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Australian dryland soils are acidic and nutrient-depleted, and have unique microbial communities compared with other drylands

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Abstract

Aim: To compare Australian dryland soils with dryland soils globally.

Location: Australian and global drylands.

Methods: We used data from standardized surveys of soil properties (C, N, and P content and stoichiometry, and pH) and microbes (diversity, composition, and correlation networks) from Australian and global drylands, which occupy three-quarters of the Australian land mass and are the largest biome on Earth.

Results: We found that Australian dryland soils were different, exhibiting characteristics of ancient weathered soils. They had lower pH, total and available P, and total N, and greater C:N and C:P ratios than global dryland soils. Australian soils had distinctive microbial community composition and diversity, with more Proteobacteria and fewer Basidiomycota than global dryland soils, and promoted the abundance of specific microbial phylotypes including pathogens, mycorrhizae, and saprobes.

Main conclusions: Australian dryland soils are clearly different from dryland soils elsewhere. These differences need to be considered when managing dryland soils to avoid unreasonable expectations about plant productivity and carbon stocks, or when predicting likely changes in ecosystem processes resulting from global environmental change.

KEYWORDS
Australasia, global survey, nutrient cycling, soil microbes, soil nutrients, soil pH

1 | INTRODUCTION

Comparisons of the biogeography of the Australian continent with the rest of the world have fascinated scientists for decades (Orians & Milewski, 2007). The literature is replete with statements referring to Australia as uniquely different in the world, being the largest island continent, and characterized by flat, barren, and heavily eroded landscapes that are largely unproductive for agriculture (Andrewarthy & Birch, 1984; Orians & Milewski, 2007). Australia also supports a diverse range of unusual plants and animals such as egg-laying "marsupials", and has had a long history of aboriginal occupation, but a relatively short history of European settlement coupled with European farming practices (Gammage, 2011). Unlike other continents, more than 90% of Australia's land mass still supports native vegetation, and less than 6% is arable. Australian soils are commonly described as being nutrient-poor or infertile, and unsuitable for farming (Lindsay, 1985; Northcote & Skene, 1972; Stafford Smith & Morton, 1990; Taylor, 1994). Strikingly, despite this widely held view, and unlike what we know about the uniqueness of Australia's plants and animals, there is a general lack of empirical evidence to support statements about the low fertility of Australia's soils (Lindsay, 1985), particularly when compared to other regions of the globe.

Drylands, ecosystems characterized by a scarcity of water, are particularly relevant when comparing Australian soils from those of

the rest of world. These ecosystems occupy almost 75% of Australia's land mass (Dunkerley, 2010) and are globally highly important, occupying about 45% of Earth's global land area and supporting about 40% of its human population (Prăvălie, 2016). At a continental scale, Australian drylands exhibit three unique characteristics compared with other drylands. First, the Australian continent is situated in the mid to lower latitudes. Therefore, unlike many other terrestrial ecosystems from the Northern Hemisphere, its soils were not strongly influenced by the last glaciation, which occurred about ~21 kyr BP. Because of the lack of glacial disturbance on Australian soils, they are considered, on average, to be extremely ancient (i.e., many millions of years). For example, many of Australia's soils had their origins in the late Cainozoic period (10–20 Myr BP), where they experienced long periods of relative stability (Hubble, Isbell, & Northcote, 1983). Consequently, soils from Australia are likely to have characteristics consistent with strongly weathered soils with a long history of development, including low soil phosphorus (P), low pH, or low concentrations of soil carbon (C), which all contribute to the uniqueness of its soils (Laliberté et al., 2013; Vitousek, Porder, Houlton, & Chadwick, 2010; Wardle, Walker, & Bardgett, 2014). Second, unlike other dryland ecosystems worldwide, forests and dense woodlands dominated by *Eucalyptus* spp. typically occur in environments that elsewhere, would normally be occupied by drought-tolerant shrubs or grasses (Dunkerley, 2010; but see Bastin et al., 2017). These densely wooded or forested systems are often characterized by a higher amount of organic matter and lower levels of soil P and pH due to weathering related to plant productivity, contributing to the unique signature of Australian soils.

Australia has only recently been occupied by Europeans, and traditional cultures did not cultivate the land (Hubble et al., 1983). Therefore, there are almost no anthropogenic soils, i.e., completely human-produced soils resulting from direct human impact. The lack of soil rejuvenation from human disturbance may also contribute to the maintenance of soils showing characteristics of strongly weathered profiles. All of these characteristics distinguish Australia from other continents where drylands form a large proportion of the land mass, such as Africa and North America. It is known that Australian soils are low in P, and soil pH levels could change in response to small changes in the water balance (Slessarev et al., 2016). Further, given the global relationship between pH and soil microbial communities (Fierer & Jackson, 2016; Lauber, Hamady, Knight, & Fierer, 2009; Maestre et al., 2015), we might expect Australian soils to be characterized by a different microbial community. However, there have been no continental-wide assessments evaluating whether Australian soils and their microbial communities might differ or resemble from those from other drylands.

Here, we compared soil properties (total C and pH), soil nutrient availability, and microbial communities of Australian soils with those across the globe. We pose the following question: To what extent do Australian dryland soils exhibit characteristics similar to other drylands globally? To address this question, we gathered information from five independent datasets that contained a total of 612 dryland locations and information on nutrient availability, soil C, pH, and/or microbial communities globally and in Australia. We report on these soil properties because they have been used for over half a century as classic indicators of soil weathering (McGill & Cole, 1981; Walker & Syers, 1976). Similarly, soil microbial communities have recently been suggested to change strongly in response to ecosystem development (Alfaro, Manzano, Marquet, & Gaxiola, 2017; Noll & Wellinger, 2008), giving us further insights into the uniqueness of Australian soils. Given the nature of the Australian landscape described above, we hypothesized that, compared with global drylands elsewhere, Australian soils should be characterized by ancient, deeply weathered soils, i.e., that are acidic and nutrient-depleted. These characteristics might have also led to a very specific microbial community assembly in the continent.

