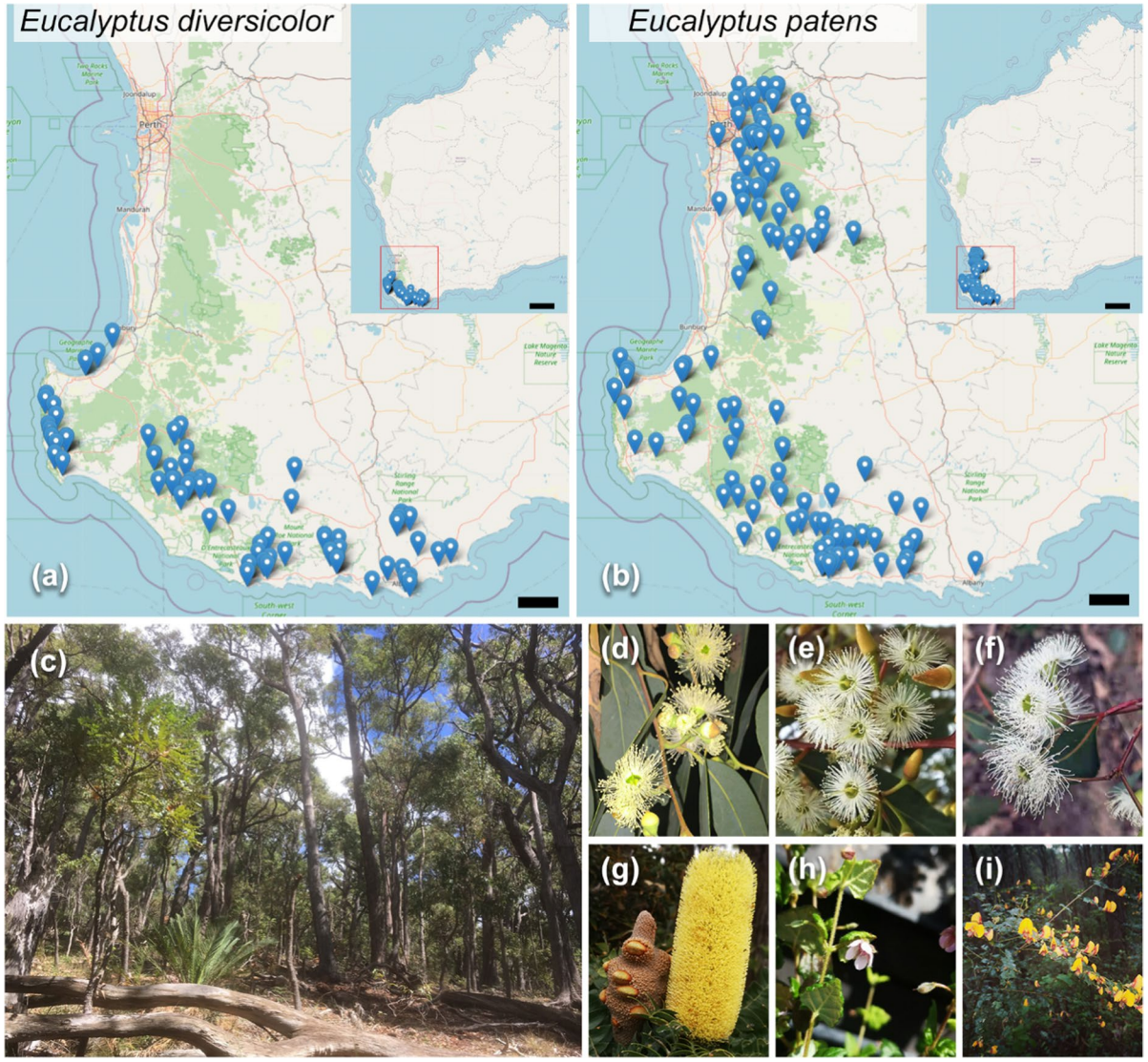

Fig. 1 Distribution of (a) *Eucalyptus diversicolor* (karri) and (b) *E. patens* (yarri) in southwest Australia, including inset maps of Western Australia. Scale bars on main maps: 30 km; on insets: 200 km. Source: https://florabase.dpaw.wa.gov.au/. (c) Habitat and some of the studied species at the *E. patens* site in Waroona, located ~100 km south of Perth; (d) *E. patens*; (e) *E. marginata*; (f) *Corymbia calophylla*; (g) *Banksia grandis*; (h) *Tremandra diffusa;* (i) *Bossiaea aquifolium*. Photos: (c) Hans Lambers; (d) Kingsley Dixon; (e, f) Sophie Xiang (g) Hongtao Zhong; (h, i) Xue Meng Zhou

Dry finely-ground leaf samples of selected species were analysed for N concentration ([N]) and ^{15}N. Total [N] was measured by the combustion method using a Leco analyser (FP628, St. Joseph, MI, USA). Stable isotope ^{15}N was measured using a Flash 1112 Elemental Analyser coupled via a continuous flow interface to Delta V Plus isotope ratio mass spectrometer (Thermo-Finnigan, Bremen, Germany) (Skrzypek and Debajyoti 2006). The natural stable isotope ratios were expressed as parts per thousand (‰).

The percentage of N derived from the atmosphere (%Ndfa) was calculated as: %Ndfa = 100 (average $\delta^{15}N$ of the reference species - $\delta^{15}N$ of N_2-fixing species)/(average $\delta^{15}N$ of reference species - 'B'). We used a 'B' value of −1.4‰ to account for the isotopic fractionation within a plant fully reliant on N fixation following Png et al. (2017). This 'B' value is an

average of several published shoot 'B' values of shrub and tree species and within the range of most species (between 0‰ and −2‰) (Andrews et al. 2011). We re-designated values of %Ndfa that were > 100% as 100%, and values <0% as 0% (Unkovich et al. 2008). For each N_2-fixing species, the reference plant species selected was *M. stipoides*, a co-occurring non-N_2-fixing grass, which is presumably arbuscular mycorrhizal (Table 1). We aimed to avoid potential isotopic differences between the forms of soil N accessible by the different mycorrhizal types (Högberg 1990), but acknowledge that two of the sampled Fabaceae are both arbuscular mycorrhizal and ectomycorrhizal (Table 1). Only youngest fully expanded leaves from the same growing season were collected for analyses to reduce seasonal variation of leaf $\delta^{15}N$ (Shearer and Kohl 1986).

