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Plant attributes explain the distribution of soil microbial communities in two contrasting regions of the globe

Manuel Delgado-Baquerizo[1,2], Ellen L. Fry[3], David J. Eldridge[4], Franciska T. de Vries[3], Peter Manning[5], Kelly Hamonts[6], Jens Kattge[7], Gerhard Boenisch[7], Brajesh K. Singh[6,8] and Richard D. Bardgett[3]

[1]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA; [2]Departamento de Biología, Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, c/Tulipán s/n, 28933, Móstoles, Spain; [3]School of Earth and Environmental Sciences, The University of Manchester, Michael Smith Building, Oxford Road, Manchester, M13 9PT, UK; [4]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; [5]Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, Frankfurt, Germany; [6]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia; [7]Max Planck Institute for Biogeochemistry, PO Box 10 01 64, Jena 07701, Germany; [8]Global Centre for Land-Based Innovation, Western Sydney University, Penrith South DC, NSW 2751, Australia

Authors for correspondence:
Manuel Delgado-Baquerizo
Tel: +13037355185
Email: m.delgadobaquerizo@gmail.com

Richard D. Bardgett
Tel: +44 0161 2755571
Email: richard.bardgett@manchester.ac.uk

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Summary

- We lack strong empirical evidence for links between plant attributes (plant community attributes and functional traits) and the distribution of soil microbial communities at large spatial scales.
- Using datasets from two contrasting regions and ecosystem types in Australia and England, we report that aboveground plant community attributes, such as diversity (species richness) and cover, and functional traits can predict a unique portion of the variation in the diversity (number of phylotypes) and community composition of soil bacteria and fungi that cannot be explained by soil abiotic properties and climate. We further identify the relative importance and evaluate the potential direct and indirect effects of climate, soil properties and plant attributes in regulating the diversity and community composition of soil microbial communities.
- Finally, we deliver a list of examples of common taxa from Australia and England that are strongly related to specific plant traits, such as specific leaf area index, leaf nitrogen and nitrogen fixation.
- Together, our work provides new evidence that plant attributes, especially plant functional traits, can predict the distribution of soil microbial communities at the regional scale and across two hemispheres.

Introduction

Soil microbial communities play important roles in driving multiple ecosystem functions and services, including climate regulation, nutrient cycling, water regulation, and food and fibre production (Bardgett & van der Putten, 2014; Delgado-Baquerizo *et al.*, 2017). Previous studies have provided evidence that abiotic factors such as climate (Maestre *et al.*, 2015; Zhou *et al.*, 2016) and soil chemical properties (pH, soil carbon (C) and nutrients; Lauber *et al.*, 2009; Tedersoo *et al.*, 2014; Maestre *et al.*, 2015) are the main predictors of the distribution of soil microbial communities across the globe. Much less is known, however, about the role of plant attributes, including community-level attributes such as diversity and cover, and functional traits in regulating the distribution of soil microbial communities at regional scales (i.e. hundreds of kilometres). Identifying the relative importance of plant attributes in predicting the distribution of soil microbial communities is of paramount importance, as plant communities are highly sensitive to climate, nitrogen (N) enrichment, and land-use intensification (Allan *et al.*, 2015; Le Bagousse-Pinguet *et al.*, 2017), and resulting shifts in vegetation might have cascading effects on the diversity and functioning of soil microbial communities (Deraison *et al.*, 2015; García-Palacios *et al.*, 2016; Le Bagousse-Pinguet *et al.*, 2017).

The identity of plant genotypes or lichen species, major biological components of cold and warm deserts, has recently been highlighted as a major predictor of the distribution of soil bacteria at the local scale (Leff *et al.*, 2017; Liu *et al.*, 2017). Much less is known, however, about the role of other plant attributes, such as plant diversity (number of species) and plant cover, and plant functional traits as predictors of the diversity (number of phylotypes) and community composition of soil bacterial and fungal communities. While empirical evidence is lacking, the conceptual links among plant attributes and microbial community composition are reasonably well established (Hooper *et al.*, 2000;

Wardle *et al.*, 2004; Lavorel, 2013; Bardgett, 2017). Plant community attributes and functional traits can directly affect soil microbes by altering the quality (which can be represented by measures such as specific leaf area (SLA) and tissue nutrient content; Cornelissen *et al.*, 2003) and quantity of resource inputs via litter and detritus (which can be represented via measures such as plant biomass and canopy cover). Both the quantity and quality of resources have been demonstrated to regulate the diversity and community composition of soil microbial communities (Hooper *et al.*, 2000; Wardle *et al.*, 2004; Schneider *et al.*, 2012; Zhou *et al.*, 2015). Moreover, microcosm studies have demonstrated that changes in litter quality during decomposition strongly influence the composition and diversity of soil microbial communities (Schneider *et al.*, 2012; Zhou *et al.*, 2015). Plant diversity could also alter the distribution of microbial communities by promoting a greater diversity of litter types, promoting niche differentiation and resource partitioning (Wardle *et al.*, 2004; Gould *et al.*, 2016), and facilitating the existence of multiple mutualism (e.g. mycorrhizae and rhizobia) and antagonistic (e.g. plant–pathogen) interactions with soil microbes. Other effects on plant community attributes and functional traits of soil microbes include changes in habitat conditions (e.g. soil structure, shading, water regulation) and soil chemistry (e.g. root exudation and nutrient uptake), which are both known to strongly affect the structure and function of microbial communities (Bardgett, 2017; Le Bagousse-Pinguet *et al.*, 2017).

Plant traits have been used to predict broad-scale shifts in the biomass of fungi and bacteria at the individual plant (Orwin, 2010), community (Legay *et al.*, 2014) and regional scales (hundreds of kilometres; de Vries *et al.*, 2012; Grigulis *et al.*, 2013). Further, plant functional traits are also known to influence the abundance of particular groups of soil microorganisms, such as mycorrhizal fungi (e.g. López-García *et al.*, 2014, 2017), and specific groups involved in N cycling, such as archaeal ammonia oxidizers (Moreau *et al.*, 2015; Thion *et al.*, 2016). However, the role of plant functional traits in regulating the diversity (number of phylotypes; richness) and community composition (relative abundance of phylotypes) of soil bacteria and fungi remains relatively poorly understood. Recent studies that have evaluated the link between plant functional traits and the taxonomic diversity of soil microbial communities at a local scale have revealed no clear relationships, despite strong effects of plant species identity (Barberán *et al.*, 2015; Fry *et al.*, 2017; Leff *et al.*, 2018). However, whether plant traits can explain variation in microbial diversity and composition at larger spatial scales, and across regions and ecosystem types at the global scale, remains largely unexplored. This is despite the suggestion that the relationship between plant traits and the diversity and community composition of soil microbial communities is likely to be strongest at regional scales (hundreds of kilometres) where taxonomic and trait diversity are considerable, and the effect of plant attributes on microbial communities could be statistically detected (Wardle, 2005). We posit, therefore, that regional-scale variation in plant traits will be strongly correlated with changes in diversity and community composition of bacterial and fungal communities.