Identifying whether Australian soils are really unique and whether their microbial communities are distinct or merely a subset of those found in drylands globally is important for several reasons. First, it would fill an important gap in our knowledge that could also advance our understanding of observed biogeographical patterns of other organisms (e.g., plants). Second, we would be able to manage these soils more effectively if we have a better understanding of their inherent fertility compared with similar ecosystems worldwide that have formed under the influence of different geological and historical influences. Farming practices in Australia are still largely based on ideas imported from Europe where soils, landscapes and the response to land management practices are markedly different. Indeed, Australian ecosystems are often managed on the basis that they are assumed to be similar to other global drylands (Pickard, 1994). Understanding what makes Australian soils unique is also important to anticipate how ongoing environmental changes can affect their capacity to maintain multiple essential ecosystem functions and services (e.g., nutrient cycling, carbon storage, and food and fibre production).

2 | MATERIALS AND METHODS

2.1 | Study sites

We gathered information from five independent, large-scale datasets containing information on nutrient availability, soil C, pH, and/or microbial communities, which were all measured using the same protocols. These datasets included: (a) 236 sites from the BIOCOM project (Maestre et al., 2012), which included 18 Australian sites (Global Network Study, hereafter); (b) 22 sites from a regional study across eastern Australia (Delgado-Baquerizo et al., 2015; East Australia Study, hereafter); (c) 54 sites from a regional study of grazing impacts on eastern Australian soils (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2016; NSW Grazing Study, hereafter); (d) 109 samples from uncultivated dryland sites from the Australian BASE project (Bissett et al., 2016; BASE Project, hereafter, and available online from Delgado-Baquerizo et al., 2016); and (e) 191 soils collected as part of a regional study of biocrusts across eastern Australia (Eldridge, 1996; Biocrust Study, hereafter; see Table S1.1,

Appendix S1 in Supporting Information). Drylands are by definition located in areas with aridity index <0.65, but we also included in our analyses dry subhumid areas because these areas also severely water limited, and are likely to become increasingly arid under current climate change prediction scenarios (Huang, Yu, Guan, Wang, & Guo, 2016). Our study included data from soil samples collected from 612 dryland (aridity index 0.06–0.92; UNEP 1992) sites located in 19 countries (Argentina, Australia, Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, USA and Venezuela) from six continents (Figure 1; Table S1.2. Appendix S1). Moreover, this dataset included locations in temperate, arid, continental, polar, and tropical climates, as defined by the Köppen climate classification (Peel, Finlayson, & McMahon, 2007). All soil samples were collected within the top 10 cm following standardized protocols. Data availability and references to the original protocols for each dataset are available in Supporting Information Table S2. For example, in the particular case of soil microbial communities, we gathered information for 101 plots including the 79 sites in Maestre et al. (2015) and the 22 sites in Delgado-Baquerizo et al. (2017).

2.2 | Soil properties

For all 612 soil samples, we gathered information on organic C and pH. In all cases, soil organic C concentration was determined as described Anderson and Ingram (1993) and soil pH in a 1:5 soil-water extract with a pH meter. We also gathered information for 300 of these samples on total N and P. Soil total N was measured with a CN analyser (LECO CHN628 Series, Leco Corporation, St Joseph, MI, USA). Total P was determined using a SKALAR San++ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulphuric acid (3 hr at 415°C) as described in Anderson and Ingram (1993). For 246 soils, we assessed available P. Olsen inorganic P (Olsen, Cole, Watanabe, & Dean, 1954) was measured following a 0.5 M $NaHCO_3$ (pH 8.5) extraction following the soil-P fractionation protocol (Tiessen & Moir, 1993). These were measured colorimetrically (Sims, Ellsworth, & Mulvaney, 1995) using a 0.5 M soil extracts and K_2SO_4 with a 1:5 soil: extract ratio (Delgado-Baquerizo et al., 2013).

2.3 | Molecular and bioinformatics analyses

For 101 plots, we gathered information on the community composition, richness, and abundance of soil fungi and bacteria (Appendix S2). These data were generated using next generation molecular analyses (Maestre et al., 2015). In brief, DNA was extracted from 0.5 g of defrosted soil samples using the Powersoil® Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA).

Detailed explanation on bioinformatics and molecular analyses are given in Maestre et al. (2015). The community composition and richness of fungi and bacteria were analysed in the Next Generation Genome Sequencing Facility of the Western Sydney University (Australia) using the Illumina MiSeq platform and the 341F/805R (bacteria) and FITS7/ITS4 (fungi) primer sets (Herlemann et al., 2011; Ihrmark et al., 2012). Initial sequence processing and diversity analyses for both bacterial 16S rDNA and fungal ITS genes were conducted by using the 'QIIME' package (Caporaso et al., 2010). Initially, low-quality regions ($Q < 20$) were trimmed from the 5′ end of sequences, and paired ends were joined with FLASH (Magoč & Salzberg, 2011) for 16S rDNA sequences and Fastq-join (Aronesty, 2011) for ITS reads. Sequences were demultiplexed, and a further round of quality control was conducted to remove sequences containing ambiguous bases (N) and reads containing bases with a quality score <25. Chimeric 16S rDNA sequences were detected by using the UCHIME algorithm from the