Carboxylate and phytosiderophore release

We selected five to 10 seedlings for each species that had relatively high leaf [Mn] (Fig. 2). Seedlings were grown in the glasshouses at the University of Western Australia and used to analyse root exudation rates of carboxylates (mainly oxalate, malate and citrate) or phytosiderophores (for *M. stipoides* only). Seedlings of *Corymbia calophylla*, *E. diversicolor* and *Tremandra diffusa* were purchased from Australian Native Nursery (Oakford, Western Australia), *E. marginata* was grown from seeds collected at Aroona Sanctuary, along Warren Beach Road and Warren River in Callcup, Western Australia, and plants of *M. stipoides* were collected at Cypress Form. All seedlings were grown in a low-P nutrient solution commonly used for growing southwest Australian native plants (Hayes et al. 2019).

After about 10 weeks in nutrient solution, root exudates were collected from excised whole or a part of root systems of seedlings, except for *B. grandis*, for which we used excised mature cluster roots. Exudates were collected in 3–10 ml of aerated 1/2 strength nutrient solution without P and Ca for 1.5 h between 9:00–11:00 h (Shane et al. 2003) and analysed for carboxylates using reverse phase liquid chromatography as described by Cawthray (2003), and for oxalate by Uloth et al. (2015). The carboxylates determined and their limits of detection (μM) were: citrate (5), malate (7), iso-citrate (10), oxalate (8), trans-aconitate (0.1), cis-aconitate (0.1), fumarate (0.06), maleate (0.05), succinate (15), and malonate (8) (Cawthray 2003; Uloth et al. 2015). Total carboxylates was the sum of all di- and tri-carboxylates, mainly citrate, malate, and oxalate. All carboxylate concentrations were expressed per unit root fresh weight.

Phytosiderophores were collected in the same way in 10 ml of 1/2 strength nutrient solution without P, Ca and Fe, over a period of three hours, and

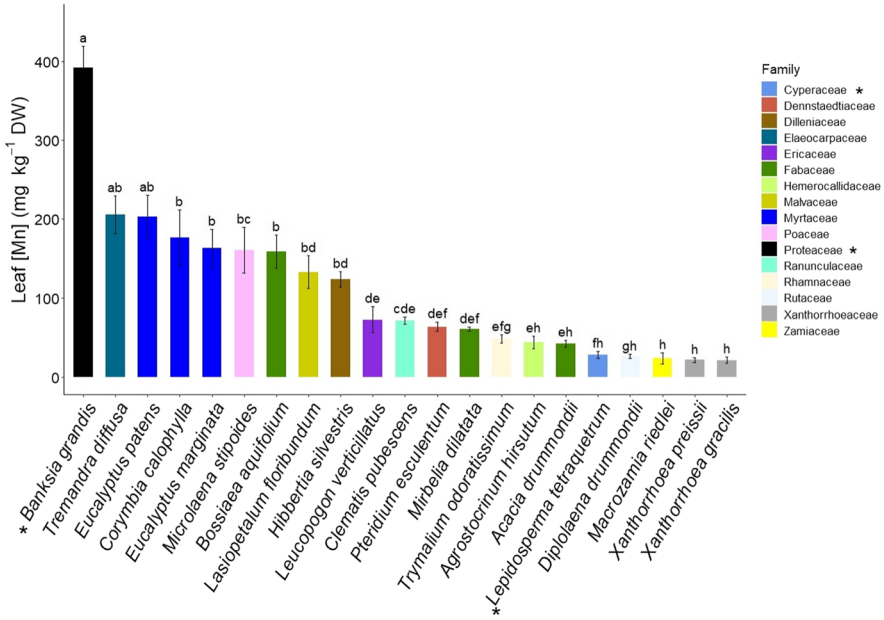

Fig. 2 Leaf manganese concentrations ([Mn]) on a dry weight (DW) basis of a range of species co-occurring with *Eucalyptus patens,* yarri (Myrtaceae) at Cypress Form, Waroona. *Banksia grandis* (Proteaceae) was used as the positive reference, and *Xanthorrhoea preissii* (Xanthorrhoeaceae) as the negative reference. Data are means ± SE (n = 5–10). Different letters indicate statistically significant differences among species ($P \leq 0.05$). Non-mycorrhizal species and the families they belong to are marked with*

quantified by measuring Fe-solubilising capacity according to Ma et al. (2003).

Statistical analyses

Individual trees were considered as the unit of replication. Differences across species, leaf ages, or soil depths were analysed using one-way ANOVA. For each model, normality of the residuals was assessed using the Shapiro-Wilk test and heteroskedasticity assessed by visual inspection. Where appropriate (leaf [Mn], leaf P concentration ([P]), and root exudation rates; Figs. 2, 3, and 4) data were $\log_{10}$ transformed. Differences among species, leaf ages, or soil depths were defined using Tukey-Kramer HSD post-hoc tests. All data are presented as mean ± standard error (SE). All analyses were conducted in R 3.6.3 (R_Development_Core_Team 2019) using base R packages.

Results

Soil characteristics

Soils were acidic (pH ($CaCl_2$) 4.1–4.8) at the *E. patens* sampling sites, and about neutral (pH ($CaCl_2$) ~6.6) at the *E. diversicolor* locations (Tables 2 and 3). Soil total P concentrations were very low (20 to 50 mg P kg^{-1}) at most locations, apart from the *E. diversicolor* location at Porongurup National Park (~140 mg kg^{-1}). Readily-available soil P, measured as resin-P, was very low (<1 mg kg^{-1}) across all sites, and organic-P was the major fraction of soil P at all sites, 65–95%.