Here, we evaluate the role of plant attributes, including plant community attributes (plant diversity and cover), and functional traits, in predicting the distribution of community composition and diversity of soil bacteria and fungi in two contrasting ecosystem types located in two different hemispheres. Given the strong theoretical link between plant attributes and soil microbial communities, we hypothesized that plant attributes would explain additional variation in microbial community composition and diversity that is unaccounted for by key drivers such as climate or soil properties. Such a hypothesis should be valid across regions differing markedly in climate, vegetation and soils. As such, we used two contrasting regional datasets (hundreds of kilometres) from Australia and England, which included natural forests and a range of grassland types (Supporting Information Fig. S1; de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2016b). The English dataset has previously been used to identify the role of plant traits in predicting the biomass of fungi and bacteria and their relative abundance (de Vries *et al.*, 2012), but the role of plant attributes as predictors of microbial community composition and diversity remain unaddressed. Our intention was not to merge the two datasets, which differed in their sampling design, vegetation, soil and climatic conditions, and plant trait information, but to test our hypotheses across two regions with markedly different vegetation, climate and soils. In doing so, we provide a general and robust test of the importance of plant traits for explaining regional-scale variation in the composition and diversity of soil microbial communities across a range of different ecosystems.

Materials and Methods

Study sites

We used two separate regional datasets (Fig. S1). The first included microhabitat-level information on three distinct vegetation classes microhabitat (grasses, N-fixing shrubs and trees) across 20 natural forest locations from eastern Australia (Fig. S1; Delgado-Baquerizo *et al.*, 2016b). Locations in Australia are distributed across a >1000 km environmental transect (Fig. S1). These sites were originally chosen to represent a wide range of aridity conditions, from arid to humid forest communities, and with perennial vegetation cover ranging from 18 to 98%. These ecosystems consistently had independent patches of vegetation dominated by trees (*Eucalyptus* spp.), N-fixing shrubs (*Acacia* spp.), and perennial grasses (*Rhytidosperma* spp.). Total annual precipitation and mean temperature ranged from 280 to 1167 mm and from 12.8 to 17.5°C respectively. The second dataset was from England and included plot-level information from 180 grasslands varying in management intensity (unimproved, semi-improved and improved grasslands) and covering the main acid, calcicolous, mesotrophic, and wet grassland types of the UK (see de Vries *et al.*, 2012; Manning *et al.*, 2015). Locations in England spanned all major grassland regions of the country, distributed across a north to south transect of *c.* 500 km^2. Across all grasslands, total annual precipitation and mean temperature ranged from 573 to 1355 mm and from 6.3 to 10.2°C respectively.

Soil sampling

Soil samples from the top *c.* 7 cm were collected in Australia and England as explained in Methods S1. In brief, in Australia, three soil cores were collected under the three most common plant functional groups' microhabitat: grasses (*Rhytidosperma* genus, including species *Rhytidosperma caespitosum*, *Rhytidosperma pilosum* or *Rhytidosperma racemosum*), N-fixing shrubs (*Acacia* genus, including species *Acacia dealbata*, *Acacia decora*, *Acacia genistifolia*, *Acacia implexa* or *Acacia wilhelmiana*) and trees (*Eucalyptus* genus, including species *Eucalyptus largiflorens*, *Eucalyptus microcarpa*, *Eucalyptus populnea*, *Eucalyptus rossii*, *Eucalyptus socialis* or *Eucalyptus tereticornis*). The same genus of these plant taxa was present across all plots. A total of 60 soil samples (20 sites × 3 microhabitats) were collected. Sampling was conducted in March (2014). In England, soil samples were collected June–July 2005 from 180 sites covering the main grassland habitat classifications in the UK, namely acid, calcicolous, mesotrophic, and wet grasslands (de Vries *et al.*, 2012; Manning *et al.*, 2015). The survey covered a wide range of grassland communities within each habitat type and included a total of 256 grassland plant species, confirming the representative nature of the national survey (Rodwell, 1992). In terms of dominant graminoid species, unimproved acid grasslands were typically dominated by *Festuca ovina*, *Deschampsia flexuosa* and *Agrostis capillaris*, calcicolous grasslands were typically dominated by *Festuca rubra*, *Festuca ovina*, *Bromus erectus* and *Carex flacca*; mesotrophic grasslands were typically dominated by *Agrostis canina*, *Festuca rubra* and *Poa trivialis*; and wet grasslands were dominated by *Carex distichia* and *Molinia caerulea*. Semi-improved grasslands in all four habitat types of grasslands became increasingly dominated by *Lolium perenne*, and improved grasslands also strongly promoted *Holcus lanatus* in acid and mestrophic grasslands, *Poa trivialis* in calcicolous grasslands and mesotrophic grasslands, and *Agrostis stolonifera* in wet grasslands.

Climate and soil properties

In all cases, we obtained information on mean annual temperature and aridity index (positively related to precipitation) (1 km) for the surveyed sites from the WorldClim database (www.worldclim.org). Moreover, we obtained information on total soil organic C, total N and phosphorus (P) and pH as explained in Methods S1.

Plant attributes

The Australian and English samples contain shared information on five plant attributes: diversity (species richness), percentage plant cover, SLA, leaf N content and N fixation (proportion of N fixing plants in England and presence of *Acacia* species – the only N-fixer microhabitat – in the Australian dataset). In addition, the two datasets include a subset of distinct plant functional traits, such as leaf C and P, plant height, canopy width and canopy height in the Australian dataset and leaf dry matter content (LDMC) and relative growth rate (RGR) in the English dataset. Both datasets were originally independently generated and with each study designed to explicitly include variables that were hypothesized to account for variation in soil properties and functions within their respective regions. For example, plant functional traits such as plant height, canopy width and canopy height may explain differences in microbial communities in forests from Australia, but not in English grasslands, where they vary little. Detailed information on how plant traits were measured in these two datasets is available in Methods S1.

Soil microbial community

Soil DNA was extracted from both sets of soil samples using the Powersoil® DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA). In England, 161 from 180 samples were included in further analyses due to DNA amplification problems. Amplicons targeting the bacterial 16S rRNA gene and fungal ITS2 region were sequenced using the Illumina MiSeq platform and the 341F/805R (bacteria) and FITS7/ITS4 (fungi) primer sets (Methods S1). Bioinformatic analyses were conducted using UPARSE and MOTHUR (Methods S1). Operational taxonomic units (OTUs) were picked at 97% sequence similarity in both cases. The resulting OTU abundance tables were rarefied. As these analyses were done together for the Australian and English datasets, OTU identities are directly comparable between them.

Statistical analyses

All statistical analyses were independently done for each dataset (Australia and England) and microbial group (bacteria or fungi). First, we evaluated the relationship between bacterial and fungal community dissimilarity with the dissimilarity of plant attributes (plant cover, diversity and functional traits) across plots. To do this, we calculated Bray–Curtis dissimilarities to generate independent community distance matrices at the OTU level for bacterial and fungal communities in the Australian and English datasets. Similarly, the Euclidean distance was used to independently create a matrix of distance for plant drivers for the Australian and English datasets. We then correlated the matrix of plant community attributes and traits distances to the dissimilarity matrix of bacteria and fungi in Australia and England using Mantel test correlations.

Second, we used two independent approaches to assess whether plant attributes can predict a unique portion of the variation of soil microbial diversity and community composition. We first conducted variation partitioning (R package VEGAN; Oksanen *et al.*, 2015) as an exploratory analysis to identify whether plant attributes (plant functional traits, and plant diversity and cover) explain a unique portion of the variation in microbial diversity and composition, after accounting for key microbial drivers such as location (latitude and longitude), climate (aridity index and mean annual temperature) and soil properties (total C, N and P and pH; Table 1).