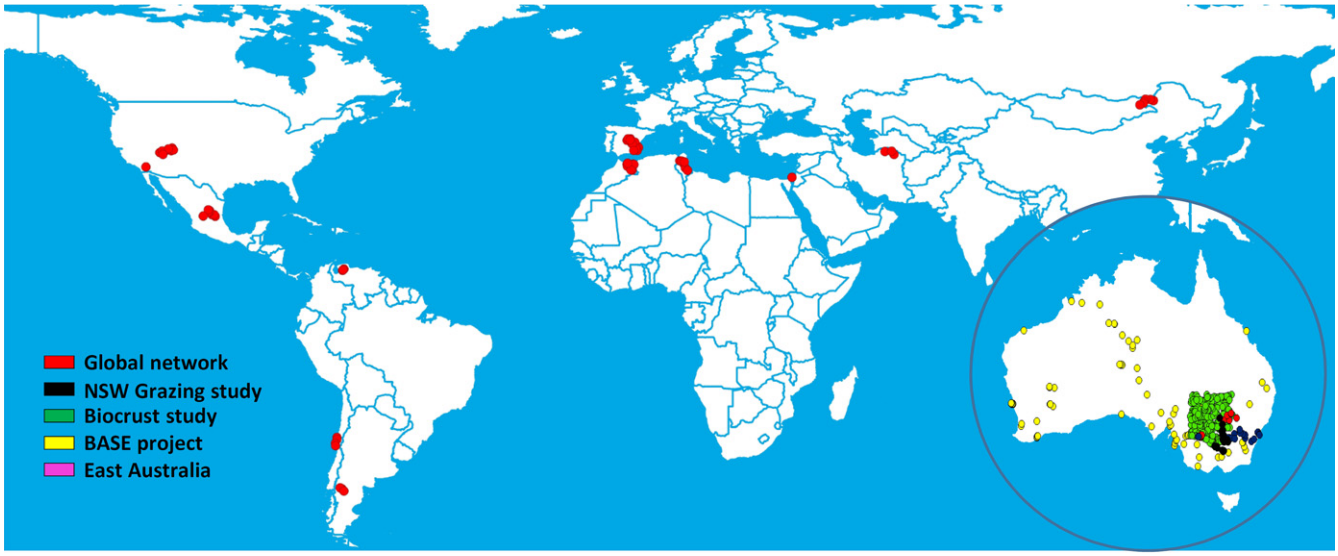

FIGURE 1 The global distribution of the 612 study sites used in this study. The map of Australia is enlarged to provide a better representation of the distribution of sites surveyed there [Colour figure can be viewed at wileyonlinelibrary.com]

'USEARCH' package (Edgar, 2010) implemented within VSEARCH (https://github.com/torognes/vsearch). The RDP training dataset (version 9; Cole et al., 2005) was used as a reference for chimera detection, as recommended by the UCHIIME documentation. De novo (abundance-based) chimera detection was used for ITS data using 'USEARCH' (Edgar, 2010). The remaining high-quality chimera-free sequences were used for downstream analysis. Operational taxonomic units (OTUs) were defined as clusters of 97% sequence similarity using UCLUST (Edgar, 2010). Taxonomy was assigned using UCLUST (Edgar, 2010) against the Greengenes database (version 13_850) for 16S rDNA OTUs (DeSantis et al., 2006; McDonald et al., 2012). For fungal ITS sequences, taxonomy was assigned by using BLAST (Altschul, Gish, Miller, Myers, & Lipman, 1990) against the UNITE database (version 6.9.7; Kõljalg et al., 2013) ($E < 10^{-5}$). This database, however, considers the Zygomycota as a phylum, whereas the most recent taxonomical references no longer do so (McLaughlin & Spatafora, 2014). We thus refer to Zygomycetous fungi when referring to the different taxonomical units formerly included in the Zygomycota (McLaughlin & Spatafora, 2014). The resultant OTU abundance tables for both primer sets were filtered to remove singletons and rarefied to an even number of sequences per samples to ensure an equal sampling depth (11,925 and 17,000 for 16S rDNA and ITS respectively). Shannon diversity was calculated on these rarefied OTU tables by using 'QIIME' (Caporaso et al., 2010). We estimated diversity using this metric because it has been recommend when quantifying and comparing microbial diversity (Haegeman et al., 2013). The number of bacterial sequences obtained from two of the sites surveyed was too low to estimate microbial diversity accurately, so they were not used in further analyses. Quantitative PCR (qPCR) reactions were carried out in triplicate on an ABI 7300 real-time PCR (Applied Biosystems, Foster City, CA, USA). The total abundance of bacterial 16S-rRNA genes and fungal internal transcribed spacer (ITS) were amplified with the Eub 338-Eub 518 and ITS 1-5.8S primer sets (Evans & Wallenstein, 2012).

2.4 | Statistical analyses

Differences in soil chemical properties and relative abundance of microbes between Australia and elsewhere were explored using a simple mixed model, based on a one-way ANOVA with subsamples. The contrast of interest, namely samples representing the Australian continent versus samples from countries in the rest of the world, was compared with an experimental error term formed from the stratum variance among 31 survey "units". The survey units were the different countries, but the number of survey units (n = 31) was larger than the number of countries surveyed (n = 19) simply because multiple independent surveys were conducted in some countries. Therefore, in the case of samples from Argentina, there were three independent survey units, each carried out by a specific sampling team and research group. A survey "unit" was considered to be independent if it were undertaken by a particular survey team within a specific area. Analyses were conducted using GENSTAT (VSN International, 2015).

We supported these analyses with structural equation modelling (SEM; Grace, 2006) of the direct effects of two important climatic variables, mean annual temperature (MAT) and aridity on the five soil response variables (pH, C, total and available P, total N) and the three N, P, and C ratios (C:N, C:P, NP). We also included in the model geographical location (distance from the Equator), Australia (compared with elsewhere), and community type (grasslands vs. woodlands). Our SEM is based on the plausibility of an a priori model explaining the relationships among a group of variables of interest (Appendix S3). The a priori model examined the direct and indirect effects of climate, distance from the Equator, community type, and Australia versus elsewhere on our soil variables. We were particularly interested in whether the path coefficient between Australia and the variable of interest increased, reduced, or had no effect on the variable of interest while excluding the effects of distance from the Equator, community type, temperature, or aridity. Data on aridity, which expresses precipitation in relation to potential evapotranspiration, were calculated as 1-FAO aridity index using FAO's global aridity map (http://ref.data.fao.org/). Mean annual temperature data were obtained from the WorldClim database (Fick & Hijmans, 2017).