Leaf [Mn] and [P] at the E. patens site

The two reference species exhibited the highest (*B. grandis*) and almost lowest (*X. preissii*) leaf [Mn], respectively (Fig. 2). *Eucalyptus patens*, which releases oxalate as the main carboxylate (Lambers et al. 2021), showed a relatively high leaf [Mn]. Species with the highest leaf [Mn] did not have the highest leaf [P] (Fig. 3). None of the Fabaceae exhibited a high leaf [P]. *Microlaena stipoides*, *Pteridium esculentum* and *Diplolaena drummondii* exhibited the highest leaf [P], ~0.90 mg g^{-1} dry weight (DW) (Fig. 3).

Leaf [Mn] of *X. gracilis*, *M. riedlei* and *D. drummondii* were indistinguishable from that of *X. preissii*, our negative reference. The low leaf [Mn] of *Lepidosperma tetraquetrum* was unexpected, since Cyperaceae, whether they produce dauciform roots or not (Güsewell and Schroth 2017) tend to release

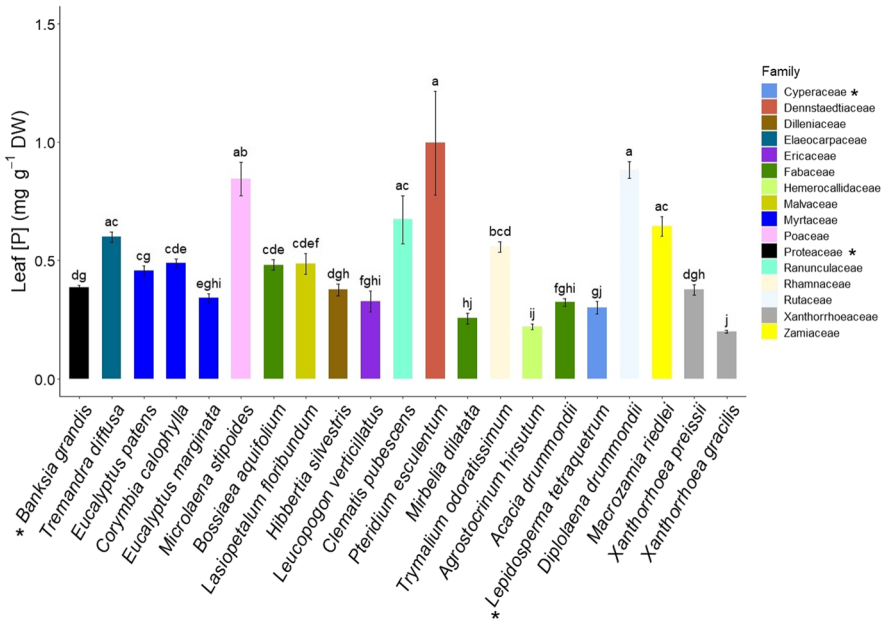

Fig. 3 Leaf phosphorus concentrations ([P]) on a dry weight (DW) basis of a range of species co-occurring with *Eucalyptus patens*, yarri (Myrtaceae) at Cypress Form, Waroona. Data are means ± SE (n = 5–10). Different letters indicate statistically significant differences among species ($P \leq 0.05$). Non-mycorrhizal species and the families they belong to are marked with*