We then used a multi-model inference approach based on information theory and nonparametric distance-based linear regressions (DISTLM; McArdle & Anderson, 2001) to evaluate

Table 1 Complete list of predictors used in this study

Group of predictors	Variable	Acronym	Value range		Units
			Australia	England	
Location	Latitude	Lat	−34.7 to −33.3	50.7–54.6	Decimal degrees
	Longitude	Lon	145.7–151.1	−4.4 to +0.9	Decimal degrees
Climate	Aridity index	AI	0.3–0.9	0.9–2.4	Unitless
	Mean annual temperature	MAT	12.8–17.5	6.3–10.2	°C
Soil properties	Soil C	C	1.3–12.3	1.4–12.8	%
	Soil N	N	0.1–0.6	0.2–1.1	%
	Soil P	P	3.1×10^{-3}–6.0×10^{-2}	1.6×10^{-2}–0.2	%
	pH	pH	4.8–8.9	4.1–7.8	Unitless
Plant community-level traits	Plant richness	PDiv	11–41	2–36	Number of species
	Plant cover	PCov	18.3–98.3	78.3–249.5	%
Plant functional traits	Specific leaf area	SLA	6.1–127.1	5.8–16.3	$cm^2\ g^{-1}$
	Leaf N	LN	0.5–2.9	1.7–3.5	%
	N fixation	NFix	0–1	0–0.42	Australia: presence/absence N fixers England: proportion of N fixers (0–1)
	Leaf C	LC	0.5–2.9	—	%
	Leaf P	LP	2.1×10^{-2}–0.2	—	%
	Plant height	PHeight	0.2–22.0	—	m
	Canopy width	CWidth	0.1–21.0	—	m
	Canopy height	CHeight	6.0×10^{-2}–7.0	—	m
	Leaf dry matter content	LDMC	—	14.9–34.8	$g\ g^{-1}$
	Relative growth rate	RGR	—	0.1–0.3	$g\ g^{-1}\ d^{-1}$

whether plant attributes (plant cover, diversity and traits) explained a unique proportion of the variation in bacterial and fungal diversity (richness; number of phylotypes) and community composition (at the OTU level) after accounting for other important microbial drivers such as soil properties (total C, N and P and pH) and climate (aridity index and mean annual temperature). Location (latitude and longitude; Table 1) was included in all models to account for spatial autocorrelation. The Euclidean and Bray–Curtis distances were used for microbial diversity and composition respectively in these analyses. We carried out these analyses using the PERMANOVA+ for PRIMER statistical package. We ranked all the models that could be generated with different combinations of our independent variables according to the second-order Akaike information criterion (AIC) and considered a $\Delta AIC > 2$ threshold to differentiate between two substantially different models (Burnham & Anderson, 2002). Differences < 2 in AIC between alternative models indicate that they do not differ significantly in their explanatory power. The full statistical reasoning for this approach can be found elsewhere (e.g. Zuur *et al.*, 2009). We then selected the best of those models, including all parameters in Table 1, and compared the AIC of the best model with competing models containing: all parameters in model A, but plant functional traits (model B); included all parameters in model A, but plant community attributes (cover and PDiv) (model C); or all parameters in model A, but plant functional traits and community attributes (model D) (Table 2).

Third, we conducted two independent analyses to assess the importance of plant attributes, soil properties, and climate as predictors of soil microbial community composition and diversity. We first used random forest analyses (Archer, 2016), as explained in Delgado-Baquerizo *et al.* (2016a), to identify the most important predictors (Table 1) of bacterial and fungal diversity and community composition. For simplicity, and given that, at this point, we were interested in the responses of the entire microbial community composition rather than on single taxa, in the case of bacterial and fungal community composition, we conducted these analyses on the axes of a nonmetric multidimensional scaling conducted on bacterial and fungal composition data at the lowest taxonomic rank (Fig. S3; stress, 0.08 and 0.12 respectively). We then used structural equation modelling (SEM) to build a system-level understanding of the major direct and indirect effects of climate, soil properties and plant attributes on the composition and diversity of soil bacteria and fungi (an *a priori* model is available in Fig. S2, and see Methods S1 for details). For simplicity, and due to the data constraints of fitting structural equation models with many paths, we only included in these models those variables that were identified as major predictors of the diversity and composition of bacteria from the best models of our distance-based multi-model approach. Importantly, in general, similar variables were identified as important predictors in our random forest results (see the Linking plant attributes and microbial community composition section). Therefore, although we used the same *a priori* model in all cases (Fig. S2), structural equation models conducted for the different datasets contain different predictors and were constructed independently. The only exception to this was latitude and longitude, which were included in all the models to account for spatial autocorrelation in our models, and to represent other variables that might co-vary with latitude and longitude but which are not included in our analyses. Analyses were performed independently for each dataset.

Table 2 Best-fitting model predicting the distribution of microbial PDiv and composition (bacteria and fungi)

Database	Microbial	Model	Climate	Soil	Plant predictors	R^2	AIC	ΔAIC
Australia	Bacterial composition	A	AI	pH	CHeight	0.380	451.20	0
		B	AI	pH		0.334	453.44	2.24
		C	AI	pH	CHeight	0.380	451.20	0.00
		D	AI	pH		0.334	453.44	2.24
	Bacterial richness	A	MAT	C + P	PCov + LP	0.462	283.44	0
		B	MAT	C + P	PCov	0.441	283.73	0.29
		C	AI			0.357	286.09	2.65
		D	AI			0.357	286.09	2.65
	Fungal composition	A	AI		CWidth	0.172	497.37	
		B	AI	pH		0.170	497.55	0.18
		C	AI		CWidth	0.172	497.37	0.00
		D	AI	pH		0.170	497.55	0.18
	Fungal richness	A		C + N + pH	PCov + PHeight + CWidth	0.222	218.51	
		B		C + N + pH	PCov	0.159	219.13	0.62
		C		pH		0.049	220.82	2.31
		D		pH		0.049	220.82	2.31
England	Bacterial composition	A	AI + MAT	C + N + pH	PDiv + LN + LDMC	0.412	1150.00	
		B	AI + MAT	C + N + P + pH	PDiv	0.394	1152.60	2.60
		C	AI + MAT	C + N + pH	RGR + LN + LDMC	0.406	1151.70	1.70
		D	AI + MAT	C + N + P + pH		0.377	1155.10	5.10
	Bacterial richness	A	AI + MAT	C + N + pH	PDiv + RGR + LN + LDMC + NFix	0.485	647.88	
		B	AI + MAT	C + N + P + pH		0.360	673.52	25.64
		C	AI + MAT	C + N + pH	LDMC + NFix	0.459	649.27	1.39
		D	AI + MAT	C + N + P + pH		0.360	673.52	25.64
	Fungal composition	A	AI	C + pH	PDiv + LN	0.233	1269.70	
		B	AI	C + pH	PDiv	0.237	1270.90	1.20
		C	AI	C + pH	RGR + LN + LDMC	0.237	1271.10	1.40
		D	AI	C + pH		0.215	1273.50	3.80
	Fungal richness	A	AI	C + pH	PCov + PDiv + RGR + SLA	0.282	802.24	
		B	AI	C + pH	PCov + PDiv	0.250	805.05	2.81
		C	AI	C + pH	RGR + SLA	0.240	807.25	5.01
		D	AI	C + pH		0.210	809.37	7.13

Model A includes all parameters in Table 1. Model B includes all parameters in model A except plant functional traits. Model C includes all parameters in model A except plant community attributes (cover and PDiv). Model D includes all parameters in model A except plant functional traits and community attributes. Location (latitude and longitude) inclusion was forced in all models to account for spatial autocorrelation. Models are ranked by Akaike information criterion (AIC). AIC measures the relative goodness of fit of a given model; the lower its value, the more likely the model is to be correct. ΔAIC is the difference between the AIC of each model and that of the best model. See Table 1, for the acronyms of the variables included in this table.