The a priori model was compared with the variance-covariance matrix of our data to enable an overall goodness-of-fit to be assessed, using the χ^2 statistic. The goodness-of-fit test estimates the likelihood of the observed data given the a priori model structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. For each of our models, those with low χ^2, high goodness-of-fit index (GFI) and high normal fit index (NFI) were interpreted as showing the best fit to our data (Appendix S3).

Finally, we tested for differences in bacterial and fungal community composition between Australia and elsewhere using one-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) on relatively abundant (>70%) taxa. Non-metric multidimensional scaling ordination (nMDS) and the Bray–Curtis dissimilarity metric were used to explore overall differences in microbial composition (at the OTU level) between Australia and elsewhere. PERMANOVA and nMDS analyses were done using PRIMER-E Ltd. & PERMANOVA version 6 (Plymouth Marine Laboratory, UK).

2.5 | Microbial network analyses

These analyses were conducted using the two datasets, including microbial data for fungi and bacteria (Global Network study and East Australia study). Bioinformatic analyses were done together for these two datasets so that OTUs of fungi and bacteria are directly comparable (see Section 2.3). Using these data, we identified ecological clusters (or "modules") of strongly associated taxa using correlation networks ("co-occurrence networks") and the following protocol. First, because of the enormous number of OTUs (synonymous with species) detected for fungi and bacteria, and to obtain a practicable network of interactions, we focused on the common species for these organisms (taxa accounting for 70% of the relative abundance

of bacterial or fungal communities). These analyses were done independently for fungi and bacteria. These bacterial and fungal taxa were then merged into a single abundance table. This resulted in a dataset with 4,192 taxa including 3,608 bacterial and 584 fungal phylotypes. We then calculated all pairwise Spearman's rank correlations (ρ) between all soil plant/animal and soil microbial/animal taxa. We focused exclusively on positive correlations because they provide information on microbial taxa that may respond similarly to environmental conditions (Barberán, Bates, O'Casamayor, & Fierer, 2012). We considered a co-occurrence to be robust if the Spearman's correlation coefficient was >0.25 and $p < 0.01$ (see a similar approach Bastian, Heymann, & Jacomy, 2009). The network was visualized with the interactive platform GEPHI (Bastian et al., 2009). Finally, we used default parameters from GEPHI to identify modules of soil taxa strongly interacting with each other.

We then computed the relative abundance of each module by averaging the standardized relative abundances (*z*-score) of the taxa that belong to each module. By standardizing our data, we ruled out any effect of merging data from bacteria and fungi. To further explore differences in microbial phylotypes (analogous to species) in dryland soils between Australia and elsewhere, we generated an ecological network of soil microbes using information from the microbial dataset (see above). We identified and calculated the relative abundance of six major ecological clusters ("modules") of phylotypes strongly co-occurring (Appendix S2).

3 | RESULTS

3.1 | Soil chemistry

Australian soils had significantly lower pH values than elsewhere ($F_{1,29} = 8.52$, $p = 0.007$; Figure 2a). Averaged over all 612 sites, we found no differences in organic C between Australia and elsewhere ($p = 0.94$), but values were 40% lower in Australian soils when we restricted our analyses to grasslands and shrublands ($F_{1,24} = 5.40$, $p = 0.029$; Figure 2b). These results were maintained even when we accounted for differences in distance from the Equator, mean annual temperature, and aridity using SEM (Figure S4.1). Total ($F_{1,22} = 4.66$, $p = 0.043$) and available ($F_{1,21} = 8.78$, $p = 0.007$) *p* were significantly lower in Australian soils (Figure 3a,b), but there were no differences in total N ($p = 0.45$, Figure 3c). Ratios of soil C:N and C:P were significantly greater in Australian soils ($F_{1,23} > 12.2$, $p < 0.002$; Figure 3d,e), but the N:P ratio did not differ ($p = 0.95$; Figure 3f). As with soil pH and organic C, our results were maintained after accounting for differences in distance from the Equator, mean annual temperature, and aridity using SEM (Figures S4.2 & S4.3).

3.2 | Microbial communities

Australian soils had lower bacterial richness (3,108 cf. 3,923; $F_{1,14} = 20.3$, $p < 0.001$) but similar fungal richness (626 cf. 549, $p = 0.19$) to soils from global drylands (Figure 4). The fungal to bacterial ratio was almost three times lower in Australian soils (ratio: 0.05) than elsewhere (ratio: 0.14; $F_{1,11} = 6.06$, $p = 0.015$; Figure 4). When we partitioned these data between woodland and grassland sites, bacterial richness and the fungal to bacterial ratio were always lower in Australia than elsewhere, but there were no community effects for fungal richness (Figure 4).

Proteobacteria ($F_{1,11} = 7.89$, $p = 0.013$) was relatively more abundant, and Actinobacteria ($F_{1,11} = 5.84$, $p = 0.056$) relatively less abundant, in Australian soils (Figure S5.1). For fungi, Australian soils had a greater relative abundance of Basidiomycota (29.3 cf. 19.5; $F_{1,11} = 15.58$, $p < 0.001$), but lower relative abundance of Glomeromycota (0.37 cf. 3.92; $F_{1,11} = 11.42$, $p = 0.002$) than elsewhere. When we correlated microbial relative abundance with soil chemical data, we found that Proteobacteria was strongly correlated with low pH and low total P (Table S6). Conversely, abundance of Gemmatimonadetes and Verrucomicrobia was positively associated with soil pH, total and available P. For fungi, Basidiomycota were relatively more abundant ($F_{1,100} = 14.07$, $p < 0.001$) and Chytridiomycota less abundant in Australian soils (Table S6).