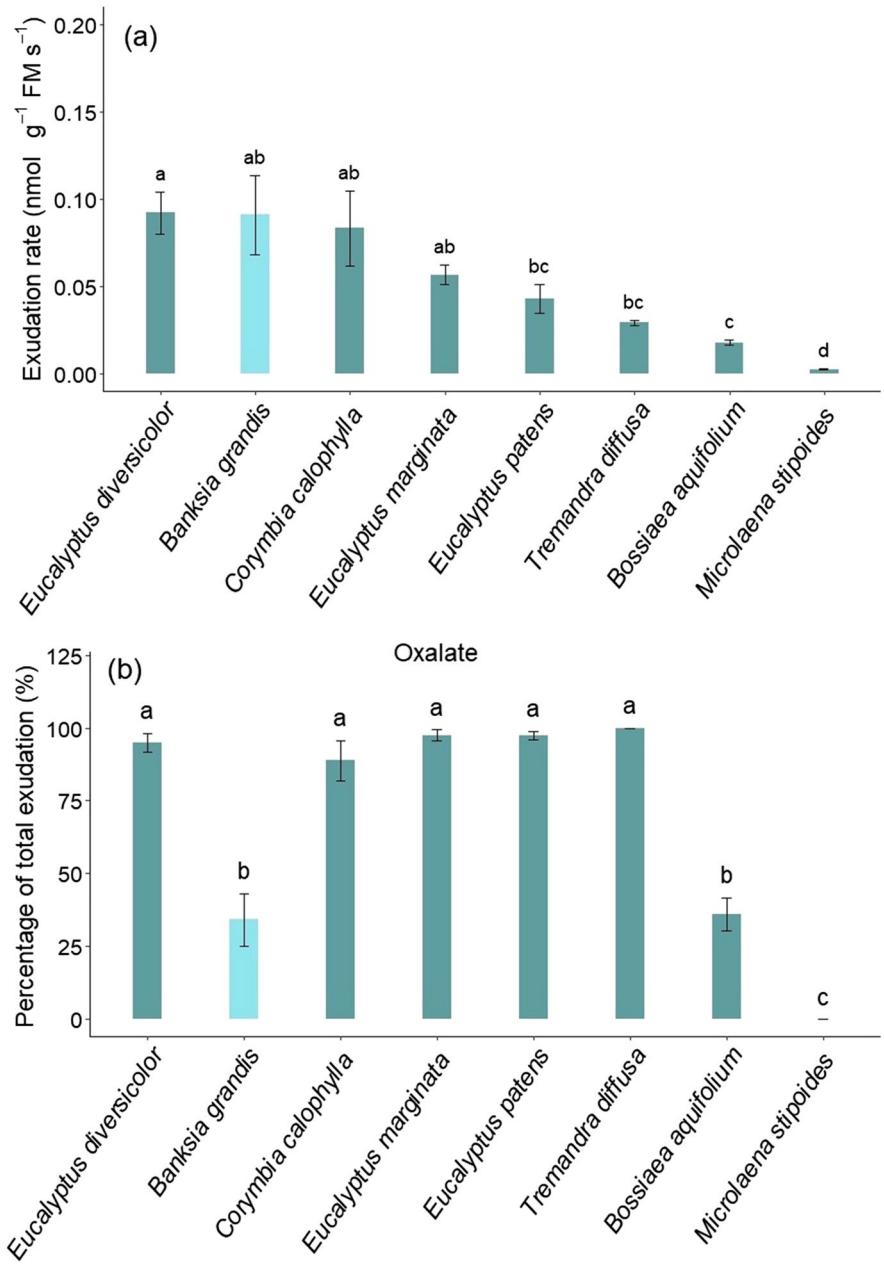

Fig. 4 Carboxylate exudation rates per unit root fresh mass (FM) of a range of species, for which leaf manganese concentrations ([Mn]) were available in their natural habitat which suggested carboxylates might play a role in their phosphorus (P) uptake. Seedlings of a range of species co-occurring with *Eucalyptus patens*, yarri (Myrtaceae) as well as *Eucalyptus diversicolor*, karri (Myrtaceae) were grown in an aerated low-P nutrient solution in a glasshouse for up to about 10 weeks. Root exudates were collected from excised whole or parts of root systems, except for *Banksia grandis*, for which we used excised mature cluster roots. (a) Rates of carboxylate exudation; (b) oxalate as a percentage of total carboxylates exuded. Data are means ± SE (n = 5). Different letters indicate statistically significant differences among species ($P \leq 0.05$)

carboxylates. These species likely do not depend on carboxylates to acquire P.

Tremandra diffusa exhibited a high leaf [Mn] (Fig. 2), closest to that of *B. grandis*. In accordance with its high leaf [Mn], *T. diffusa* seedlings grown in nutrient solution released a similar amount of carboxylates as other investigated species from the same site with a relatively high leaf [Mn] (Fig. 4a). *Bossiaea aquifolium* also showed relatively high leaf [Mn] (Fig. 2) and released carboxylates in nutrient solution (Fig. 4a). *Corymbia calophylla*, *M. stipoides*, *E. marginata* and *E. patens* had similar leaf [Mn] (160–203 mg kg^{-1}). As shown in Fig. 4a and in a previous paper for *E. patens* (Lambers et al. 2021), these Myrtaceae species released carboxylates. All other species had intermediate leaf [Mn] and likely did not release significant amounts of carboxylates.

Table 2 Soil characteristics of the horhizon at 0–100 mm depth at *Eucalyptus diversicolor,* karri (Myrtaceae) sites collected at two different locations, Torndirrup and Porongurup National Parks. In Torndirrup National Park, as the reference plant species were not at the exact same location of *E. diversicolor*, we also compared soil chemical properties at the site of the reference species (*Adenanthos obovatus*). Data are means (SE) (n = 5). Different letters indicate significant differences among the three sites ($P \leq 0.05$)

Plant species	Location	Soil characteristic						
		pH (H_2O)	pH ($CaCl_2$)	EC (µS m^{-1})	Total P (mg kg^{-1})	Organic P (mg kg^{-1})	Resin P (mg kg^{-1})	Total Mn (mg kg^{-1})
E. diversicolor	Torndirrup National Park	7.3(0.2)^{a}	6.5(0.2)^{a}	11,648(2385)^{a}	46(7) ^{b}	36(5)^{b}	0.83(0.11) ^{b}	78(5)^{b}
A. obovatus	Torndirrup National Park	4.6(0.1)^{bc}	4.0(0.1)^{b}	–	50(17)^{b}	30(2)^{b}	3.7(0.08)^{a}	62(5)^{b}
E. diversicolor	Porongurup National Park	7.3(0.2)^{a}	6.7(0.3)^{a}	15,867(3043)^{a}	140(16)^{a}	91(16)^{a}	0.36(0.10) ^{b}	819(69)^{a}

Abbreviations: EC, electrical conductivity

Table 3 Soil chemical properties at the *Eucalyptus patens* site at Cypress Form, Waroona. Data are means (SE) (n = 5). Different letters indicate significant differences among soil depth ($P \leq 0.05$). Soil nutrient concentrations are total concentrations, expressed on a dry weight (DW) basis

Soil chemical properties	Soil depth	
	0–50 mm	>50 mm
pH (H_2O)	5.7(0.1)^{b}	6.5(0.1)^{a}
pH ($CaCl_2$)	4.8(0.1)^{b}	5.3(0.0)^{a}
EC (µS m^{-1})	9321(829)^{a}	2675(217)^{b}
Total P (mg kg^{-1})	34(2)^{a}	3.0(0.6)^{b}
Organic P (mg kg^{-1})	30(2)^{a}	2.3(0.7)^{b}
Resin P (mg kg^{-1})	1.1(0.1)^{a}	0.7(0.2)^{a}
N (mg g^{-1})	4.2(0.3)^{a}	0.8(0.1)^{b}
N:P	25(1)^{a}	14.0(0.6)^{b}
Total C (mg g^{-1})	107(10)^{a}	16.3(1.6)^{b}
Mg (mg g^{-1})	0.8(0.1)^{a}	0.37(0.04)^{b}
Ca (mg g^{-1})	3.3(0.3)^{a}	0.83(0.09)^{b}
K (mg g^{-1})	0.41(0.04)^{a}	0.39(0.04)^{a}
S (mg/g)	0.44(0.04)^{a}	0.09(0.01)^{b}
Mn (mg kg^{-1})	314(18)^{a}	193(6)^{b}
Na (mg kg^{-1})	92(9)^{a}	66(6)^{b}
Zn (mg kg^{-1})	4.7(0.4)^{a}	3.9(0.3)^{a}
Cu (mg kg^{-1})	6.1(0.2)^{a}	5.6(0.2)^{a}
Fe (g kg^{-1})	15.0(0.2)^{b}	17.9(0.3)^{a}
Al (g kg^{-1})	17.5(0.9)^{b}	24.4(0.4)^{a}

Abbreviations: EC, electrical conductivity

Leaf [Mn] and [P] at the E. diversicolor sites

At Torndirrup National Park, *B. grandis* exhibited the highest leaf [Mn] (Fig. 5a), but the lowest leaf [P] and *E. diversicolor* had the highest leaf [P] (Fig. 5b). Using young leaves of *A. obovatus* as the negative reference showed that the co-occurring *E. diversicolor* had a similar leaf [Mn], but the soil pH under *E. diversicolor* was significantly higher than that under the negative reference species (pH 7.3 vs. pH 4.6) with similar soil [Mn] (Table 2). In the absence of negative reference species at the exact same location, we cannot draw a firm conclusion, but suggest *E. diversicolor* likely exuded carboxylates. This was confirmed using seedlings grown in nutrient solution (Fig. 4a).