With a good model fit, we were then free to interpret the path coefficients of the model and their associated *P* values. In the case of England, we accounted for any effect from management practices on our results by repeating the SEM analyses using the residuals from a one-way ANOVA in which management practice (managed, intermediate intensity managed and intensively managed) was treated as a fixed factor and bacterial diversity or composition as a response variable (i.e. residuals of bacterial diversity or composition). This results in a more conservative test of plant effects on microbial communities as functional traits are known to co-vary with management (see de Vries *et al.*, 2012).

Finally, we used random forest analysis (Archer, 2016) to identify the microbial phylotypes that were most strongly associated with a particular plant trait. We focused on shared dominant taxa (> 50 reads across all samples) between Australia and England for these analyses. Moreover, we focused on shared plant community attributes (cover and diversity) and functional traits (SLA, leaf N and N fixation), and microbial phylotypes for the Australian and English datasets. Analyses were conducted independently for the Australian and English datasets and for fungal and bacterial communities. For both datasets, we first identified the top unique and shared (significance, $P < 0.05$) microbial phylotypes accounting for the variation of particular plant traits (i.e. those microbial phylotypes that are selected from the random forest model as important predictors of each plant trait). The reserved approach enabled us to identify particular phylotypes that consistently characterize particular plant attributes in both Australia and England. We then conducted Spearman correlations among shared phylotypes in Australia and England with particular plant traits for which these phylotypes are good predictors. The major goal for these analyses is to provide a list of examples that could make the basis of experimental studies to look at the links between particular microbial phylotypes and plant attributes in more detail.

Data accessibility

Data associated with this paper has been deposited in figshare: http://figshare.com/s/700c8ec31c66bab57553 (10.6084/m9.figshare.6133889).

Results

Microbial and plant attributes in Australia and England

The Australian and English datasets varied markedly in fungal and bacterial community composition (Figs S3, S4). Proteobacteria and Acidobacteria were the dominant bacterial phyla in England, while Actinobacteria was the dominant phylum in Australia (Fig. S4). In both datasets, the fungal community was dominated by Ascomycota (Fig. S4), with Zygomycota and Basidiomycota being the second most abundant fungal phyla in England and Australia respectively. Fungal diversity was greater in the Australian dataset, but bacterial diversity did not differ between datasets (Fig. S3). See Methods S1 for details on the statistical analyses conducted to evaluate these general patterns in microbial diversity and composition. In both datasets, there was considerable heterogeneity in soil properties and microbial communities. For example, in Australia, pH and soil C ranged from 4.8 to 8.9 and 1.3 to 12.3% respectively (Table 1). Similarly, bacterial and fungal diversity ranged from 955 to 2833 and 489 to 813 phylotypes respectively. In England, soil pH and C ranged from 4.1 to 7.8 and 1.4 to 12.8% respectively (Table 1), and bacterial and fungal diverity from 820 to 3329 and 243 to 763 phylotypes respectively.

Plant attributes varied greatly among plots in both datasets. For example, plant cover ranged from 78.3 to 249.5% (i.e. due to multiple vegetation layers in grassland communities) in England and from 18.3 to 98.3% in Australia. Plant species diversity ranged from two to 36 species across grassland plots in England and from 11 to 41 species in forest plots in Australia. Values for community-weighted mean (CWM) SLA ranged from 5.8 to 16.3 $cm^2\ g^{-1}$ in England and from 6.1 to 127.1 $cm^2\ g^{-1}$ in Australia, and CWM leaf N ranged from 1.7 to 3.5% in England and from 0.5 to 2.9% in Australia. The percentage of N fixers in England ranged from 0 to 42.4% of total cover (presence of *Acacia* spp. microhabitats characterized the only N fixer in the Australian dataset; Table 1).

Linking plant attributes and microbial community composition

The Euclidean matrix of distance for plant attributes was positively and significantly related to the Bray–Curtis matrix of distance, including the community composition of soil bacteria and fungi in the Australian and English datasets (via the Mantel test) (Fig. 1), indicating that certain plant community attributes/traits and microbial taxa tend to co-occur in nature. Variation partitioning modelling suggested that, in general, plant attributes explained unique portions of the variation in bacterial and fungal communities from both Australia and England (Figs 2, S5, S6; Table S1). Shared variation explaining microbial community composition and diversity among different predictors (e.g. climate and location, soil properties and plant attributes) cannot be attributed to any of those groups of predictors in particular. Because of this, we only compared the unique portion of the variation in microbial communities explained in a singular manner by either climate and location, soil properties or plant attributes.

Moreover, using distance-based multi-model inference and variation partitioning modelling, we found that plant attributes explained a unique proportion of the variation in soil microbial communities that was unaccounted for by soil properties, climate or location (Table 2). Removal of all plant attributes from these models always resulted in poorer model fit in all cases ($\Delta AIC > 2.00$). In Australia, our best-fitting models selected canopy height and plant cover and leaf P as the major predictors of bacterial community composition and diversity respectively

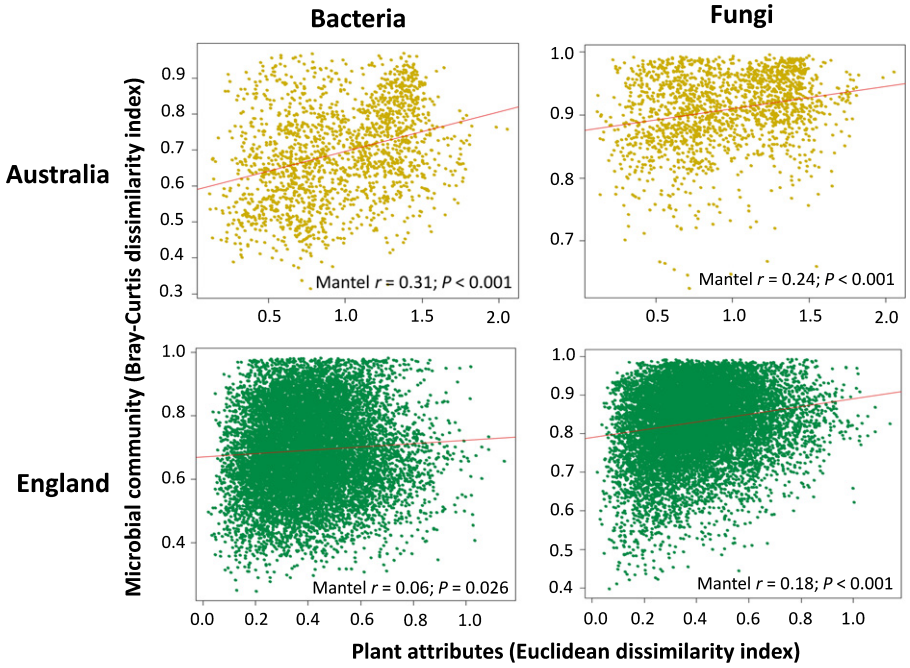

Fig. 1 Relationship between the matrix of dissimilarity from multiple plant traits, cover and diversity (Euclidean distance) and the beta diversity of bacteria and fungi (community composition dissimilarity based on Bray–Curtis distance) for the Australia ($n = 60$) and England ($n = c.\ 160$) datasets. The solid lines represent the fitted linear regressions.