Our microbial data clustered into six clear networks (Figure 5a). The relative abundance of modules 0 and 1 was significantly lower for Australian soils than elsewhere (Figure 5b), and positively correlated with increasing pH and soil P (Table S6.1). Modules 3 and 4,

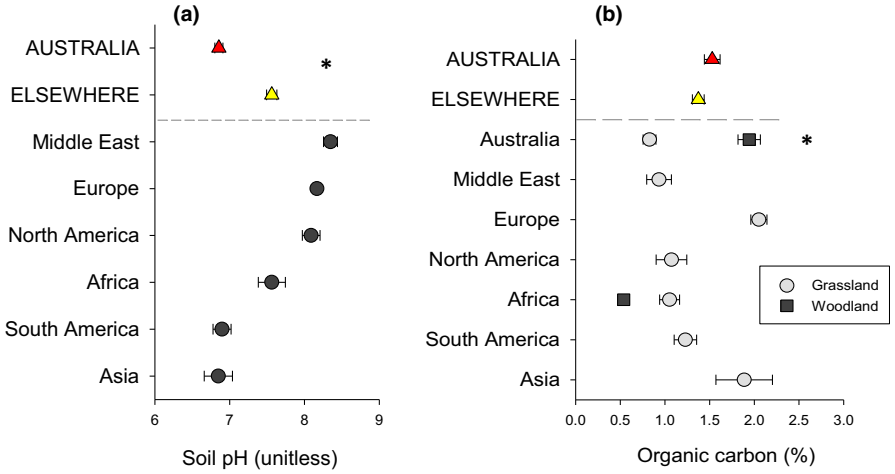

FIGURE 2 Mean (+95% CI) values of pH (a) and soil organic carbon (b) for sites in Australia and elsewhere. The upper panels show the mean values for Australia and elsewhere and the lower panels the values for different continents. *Indicates a significant different in the mean values at $p < 0.05$ (one-way ANOVA). For organic C, the lower panel separates sites into grassland and woodland communities. Woodland communities were sampled only in Australia and Africa (see Supporting Information Appendix S1) [Colour figure can be viewed at wileyonlinelibrary.com]

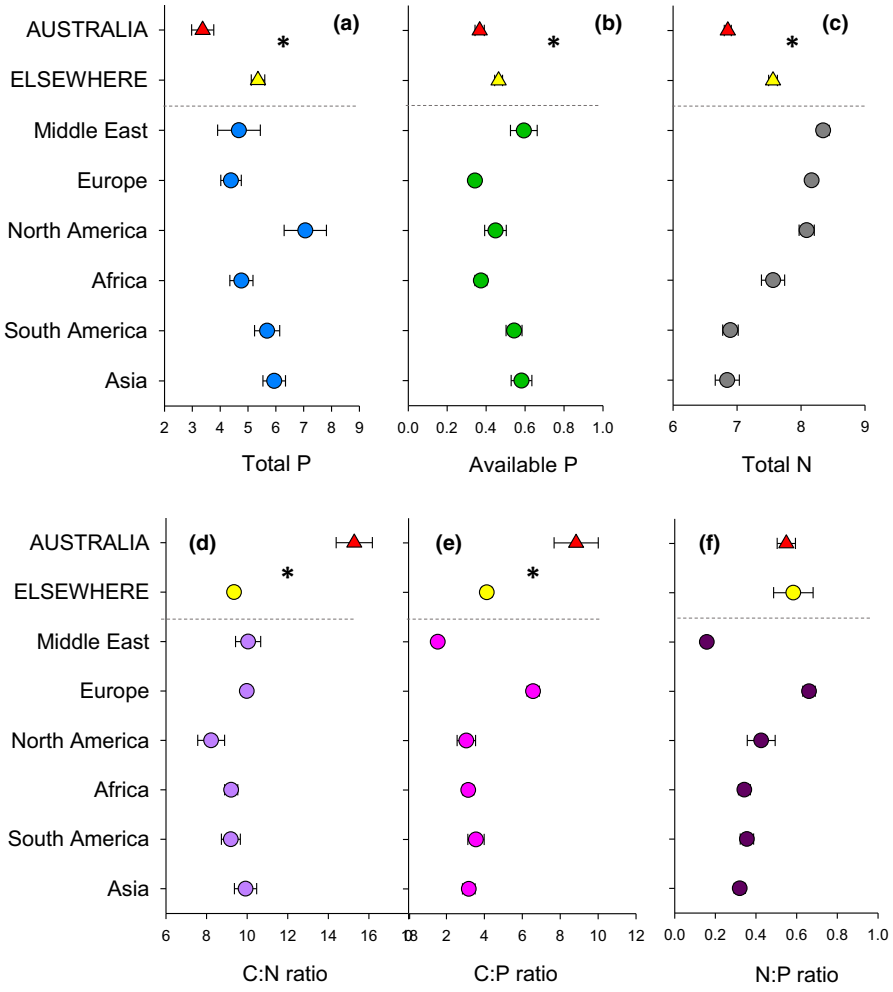

FIGURE 3 Mean (95% CI) values of (a) total P, (b) available P, (c) total N, and the (d) C:N, (e) C:P, and (f) N:P ratios for Australia and elsewhere. The upper panels show the mean values for Australia and elsewhere and the lower panels the values for different continents. *Indicates a significant different in the mean values at $p < 0.05$ (one-way ANOVA; see Supporting Information Table S2) [Colour figure can be viewed at wileyonlinelibrary.com]

however, displayed the opposite trend, being negatively correlated with pH and soil P and relatively more abundant in Australian soils (Table S6.1). The relative abundance of different bacterial and fungal phyla differed among the six modules (Figure 5c). Specific taxa comprising each module and including multiple mycorrhiza, saprobe, and pathogen species and their traits are available in Table S2.1. The two-dimensional NMDS analyses indicated clear and significant separation between both bacteria and fungi (Figure S7.1).