At the low-diversity Porongurup National Park site, no suitable reference species occurred. We sampled young leaves of *E. diversicolor*, anticipating these might be suitable as negative reference (Shane and Lambers 2005b). Leaf [Mn] (Fig. 5c) was very high in mature leaves, compared with those at the other location, and significantly different from those in young leaves. The high leaf [Mn] suggests they released carboxylates. This was confirmed using seedlings grown in nutrient solution (Fig. 4a). Leaf [P] values were relatively high in mature leaves, and considerably higher in young leaves (Fig. 5d).

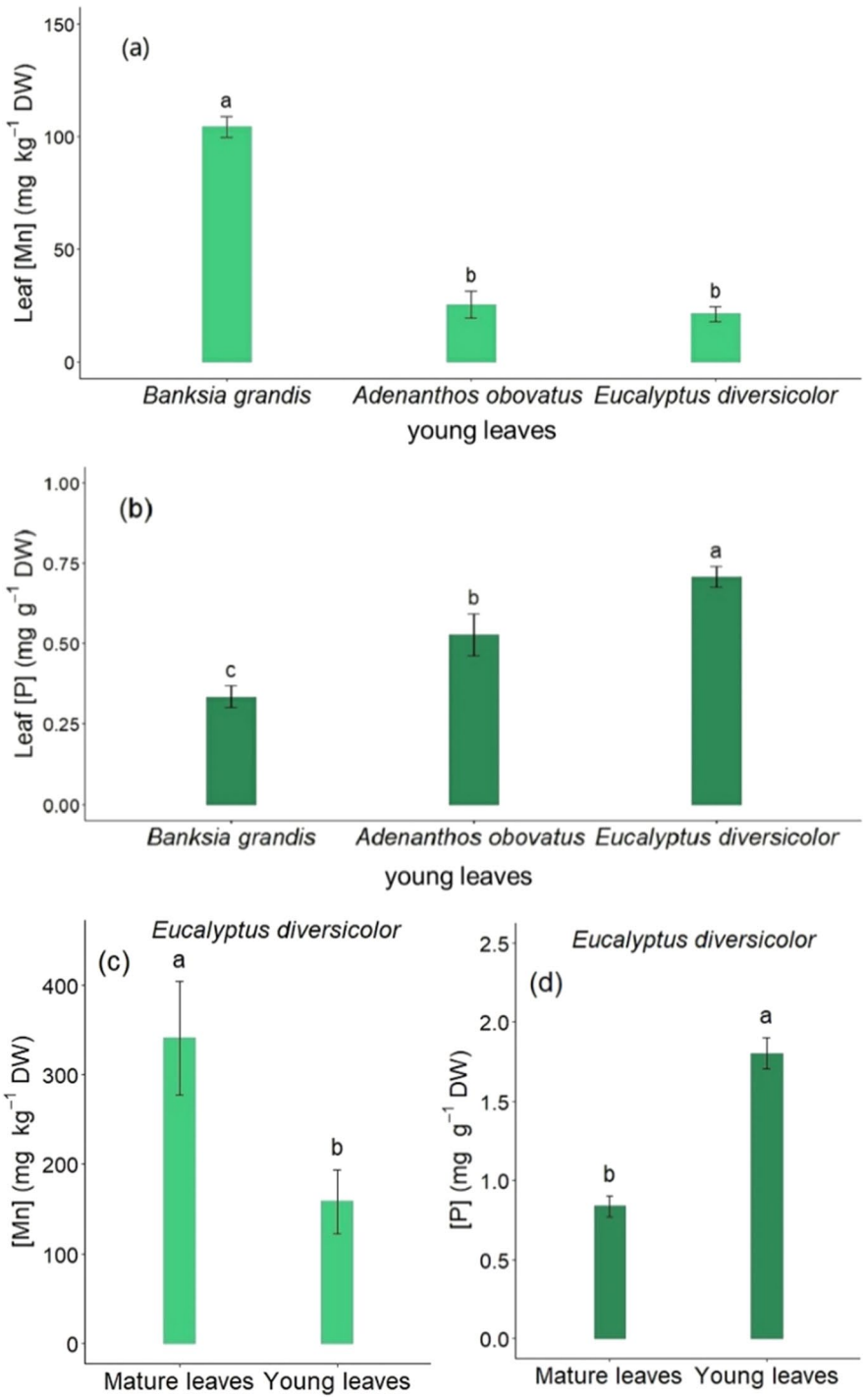

Fig. 5 Leaf manganese concentrations ([Mn]) and phosphorus concentrations ([P]) of *Eucalyptus diversicolor* (Myrtaceae) collected at two locations: (a) [Mn] and (b) [P] in Torndirrup National Park, (c) [Mn] and (d) [P] in Porongurup National Park. In Torndirrup National Park, the reference plant species were not at the exact same location of *E. diversicolor*, because none were available there, and the two locations differed significantly in soil pH, which was higher under *E. diversicolor*, and hence its leaf [Mn] would be expected to be significantly lower. In Porongurup National Park, no reference plants were available at an acceptably short distance, and young leaves of *E. diversicolor* were used instead. Data are means ± SE (n = 5). Different letters indicate statistically significant differences among species ($P \leq 0.05$)

Carboxylate and phytosiderophore release

All species that exhibited relatively high leaf [Mn] released carboxylates (Figs. 2, 4a and 5c), including oxalate (Fig. 4b), except for the grass *M. stipoides*, which released phytosiderophores. Quantitative analysis of total released phytosiderophores showed a Fe-solubilising capacity of 0.50 ± 0.09 µg Fe g^{-1} root