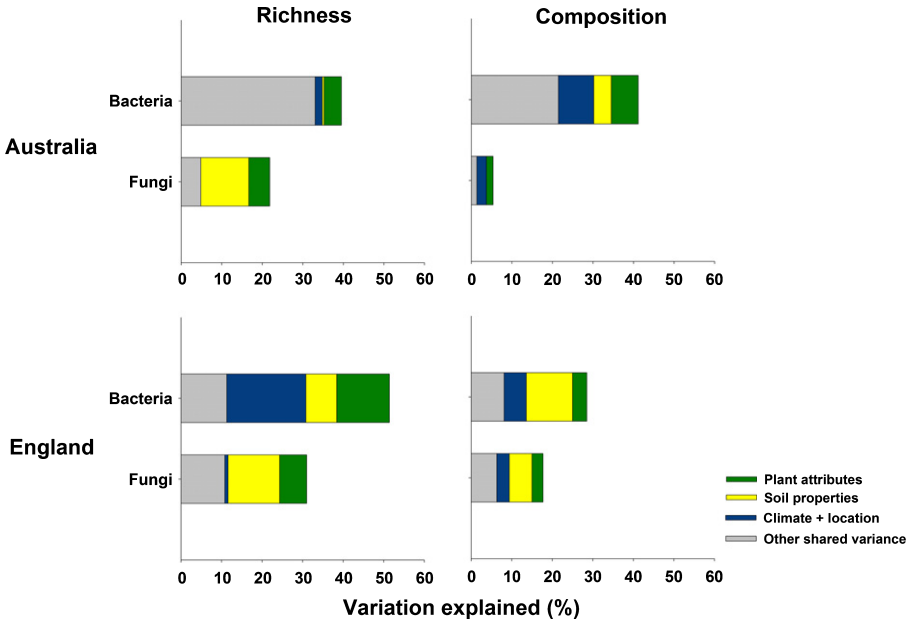

Fig. 2 Relative contribution of the different predictors used to model bacterial and fungal composition and diversity. Panels represent results from variation partitioning modelling aiming to identify the percentage variance of bacterial and fungal community composition and diversity explained by plant attributes (cover, diversity and functional traits), soil properties and climate in Australia and England. Unique and shared variance from plant cover, diversity and functional traits in predicting microbial community composition and diversity were merged in this figure for simplicity. An alternative version of this figure showing the unique and shared variance of each group of predictors can be found in Supporting Information Figs S5 and S6. *P*-values associated with the relative contribution of the different predictors are available in Table S1.

(Table 2). Plant cover, height and width were selected as major plant predictors of the diversity of soil fungi in Australia (Table 2). The only exception was the community composition of soil fungi in Australia, which was best predicted by pH and aridity index, and for which models were not improved by the inclusion of plant attributes (Table 2). In England, plant diversity, leaf N and LDMC were selected as major predictors for bacterial composition. The same predictors, but also the cover of N fixers, were also the major drivers of bacterial diversity in this dataset (Table 2). Finally, plant diversity and leaf N were selected as the major predictors of fungal composition, whereas cover, diversity, RGR and SLA were the best predictors of fungal diversity in the English dataset.

We then used random forest analyses to identify the importance of plant attributes, soil properties and climate in predicting microbial community composition and diversity (Fig. 3). Plant attributes were selected as significant predictors of the diversity and community composition of bacteria and fungi in Australia and England (Fig. 3). In addition, soil properties and climate were key significant predictors of bacterial and fungal attributes, although no soil property or climate variable was selected as a significant driver of the diversity of fungi in Australia. Most predictors in the best-fitting models (Table 2) were also selected as significant drivers of bacterial and fungal diversity and community composition by our random forest analyses (Fig. 3), thus demonstrating that the identity of the main predictors was robust to the statistical method used.

We then used SEM to gain deeper insights on the role of plant attributes and functional traits in predicting the community diversity and composition of fungi and bacteria in the two hemispheres. Each SEM included the predictors of each microbial attribute selected in the best-fitting ($\Delta AIC > 2$) models described earlier and in Table 2. We detected multiple significant direct effects of plant attributes on soil microbial community composition and diversity after accounting for other key drivers, such as climate and soil properties (Figs 4 and 5). In both the Australian and English datasets, plant cover had a negative direct effect on the diversity of bacteria and/or fungi (Fig. 4). In Australia, canopy height was the major plant attribute explaining the composition of bacteria (Fig. 4). In England, plant diversity had a positive effect on the diversity of bacteria and fungi (Fig. 4). Also, plant diversity and leaf N showed direct effects on the composition of bacteria and fungi (Fig. 5).

We also identified some indirect effects of location and climate on the composition or diversity of soil bacteria and fungi via plant attributes (Figs 4, 5) in the Australian and English datasets. For example, plant width was indirectly related to the composition of fungi via changes in soil pH for the Australian dataset (Fig. 4). In addition, we also found direct effects of climate (mainly from aridity index) on the diversity of soil bacteria and fungi in England (Fig. 5). Aridity index also operated via its effects on the plant cover, CWM SLA and CWM leaf N of temperate grassland plant communities in England, but it did not affect these attributes in Australia (Figs 4, 5).

Further correlation analyses (Spearman) exploring links among plant attributes and microbial community diversity and composition for Australia and England are available in Fig. S7. Soil pH and C were the most consistent abiotic factors explaining the community composition and/or diversity of fungi and/or bacteria for the Australian and English datasets (Figs 4, 5). Importantly, in the case of England, the direction and strength of the multiple direct and indirect effects in our SEM were mostly maintained after controlling for management practices by using the residuals of bacterial diversity or composition from a one-way ANOVA, as explained in the Materials and Methods section (Fig. S8).

Finally, we used random forest analyses to identify particular bacterial and fungal species that are associated with certain plant community attributes and plant traits in both the Australian and English datasets. A subset of phylotypes (total 57 OTUs) shared