4 | DISCUSSION

Compared with elsewhere, two of the strongest characteristics of Australian soils were their lower soil P and pH. Australian soils are known to be among the oldest soils on Earth, a consequence of the minor effect of last glaciations on their soils (McKenzie, Jacquier, Isbell, & Brown, 2004). Long-term chronosequence studies (Vitousek et al., 2002) and studies of ancient tropical systems (Delgado-Baquerizo et al., 2016) demonstrate that older soils have extremely low levels of P. This phenomenon is also apparent in drylands, as evidenced by the classic studies of Lajtha (1988) and Lajtha and Schlesinger (1988) in the Chihuahuan Desert in the western United States. Phosphorus is largely under abiotic control, and derived mainly from subsoil and P-rich parent material (Vitousek et al., 2010). However, P can also be deposited through low-distance aeolian deposition (Das, Evan, & Lawrence, 2013). Lower total and available P is consistent with the large number of studies of plant–soil relationships in Australia (see reviews by Lambers, Raven, Shaver, & Smith, 2008; Lambers, Brundrett, Raven, & Hooper, 2010), though P levels are spatially variable (Kooyman, Laffan, & Westoby, 2016). Similarly, chronosequence studies reveal that soil pH tends to be higher in young soils and declines with soil age (Alfaro et al., 2017).

The pattern of pH change in Australia is strongly controlled by precipitation and leaching (high pH in drylands), bedrock characteristics (e.g., high over calcrete, Kooyman et al., 2016), and vegetation (low organic matter in drylands; de Caritat, Cooper, & Wilford, 2011). Soil pH, which was also lower in Australian soils, typically declines with ecosystem development due to prolonged leaching of cations in the bedrock over millennia. However, the extent to which pH changes with age depends on soil type and particularly, the nature of the parent material (Lambers, Shane, Cramer, Pearse, & Veneklaas, 2006). Although the effect of low P on terrestrial biota is clear from the Australian literature (Lambers et al., 2006, 2010; McKenzie et al., 2004), we lack a comprehensive comparison of the magnitude of the differences between Australia and other

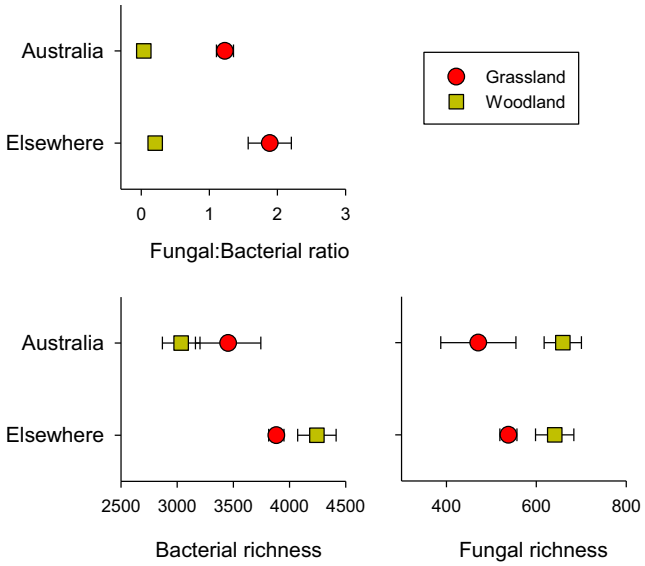

FIGURE 4 Mean (+95% CI) for the ratio of fungi to bacteria, bacterial richness and fungal richness for sites in Australia (n = 29) and elsewhere (n = 72) partitioned into grasslands and woodlands. Values differ significantly between woodland and grassland for all attributes except bacterial richness in Australia [Colour figure can be viewed at wileyonlinelibrary.com]

continents, particularly from drylands (Stafford Smith & Morton, 1990). Interestingly, many plant species from Australian drylands (e.g., family Proteaceae) have co-evolved under conditions of low soil P (Specht & Rundel, 1990) by developing proteoid or clustered root structures, or by forming close associations with N-fixing microbes or mycorrhizal fungi. These root morphologies allow plants to exude large amounts of P-mobilizing carboxylates (organic anions), making them extremely competitive in P-depleted environments (Lambers et al., 2006). Similarly, long-lived structures on plants may allow those growing on infertile soils to produce C relatively more efficiently than N, allowing Australian drylands to produce relatively high levels of biomass, even in the presence of low levels of P (Orians & Milewski, 2007). These vegetation communities, which are extremely well adapted to low P, occur widely across the Australia drylands, further supporting the notion that Australian soils have much lower levels of P than drylands elsewhere.

4.1 | Soil C levels in Australian soils are similar to soils elsewhere

Given the expectation that Australian soils should reflect characteristics of retrogressive ecosystems, we had expected their soils to have less C than global drylands elsewhere. We partially fulfilled our expectation, as soil C was lower in Australia than elsewhere, but only when forests and woodlands were excluded from our analyses. Eucalypt woodlands are a widespread vegetation community in Australian drylands and may explain the higher C:N ratio we found in Australian soils, consistent with studies of major forested biomes worldwide (Xu et al., 2013). Several reasons may support the lack of an overall difference between soils in Australia and elsewhere. First, drylands soils are naturally low in C (Plaza, Gascó, Méndez, Zaccone, & Maestre, 2018). The low capacity of dryland soils to retain C, which has recently been highlighted by Rabbi et al. (2015) is a characteristic that seems to be shared across drylands worldwide. Second, large areas of Australia's drylands support dense forests and