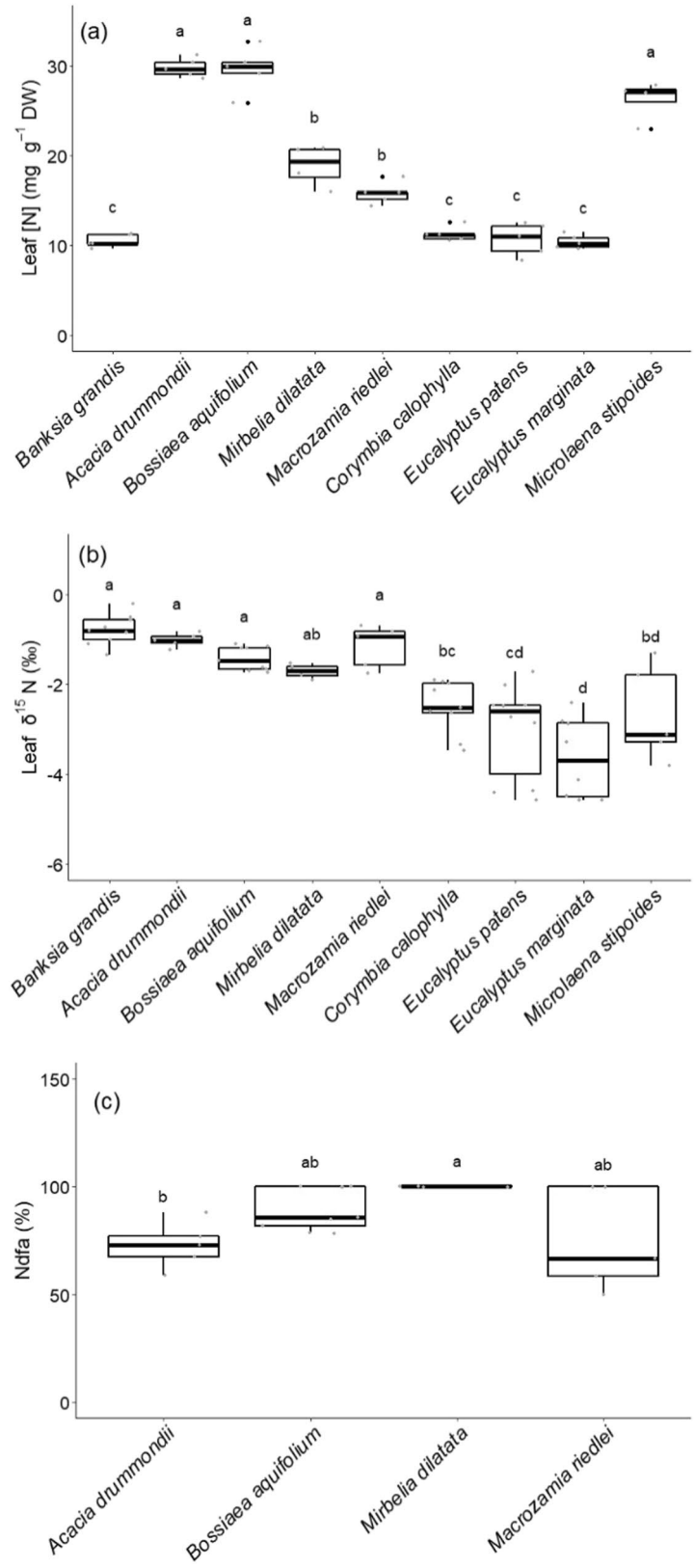

Fig. 6 (**a**) Leaf nitrogen concentrations ([N]), (**b**) leaf N isotope composition expressed as $\delta^{15}N$, and (**c**) N derived from atmospheric N_2 fixation (Ndfa) for a range of species co-occurring with *Eucalyptus patens* (Myrtaceae) at Cypress Form, Waroona. Box-plots with medians, 25th and 75th percentiles. Whiskers extend to 1.5 times the interquartile range. Data presented beyond whiskers represent outliers. Data are means ± SE (n = 5–10). Different letters indicate statistically significant differences among species ($P \leq 0.05$)

DW (n = 4), which corresponds with a phytosiderophore release rate of 8.7 ± 1.4 nmol DMA equivalent g^{-1} root DW (3 h)$^{-1}$.

The fastest exudation rate was exhibited by *E. diversicolor*, in accordance with our hypothesis and contrary to the widely held view that this species (Bougher et al. 1990) and *Eucalyptus* species in general (Brundrett and Abbott 1991; Malajczuk et al. 1982) depend on mycorrhizal associations to acquire P.

Leaf N concentrations, N-isotope composition, and N derived from the atmosphere

Leaf [N] (Fig. 6a) was lowest in *B. grandis*, *C. calophylla*, *E. marginata*, and *E. patens* (10.2–11.3 mg g^{-1} DW), higher for the putatively N_2-fixing *M. riedlei* (16.0 mg g^{-1} DW) and highest for the three Fabaceae (18.9–29.8 mg g^{-1} DW), with *M. stipoides* also showing a relatively high value (24.0 mg g^{-1} DW) (Fig. 6a). The $\delta^{15}N$ values ranged from closest to zero for *B. grandis* to the most negative values for the eucalypts and *M. stipoides* (Fig. 6b), with the putatively N_2-fixing species showing values in between. Using *M. stipoides* as a reference, we calculated the percentage N derived from atmospheric N_2 fixation (%Ndfa) for the putatively N_2-fixing species, and found values ranging from 73% in *Acacia drummondii* to 100% in *Mirbelia dilatata* (Fig. 6c).