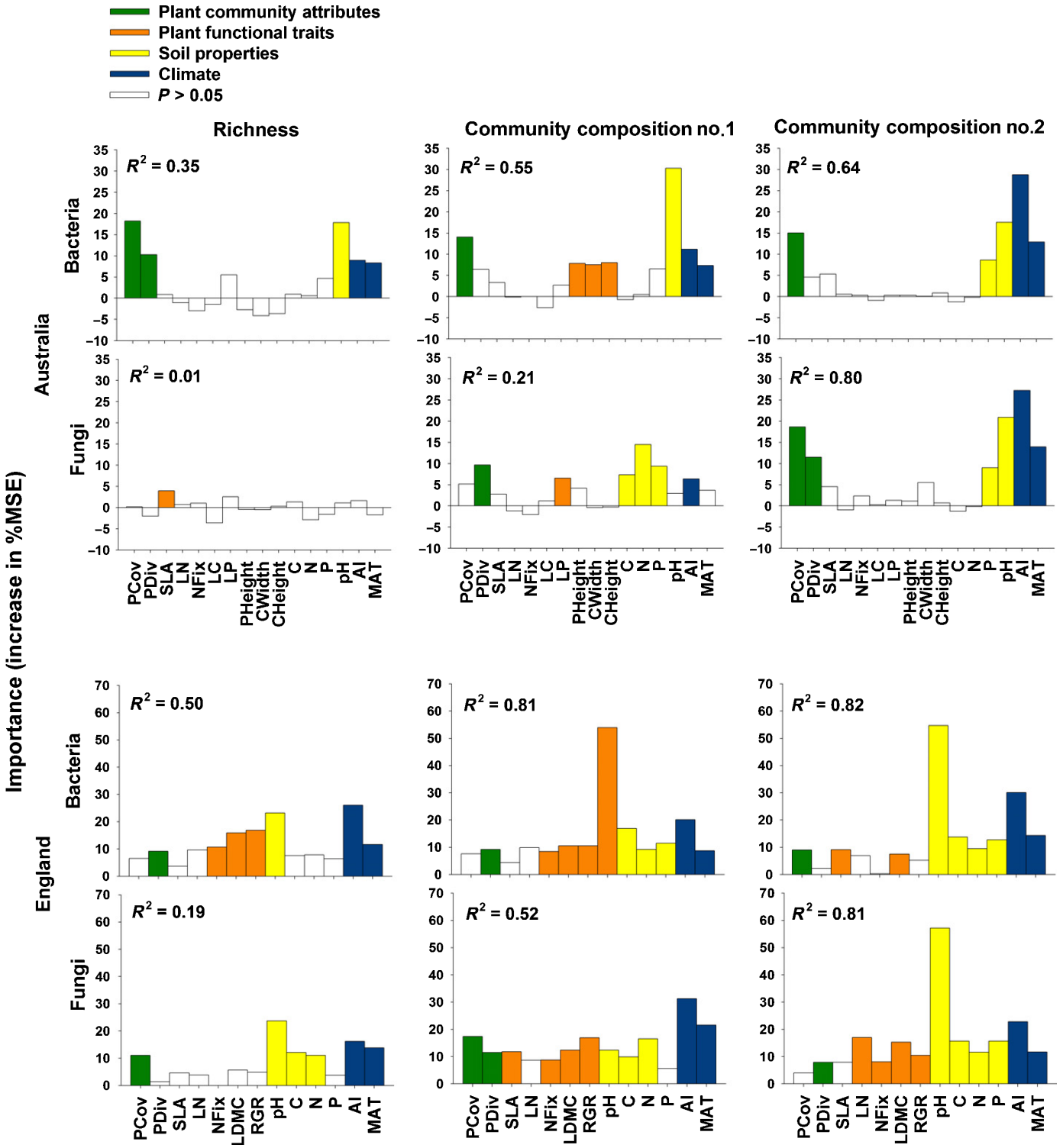

Fig. 3 Random forest analysis aiming to identify the best individual predictors of the diversity and community composition of bacteria and fungi in Australia and England. Predictors include plant attributes, soil properties and climate (Table 1). MSE, mean square error. Community compositions no. 1 and no. 2 represent the first and second axes of a nonmetric multidimensional scaling including the community composition of bacteria or fungi (see Fig. S3).

by the Australian and English datasets – bioinformatic analyses were done simultaneously for both datasets, allowing direct comparison of OTUs – were significantly associated with particular plant traits (Fig. S9). For example, the relative abundance of OTU_1699 (unidentified species from family Ellin5301; phylum Gemmatimonadetes) was strongly and positively correlated to N fixation (percentage coverage of N-fixing plants across English grasslands and presence of *Acacia* sp. in Australia) in both the

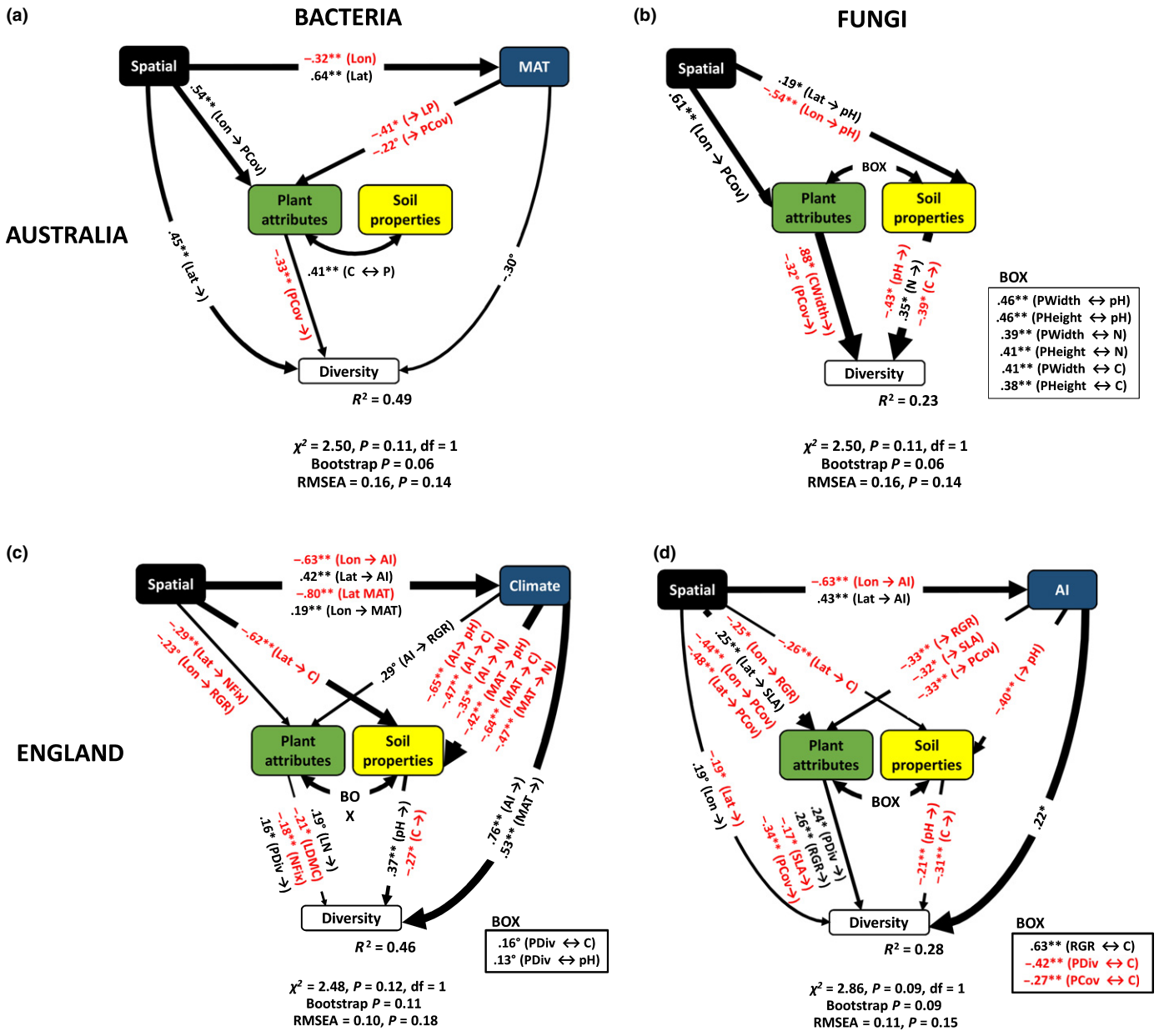

Fig. 4 Structural equation model describing the effects of multiple drivers (selected from Table 1) on the diversity of (a, c) bacteria and (b, d) fungi for the Australia ($n = 60$) and England ($n \approx 160$) datasets. Numbers adjacent to arrows are indicative of the effect size of the relationship. R^2 denotes the proportion of variance explained. Climate, soil properties and plant predictors are included in our models as independent observable variables; however, we group them in the same box in the model for graphical simplicity. All predictors within each are allowed to co-vary. This does not apply to the model in which only one predictor for a given group is included. In this case, the name of the predictor stands alone (e.g. soil pH). RMSEA, root-mean-square error of approximation. Significance levels of each predictor: °, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$. Negative effects in red.