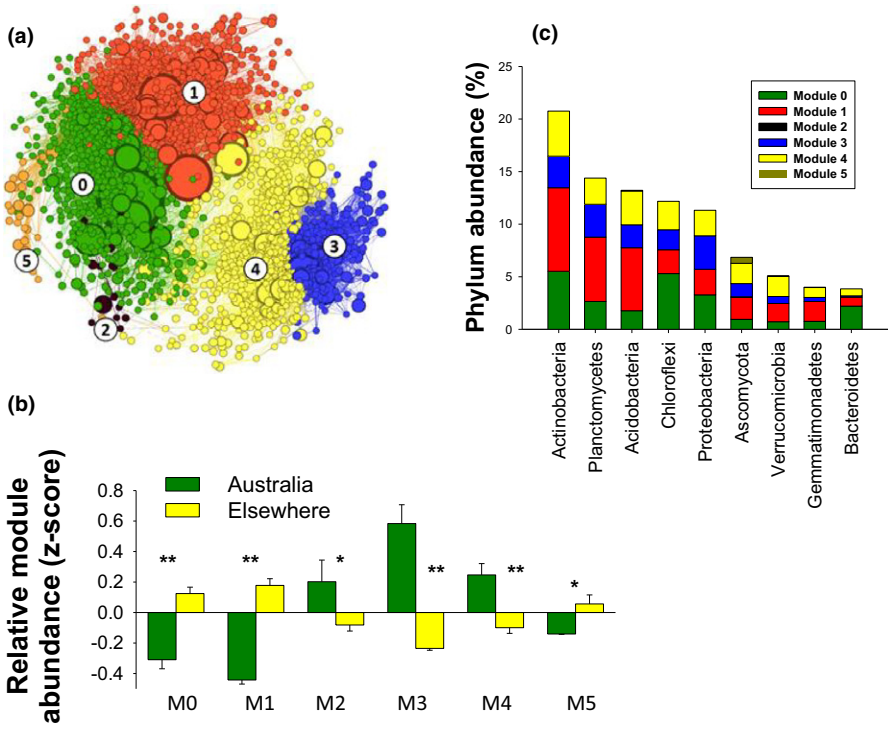

FIGURE 5 (a) Correlation network including multiple bacterial and fungal phylotypes strongly co-occurring with each other within microbial modules, (b) the relative abundance of phylotypes within the modules (*0.05 > p > 0.01, **p < 0.01), and (c) relative abundance different phyla in the six modules [Colour figure can be viewed at wileyonlinelibrary.com]

woodlands, often dominated by *Eucalyptus* spp., rather than low-stature shrubs and grasses. This may reflect the ability of these trees to access groundwater (Eberbach, 2003), releasing them from a reliance on precipitation or the redistribution of surface water. Soil C storage is known to be significantly greater beneath woody communities than grasslands (Chen, Hutley, & Eamus, 2005), a key condition that might have helped Australian soils maintain higher than expected levels of C, given their long history of development. For example, soil organic carbon stocks in northern Australian savanna woodlands are known to be almost three times greater than global averages, and similar to tropical woodlands (Chen et al., 2005). Dense woodlands and forests also have a greater capacity to develop on nutrient-poor soils (Bond, 2010). More interestingly, when we re-analysed our data excluding sites with forests, woodlands, and savannas, Australian soils had about 40% less C than dryland soils elsewhere. This is in agreement with the expectation that ecosystems in Australia might be largely retrogressive, as defined in Peltzer et al., 2010). The trajectory of soil C change during ecosystem development is nonlinear (quadratic) with time. As ecosystems develop, C production increases rapidly via microbial processes, but begins to decline in very old systems as rates of nutrient leaching exceed accumulation and old soils are no longer capable to retain organic matter, in part, a consequence of the largely leached soil cations over millennia (Vitousek et al., 2010). Interestingly, unlike total C and P, total N in Australia did not differ from elsewhere. Drylands are known to have a very active N fixer (e.g., cyanobacteria) and nitrifier microbial communities (Delgado-Baquerizo et al., 2016). Moreover, unlike P, which is linked to the bedrock availability, the major source of N is the atmosphere, explaining why Australian drylands have maintain similar levels of total N and N availability than drylands elsewhere.

4.2 | Australian soils have a unique microbial signature

Differences in aridity, soil mineralogy, and geomorphology are known to be strong drivers of surface- and subsurface-resident microbial communities (Pointing & Belnap, 2012). At the entire community composition and phylum levels, we found strong and significant differences between soils from Australia and elsewhere. For example, the NMDS plots of bacterial and fungal communities showed a significant spatial separation across locations from Australia compared with elsewhere. Also, important phyla such as Proteobacteria, the dominant bacterial taxon globally (Delgado-Baquerizo et al., 2016; Maestre et al., 2015; Ramirez, Craine, & Fierer, 2012), were relatively more abundant in Australian soils than elsewhere. A higher amount of Proteobacteria has been reported previously during long-term ecosystem development in soils from the Southern Hemisphere (Jangid, Whitman, Condron, Turner, & Williams, 2013).

Some of these general patterns might be related to the low P and pH that characterize soils from Australia compared with elsewhere. For example, soil pH values from our soils were also negatively correlated with the relative abundance of Basidiomycota (Table S6.1), a group of fungi found typically in acidic forested soils, but positively correlated with Actibobacteria and Gemmatimonadetes, and the fungal phyla Glomeromycota and Chytridiomycota (Table S6.1). Proteobacteria, particularly γ-Proteobacteria, have been shown to be important drivers of soil functioning in both field and microcosm studies from Australian soils (Delgado-Baquerizo et al., 2017). Differences in soil P and pH are known to be strong drivers of microbial communities in terrestrial ecosystems (Lauber et al., 2009), and there is considerable evidence that these differences are linked to the assembly of microbial communities in Australia (Lambers et al., 2008).