Discussion

We focused on P-acquisition strategies in 'cool spots' in a biodiversity hotspot, confirming our main hypothesis that common species in these habitats depend on a carboxylate-releasing P-mobilising strategy, while being mycorrhizal. Our results indicate that the tall eucalypt forest in southwest Australia, characterised by a low diversity of species, 'cool spots', on P-impoverished high-rainfall sites, function very differently from the hyperdiverse kwongan (or kwongkan; Hopper 2014) shrubland communities. We sampled most of the vascular plant species at the *E. patens* site; that number of 21 contrasted strongly with numbers of 40–50 per 100 m^2 quadrats with a large variation among quadrats in kwongan shrublands on the sandplains in the Southwest Biodiversity Hotspot (Zemunik et al. 2016). In kwongan shrublands, Proteaceae species with very effective P-acquisition strategies are also very sensitive to oomycete pathogens (Albornoz et al. 2017; Laliberté et al. 2015). This trade-off has been offered as an explanation for coexistence of Proteaceae with mycorrhizal plants with less effective P-acquisition strategies but better protection against oomycete pathogens (Laliberté et al. 2015; Lambers et al. 2018). In contrast, the few dominant species in the 'cool spots' are mycorrhizal but depend on a carboxylate-releasing P-acquisition strategy, with the tall eucalypts dominating the canopy and other common species also being both mycorrhizal and carboxylate-releasing. We surmise that the degree of competition by dominant carboxylate-releasing mycorrhizal species for the extraordinarily low amounts of readily-available P in these environments explains the low species diversity and paucity of nitrogen-fixing species, whereby only a few understorey species exhibit carboxylate-releasing strategies to access P. The role of mycorrhizas in these high-rainfall systems is likely very important to boost species' defence against pathogens (Albornoz et al. 2017; Laliberté et al. 2015), but given the very low availability of soil P in the studied habitats, mycorrhizas are unlikely to play a major role in inorganic P acquisition (Lambers et al. 2018; Parfitt 1979; Treseder and Allen 2002). The dominant species, being efficient at acquiring P, based on their carboxylate-releasing strategy, and protected against oomycete pathogens, because they are mycorrhizal, would not require facilitation of their P acquisition, as is common in kwongan (or kwongkan; Hopper 2014). Would it be likely that *E. patens* used both a carboxylate-releasing and mycorrhizal strategy to acquire P, possibly depending on space or time? We cannot exclude this, although our ^{15}N results do not support this, as we discuss below. To further test this, we would need experiments done with a range of Myrtaceae species that naturally grow in kwongan (Albornoz et al. 2017). These authors grew Myrtaceae species in soil from their natural habitat inoculated with mycorrhizal fungi with different levels of mycorrhizal colonisation. Albornoz et al. (2017) found that the level of mycorrhizal colonisation did not affect the growth of Myrtaceae species, as long as there were no oomycete pathogens in the soil. These results are

supported by the finding that in the natural kwongan habitat of these species, mycorrhizal fungi are commonly found inside the roots of mycorrhizal plants, but not in ingrowth soil cores outside the roots of these plants (Teste et al. 2016). We suggest that similar experiments are required in tall *Eucalyptus* forests to corroborate the present findings.

We used leaf [Mn] as a proxy for carboxylate-releasing P-acquisition strategies, based on the correlation between these two parameters in field (Lambers et al. 2021; Lambers et al. 2015b) and glasshouse studies (Pang et al. 2018; Wen et al. 2019). We then followed up with glasshouse studies to measure carboxylate exudation of seedlings grown in a low-P nutrient solution (Fig. 4). Our results lend further support for the use of leaf [Mn] as a proxy for rhizosphere carboxylate concentrations and confirm a recent contention that species in typical mycorrhizal clades may actually depend on carboxylate release to acquire P (Lambers et al. 2021). Likewise, our data show that one species in a typical non-mycorrhizal carboxylate-releasing clade (Cyperaceae) may actually not depend on carboxylate release to acquire P. Below, we discuss the wider implications of our findings.

Coexistence of P-acquisition strategies among sympatric species

Our findings provide evidence for a wide spectrum of P-acquisition strategies in tall eucalypt forests in southwest Australia (Fig. 2). At one end of the spectrum, there was *B. grandis*, our positive reference, which releases large amounts of carboxylates (Shane and Lambers 2005a), as is common in Proteaceae (Lambers 2022). At the other extreme were *X. gracilis*, *X. preissii* (our negative references) and *M. riedlei*, which grow very slowly between fires, but are among the first to resprout after a fire (Grove et al. 1980). These species likely depend on elevated soil P concentrations after a major disturbance such as fire (Lambers et al. 2022). In between the two extremes, some species released significant amounts of carboxylates, in accordance with their relatively high leaf [Mn]. *Tremandra diffusa* exhibited a leaf [Mn] closest to that of *B. grandis*, in agreement with data on the rainforest trees *Elaeocarpus ferruginiflorus* and *E. ruminatus* in the same family (Lambers et al. 2021). In agreement with its high leaf [Mn], seedlings of *T. diffusa* grown in nutrient solution released carboxylates (Fig. 4a). *Bossiaea aquifolium*, which formed a major understorey component, showed a high leaf [Mn] and released carboxylates, and likely also depends on a P-mining strategy.

One species that exhibited relatively high leaf [Mn] but did not release carboxylates, was *M. stipoides*. Its high leaf [Mn] is likely accounted for by its release of phytosiderophores, which is typical for Poaceae (Ma 2005). Grasses enhance the release of phytosiderophores when they are Fe-deficient, but *M. stipoides* in this case was grown with sufficient Fe. The present results suggest that *M. stipoides* up-regulated its phytosiderophore release in response to P deficiency. Phytosiderophores not only mobilise Fe, but also Mn (Zhang 1993), and they likely enhance P availability in soil, evidenced by findings for Fe-deficient *Zea mays* plants that accumulate more P than Fe-sufficient ones, in both roots and shoots (Zanin et al. 2017). Much inorganic P in soil is sorbed onto oxides and hydroxides of Fe, and phytosiderophores would therefore mobilise both Fe and P.

Some species with intermediate leaf [Mn] may depend on facilitation. This possibly includes *Lygodactylus verticillatus* (Fig. 2). Some species may access organic P in leaf litter, which may be accessed without involvement of carboxylates (Zhong et al. 2021). Since most of that leaf litter would have been made available by dominant P-mobilising species, we may consider this 'indirect facilitation' (Lambers et al. 2012a). We hypothesise that *D. drummondii* functions like this, whereas species with slightly higher leaf [Mn] are possibly 'directly facilitated', depending on P-mobilising carboxylates released by a neighbour. However, this contention requires further study.