Australian and English datasets ($P < 0.01$). Similarly, the relative abundance of OTU_98 (unidentified species from genus *Candidatus* 'Solibacter'; phylum Acidobacteria) was strongly positively related to SLA in the Australian and English datasets ($P < 0.05$). Finally, the relative abundance of OTU_8 (uncultured Mortierellaceae; division Zygomycota) and the relative abundance of OTU_43313 (Erythrobacteraceae; phylum Proteobacteria) were found to be strongly negatively related to plant cover and plant diversity respectively in both Australia and England (see Fig. S9 for a complete list of taxa).

Discussion

Our study provides strong observational evidence, from two contrasting regions of the globe, that aboveground plant attributes, such as diversity, cover and functional traits, can help explain the diversity and community composition of soil bacterial and fungal communities at a regional scale (hundreds of kilometres). We also provided examples for microbial phylotypes that are strongly related to particular plant traits, such as SLA, leaf N and N fixation, across two very different regions of the world. We did this

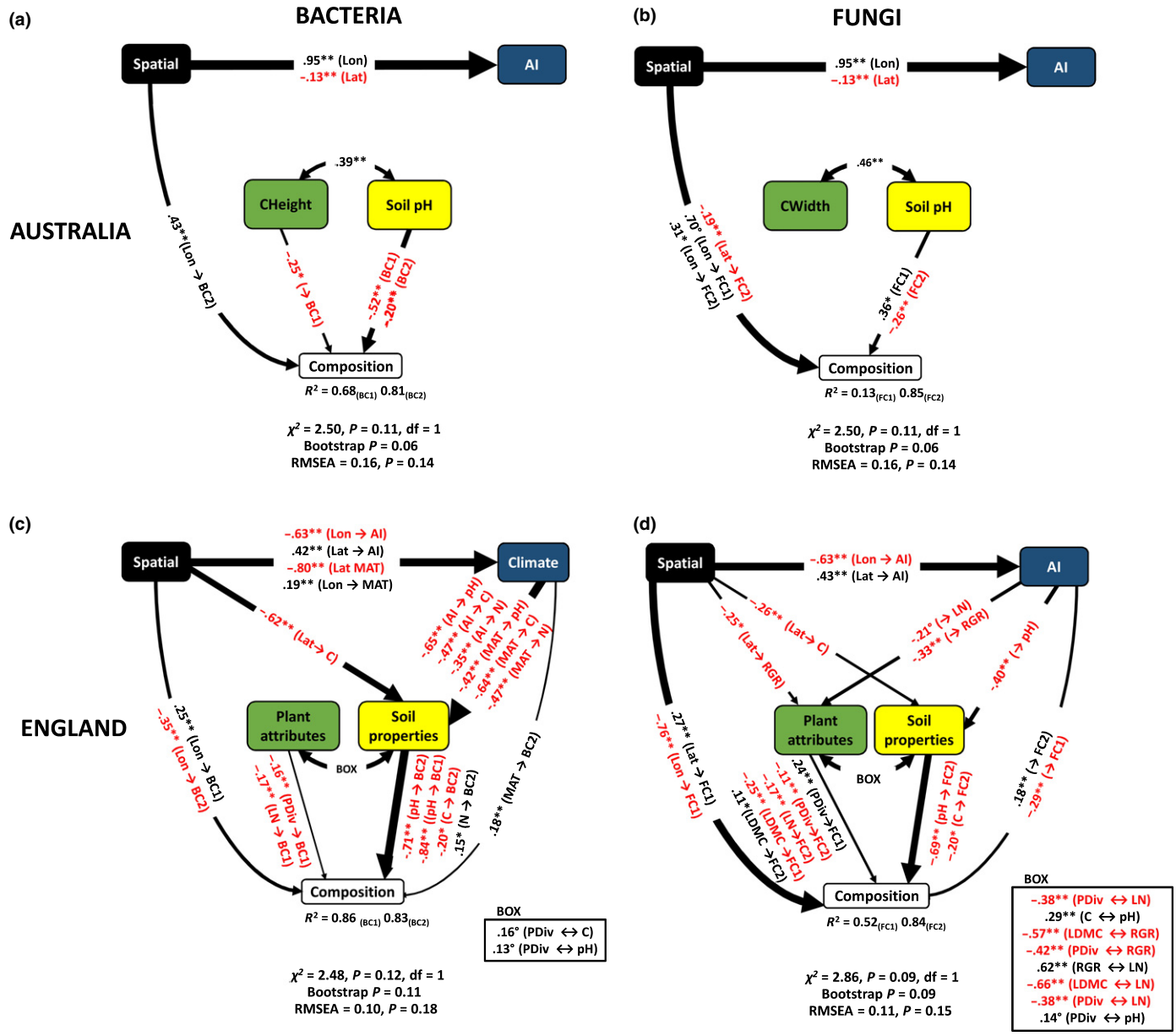

Fig. 5 Structural equation model describing the effects of multiple drivers (selected from Table 1) on the composition (two axes from a nonmetric multidimensional scaling) of (a, c) bacteria and (b, d) fungi for the Australia ($n = 60$) and England ($n \approx 160$) datasets. Numbers adjacent to arrows are indicative of the effect size of the relationship. R^2 denotes the proportion of variance explained. Climate, soil properties and plant predictors are included in our models as independent observable variables; however, we grouped them in the same box in the model for graphical simplicity. RMSEA, root-mean-square error of approximation. Significance levels of each predictor: °, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$. Negative effects in red.

using two separate datasets from Australia and England, which differed markedly in climate (dryland vs mesic), vegetation (forest vs grasslands), and microbial community composition (Figs S3, S4). Our distance-based and variation-partitioning models provided evidence that plant attributes explain a unique proportion of variation in the composition and diversity of microbial communities that is unaccounted for by other key microbial drivers, such as climate and soil properties, which are routinely proposed to be the main determinants of microbial community structure and diversity at large spatial scales. Our SEMs provided an integrative understanding of the role of plant attributes in driving soil microbial communities once we controlled for multiple environmental drivers. These results provide further evidence of strong, direct links between particular aboveground plant attributes and the diversity and composition of soil fungal and bacterial communities at regional scales.

Our findings accord with the results of microcosm experiments that demonstrate the importance of plant functional traits (e.g. litter chemistry) for soil microbial community composition (Schneider *et al.*, 2012; Zhou *et al.*, 2015). However, they are in contrast to recent studies that did not find significant relationships between the local distribution of plant traits and soil microbial

community composition within Panamanian tropical forest (Barberán *et al.*, 2015) or in grassland sites in England (Fry *et al.*, 2017; Leff *et al.*, 2018). This likely relates to the different spatial scale used in these studies; our study considers variation in microbial communities at a regional scale, whereas the studies of Barberán *et al.* (2015), Fry *et al.* (2017) and Leff *et al.* (2018) examined local scales where variation in both plant traits and microbial communities, and their drivers, is less and thus shows weaker patterns of association.