Our network analyses further indicated that some dominant taxa (accounting for >70% relative abundance of all taxa) co-occur in Australia, but are not as abundant elsewhere. Our results suggest, therefore, that the specific soil properties from Australian soils likely promote particular ecological clusters of strongly co-occurring microbial species, clusters that are different elsewhere. For instance, soils from Australia have very low relative abundance of modules 0 and 1, which however, are more abundant elsewhere (Figure 5). These differences could have important implications for soil functioning, given the role of some of microbial taxa comprising the modules, on processes such as the production of enzymes to decompose soil organic matter (i.e., starch and cellulose degradation), the release C for maintaining structural components, or the degradation of chitin, to name a few (Trivedi, Delgado-Baquerizo, Anderson, & Singh, 2016). Also, soil pH (Figure 6) and soil P (Table S6.1) seem to play an important role in explaining some of the taxa included in these modules. For example, the relative abundance of modules 0 and 1, whose members were significantly less abundant in Australian soils (Figure 5b) was positively correlated with soil pH and included members of genera *Afifella*, *Balneimonas*, *DA101*, *Lamia*, *Kaistobacter*, and *Microlunatus* (module 0), and *Gemmata*, *Lentzea*, *Rubrobacter*, *Rhodoplanes*, *Mesorhizobium*, *Opitutus*, *Nocardioides*, and *Steroidobacter* (module 1), which have been reported to be found in high pH soils across the globe (Delgado-Baquerizo et al., 2018), and that show relatively low abundant in Australian soils. In contrast, clusters 3 and 4 contain members of the family Bradyrhizobiaceae and genera *Candidatus Solibacter*, *Mycobacterium*, *Rhodoplanes*, and *Phenylobacterium* (module 3), *Methylobacterium* and *Nocardioides* (module 4), which have been reported from low pH soils globally (Delgado-Baquerizo et al., 2018), and that could be relatively more abundant in Australian soils. Although taxa related to soil P are more poorly described at the global scale, taxa from family Pseudonocardiaceae (Delgado-Baquerizo et al., 2018) and order Burkholderiales (Baas et al., 2016) in module 3 might prefer the low soil P conditions in Australia compared with elsewhere.

5 | CONCLUSIONS

Together, our study provides evidence that Australian dryland soils are different from drylands elsewhere in terms of their main properties and microbial communities. The signature of Australian soils was consistent with that of highly weathered landscapes (Vitousek et al.,

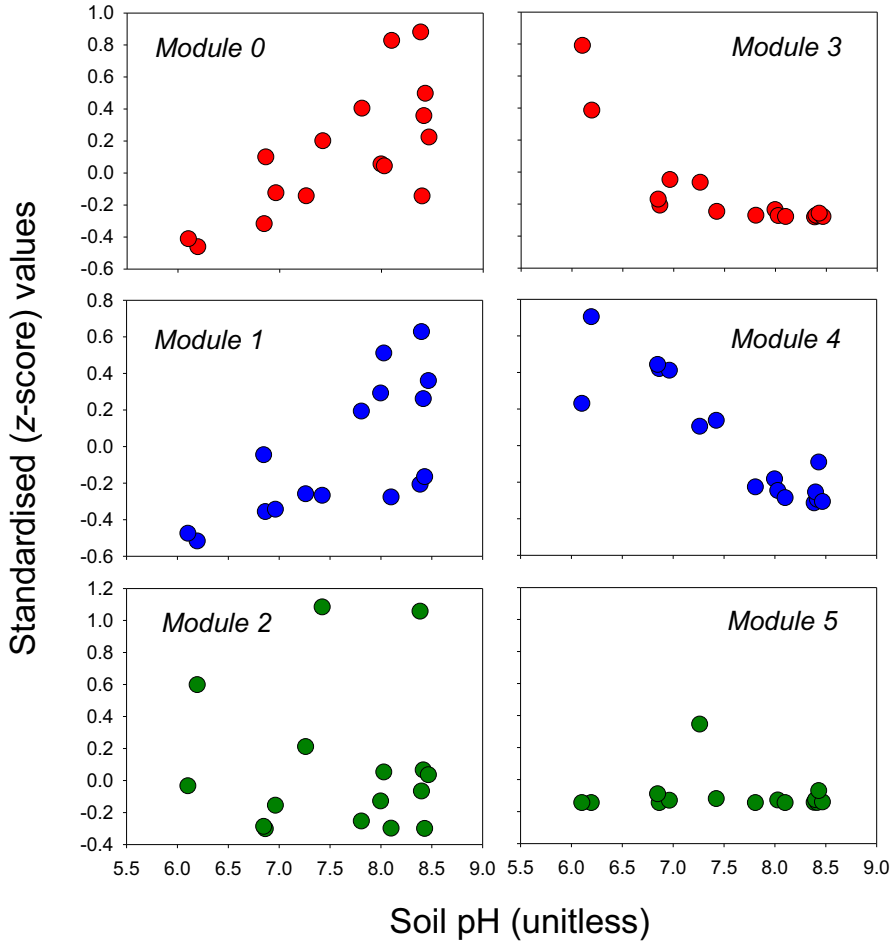

FIGURE 6 Relationships between soil pH and the standardized (z-transformed) relative abundance of microbial taxa for the six microbial modules [Colour figure can be viewed at wileyonlinelibrary.com]

2010; Wardle et al., 2014) low in pH, lower contents of total and available P, and generally higher C:N and C:P ratios, a greater relative proportion of Proteobacteria and lower abundance of Actinobacteria and, more importantly, higher relative abundance of specific microbial assemblies linked to low soil pH. It is critically important that we understand how Australian soils differ from those of other drylands because it will shield us against unrealistic expectations about the extent to which current land management practices such as conservation farming or low risk stocking might lead to better environmental outcomes for them. Second, knowledge about Australian soils will help to explain why, for example, Australian ecosystems and their biota behave in idiosyncratic ways; adding to the growing body of knowledge and attempts to evaluate whether Australian dryland soils are indeed resource poor, or whether this notion is an artificial construct arising from a Eurocentric view of ecosystem productivity. This knowledge will ultimately provide us with a greater understanding of the mechanisms underpinning the processes shaping the Australian environment and its biota.

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DATA ACCESSIBILITY

Supporting information is included in this manuscript. The data have been lodged with Figshare https://figshare.com/s/1fad93838beef73175e8.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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