Leaf [Mn] and [P]

Plants with the highest leaf [Mn] did not have the highest leaf [P] (Figs. 2, 3). This indicates that species with a high P-acquisition efficiency also exhibited a high P-use efficiency, which is well documented for Proteaceae (Lambers et al. 2012b; Sulpice et al. 2014) and co-occurring species (Guilherme Pereira et al. 2019). Interestingly, all species functioned at less than half of the leaf [P] that is considered adequate for crop plants, which is 2.00 mg g^{-1} leaf DW (Epstein and Bloom 2005) and also less than

the global median leaf [P], which is 0.99 mg g^{-1} DW (Wright et al. 2004). Some of the low leaf [P] will be accounted for by the presence of sclerenchyma, but this does not offer a full explanation (Lambers et al. 2010). Leaves of the present species differed in their leaf dry matter content (Fig. S1a) but expressing leaf [P] on a FW basis did not substantially change the ranking (Figs. 3, S1b). *Microlaena stipoides*, *P. esculentum* and *D. drummondii* exhibited the highest leaf [P], about 0.90 mg g^{-1} DW (Fig. 3).

Leaf [N] and [P], and $\delta^{15}N$ values

The leaf [P] and [N] of *B. grandis* were the same as recorded for two other populations of this species (Barrick 2003). Likewise, leaf [P] and [N] of *C. calophylla* and *E. marginata* were similar to or somewhat lower than published data (Hingston et al. 1980). For *M. riedlei*, the present leaf [N] and [P] data were in accordance with published data (Grove et al. 1980). We did not find data on leaf [N] and [P] in the literature for *B. aquifolium*, but published values for *B. laidlawiana* (regarded by some as *B. aquifolium* subsp. *laidlawiana*) growing in karri forest (Grove 1990) are similar to the ones for *B. aquifolium* we studied. We did not find pertinent data for the other species we studied in the literature.

Based on $\delta^{15}N$ data (Fig. 6b), we conclude that 70–100% of all leaf N was acquired through symbiotic N_2 fixation in *M. riedlei* and the three Fabaceae (Fig. 6c). These values are high compared with those for Fabaceae on severely P-impoverished Bassendean sands in Jurien Bay in southwest Australia, but similar to those on younger Spearwood sands, where the availability of both P and N is greater (Png et al. 2017). Since two of the Fabaceae appeared not to exhibit P-mobilising strategies, but possibly depended on facilitation, competition with the large eucalypts was likely severe. This strong competition with tall eucalypts likely explains why the dependence of the N_2-fixing species on atmospheric N_2 was very large, because legumes tend to increase their dependence on N_2 fixation when neighbours compete with them for combined N (Li et al. 2009).

The high $\delta^{15}N$ values for *B. grandis* suggest that this species accessed organic N, as shown for *Hakea actites* (Proteaceae) (Schmidt et al. 2003). Relatively high $\delta^{15}N$ values are common for Proteaceae (Schmidt and Stewart 1997). Conversely, the very negative values for both *M. stipoides* and the eucalypts suggest that they predominantly accessed inorganic N. Being ectomycorrhizal (Brundrett and Abbott 1991), we might have expected the eucalypts to access organic N (Abuzinadah and Read 1986; Högberg 1990), but the stable isotope values do not support this expectation (Fig. 6b). We surmise that this is because in severely P-impoverished habitats, mycorrhizal fungi are largely restricted to roots, with very few hyphae extending into the soil (Teste et al. 2016). The leaf [Mn] data support this contention, because mycorrhizal hyphae (Bethlenfalvay and Franson 1989) including ectomycorrhizal hyphae (Canton et al. 2016) in soil tend to intercept Mn and cause low leaf [Mn].

Phosphorus acquisition in *E. diversicolor*

Grove (1990) reported high leaf [Mn] for unfertilised *E. diversicolor* of 857 mg kg^{-1} DW in comparison with 95 mg kg^{-1} DW for *B. aquifolium* subsp. *laidlawiana* (formerly *B. laidlawiana*) at the same location. Leaf [Mn] for *E. diversicolor* was 222 mg kg^{-1} DW in comparison with 70 mg kg^{-1} DW for *C. calophylla* at the same yellow podzolic soil site (Hingston et al. 1979), suggesting that *E. diversicolor* released carboxylates more vigorously than *C. calophylla*; our data on carboxylate exudation support this contention (Fig. 4a).

The present results suggest that *E. diversicolor* forests function like *E. patens* forests, with *E. diversicolor* releasing large amounts of carboxylates to acquire P, while its mycorrhizal associations protect it from pathogens. These traits make them independent of neighbours facilitating their P uptake, strong competitors, and dominant species in a low-diversity habitat.

Concluding remarks

The present results provide insights into some 'cool spots' in a biodiversity hotspot; some species in mycorrhizal families may actually depend on carboxylate release to acquire P in their natural habitat. They also indicate that the tall eucalypt forest in southwest Australia function differently from what we might believe, based on mycorrhizal surveys (Albornoz et al. 2021a; Brundrett and Abbott 1991). We do not know how common carboxylate-releasing strategies are amongst Myrtaceae and Elaeocarpaceae (Lambers et al. 2021),

or if this trait is associated with high-rainfall locations in Australia.

Even in the severely P-impoverished habitats of the present study, a range of P-acquisition strategies co-exist, ranging from carboxylate release in species with high leaf [Mn] to direct facilitation by carboxylate-releasing neighbours in species with intermediate leaf [Mn]. Some species with low leaf [Mn] likely depended on indirect facilitation and accessed readily-available organic P in litter made available predominantly by the dominant P-mobilising species. Leaf [Mn] of Fabaceae indicates that they depended to a greater (*B. aquifolium*) or lesser (*A. drummondii*) extent on carboxylates, but they likely also accessed organic P (Houlton et al. 2008; Png et al. 2017). Our findings provide further incentive to revisit some of the species in 'mycorrhizal families' (Elaeocarpaceae, Myrtaceae) that have unusually high leaf [Mn] (Lambers et al. 2021). The present results show that significant carboxylate release associated with mobilisation of P and Mn, even without involvement of cluster roots, is more pervasive than commonly believed.

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