Our SEM results indicate that plant cover had a strong negative effect on the diversity of bacteria and/or fungi in both Australia and England. More specifically, our results suggest that increases in percentage plant cover might lead to the exclusion of microbial species via the competition-to-exclusion principle (Eldridge *et al.*, 2017). In addition, unlike Australia, in England, plant leaf N content (e.g. positive for bacterial diversity), SLA (e.g. negative for fungal diversity) and species diversity (e.g. positive for fungi and bacteria) were also important drivers of the distribution of the diversity and community composition of fungi and bacteria. All these plant attributes are considered key functional markers which relate to soil fertility and the quantity and quality of plant inputs (Garnier *et al.*, 2004). This finding suggests that, in temperate grasslands, the community composition and diversity of soil microbial communities may be strongly affected by both the range and quality of the resources entering soil from plant communities, in the form of litter (note that we used leaf nutrients in our study), but they may also be related to an effect of root turnover and exudation (de Vries *et al.*, 2012; Grigulis *et al.*, 2013). For example, highly diverse plant communities can influence the community composition and diversity of soil microbial communities via greater variability in litter quality (niche partitioning), but also by promoting a higher diversity of resources (e.g. via rhizodeposition; Paterson *et al.*, 2007). Plant leaf N and diversity were also major drivers of microbial community composition in the grasslands studied, suggesting that these plant attributes can promote/inhibit the relative abundance of particular microbial taxa. Conversely, other plant traits not measured in England, such as canopy height (likely to be relatively constant in temperate grasslands, and therefore uninformative in England), regulated the community composition of bacteria in Australian forests. Together, these results suggest that litter quality might be the major plant driver of microbial community composition in temperate grasslands, where plant inputs to soil are relatively large. Further, in the English dataset, there was almost complete vegetation coverage across grassland sites. Conversely in Australia, where plant cover was always < 100% (18–98%), litter quantity rather than quality likely plays a more important role in influencing the composition of soil microbial communities. We would like to highlight that our study focused on aboveground plant attributes, which were found to account for a unique portion of the variation in the distribution of soil microbial community composition and diversity. However, we did not have available information on belowground attributes for our study sites. As such, we can only guess that including belowground plant attributes would have increased the explanatory power of our models; however, further research needs to be done to support this assumption.

In addition to demonstrating that plant attributes can explain regional-scale variation in bacterial and fungal community composition, our study provides a unique inventory of phylotypes (i.e. species equivalent) that are strongly associated with particular plant traits, such as SLA index, leaf N content and/or N fixation, in two markedly different regions of the globe. This information and approach could be used to predict the distribution of particular microbial taxa using plant functional traits (with potential implications for the understanding of ecosystem functioning) and help to identify the potential role of certain microbial species (with as yet unestablished functional roles) in driving particular ecosystem functions (e.g. decomposition rates). Some of these phylotypes responded in a similar manner to increases in the values for particular plant traits. For example, the relative abundance of OTU_1699 (family Ellin5301) was strongly positively related to N fixation (percentage coverage of N fixers across English grasslands and presence of *Acacia* sp. in Australia) in both Australian and English datasets. Regrettably, little is currently known about the ecology of these bacterial taxa. Furthermore, the relative abundance of OTU_98 (*Candidatus* 'Solibacter' sp.) was strongly positively correlated to SLA in both datasets ($\rho > 0.164$, $P < 0.05$). Species from the genus *Candidatus* 'Solibacter' are known to be chemoorganotrophic organisms that use organic C for growth and energy (Ward *et al.*, 2009); as such, they might gain resources from litter inputs, especially those of high decomposability (i.e. often characterized by a higher SLA). In the same vein, OTU_8 (Mortierellaceae sp.), a saprophyte that can act as a facultative parasite (Fitzpatrick, 1930), was negatively related to plant cover in England and Australia (see extended discussion on phylotypes showing opposite patterns in both datasets in Methods S2).

Plant attributes such as diversity, vegetation cover and plant traits are highly sensitive to climate change and land-use intensification (Allan *et al.*, 2015; Deraison *et al.*, 2015; García-Palacios *et al.*, 2016; Le Bagousse-Pinguet *et al.*, 2017). Supporting this notion, our SEM identified multiple indirect effects of climate on fungal diversity and community composition, driven indirectly by changes in plant attributes. For example, increases in aridity related to changes in plant cover, SLA and leaf N of temperate grasslands in England, which could be taken to suggest that predicted increases in aridity resulting from climate change (Huang *et al.*, 2016), might indirectly alter the diversity and composition of grassland soil fungal communities. In this respect, our SEM results could be used to generate new hypotheses that could potentially lead to management strategies. For instance, our approach could help identify how plant traits mediate climate effects, and lately provide strategies for the management of these traits that mitigate climate impacts on soil microbial communities and soil processes. This is especially significant given the known importance of changes in fungal communities for biogeochemical cycles and plant community dynamics in grasslands (van der Heijden *et al.*, 2008), and hence the potential for this to alter the capacity of these ecosystems to provide essential goods and services, such as food production and climate regulation (Bardgett & van der Putten, 2014; Delgado-Baquerizo *et al.*, 2016a).

Together, our work provides new evidence, from an observational study, for the important role of plant attributes in

explaining variation in soil microbial communities across two markedly different mesic and dryland ecosystem types of the world. More precisely, in both forested ecosystems and temperate grasslands, plant attributes explained a unique proportion of the variation in soil microbial communities that could not be explained by factors such as soil abiotic properties and climate. Our findings also advance understanding of the links between plant traits and soil microbial communities by identifying a suite of phylotypes strongly associated with particular plant traits such as SLA, leaf N and N fixation across a broad range of ecosystem types. Such information suggests that it might be possible to predict the distribution of certain microbial taxa at large spatial scales using plant functional traits. Given the importance of soil microbial communities for ecosystem functioning, such knowledge is critical to improve our ability to predict likely changes in ecosystem function under global change and to manage terrestrial ecosystems sustainably.

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Author contributions

M.D-B., R.D.B. and B.K.S. designed this study. The Australia dataset was compiled by D.J.E. and M.D-B. The England dataset was compiled by R.D.B., F.T.d.V. and P.M. Lab analyses were conducted by E.L.F. and M.D-B. J.K., G.B., D.J.E. and M.D-B. provided plant trait data. B.K.S. provided Miseq Illumina data. K.H. performed bioinformatic analyses. M.D-B. conducted statistical modelling. The manuscript was written by M.D-B. with contributions from all co-authors.

ORCID

Manuel Delgado-Baquerizo http://orcid.org/0000-0002-6499-576X

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Locations of the sites included in this study for the Australia and England datasets.

Fig. S2 *A priori* structural equation model including direct and indirect effects of geographical location, climate, soil properties and plant attributes on the community composition or richness of soil bacteria and fungi.

Fig. S3 Community composition and diversity of bacteria and fungi for the Australia and England datasets.

Fig. S4 Composition of bacteria and fungi at the phyla level for the Australia and England datasets.

Fig. S5 Variation partitioning modeling aiming to identify the relative contribution of plant traits, plant diversity and cover, location and climate and soil properties as predictors of the composition of bacteria and fungi at the OTU level.

Fig. S6 Variation partitioning modeling aiming to identify the relative contribution of plant traits, plant diversity and cover, location and climate and soil properties as predictors of the diversity of bacteria and fungi at the OTU level.

Fig. S7 Correlations between plants traits, cover and diversity with the diversity and composition of bacteria and fungi for the Australia and England datasets.

Fig. S8 Structural equation model describing the effects of multiple drivers on the residuals of diversity and community composition of bacteria and fungi for the England dataset.

Fig. S9 Shared phylotypes in the Australia and England dataset that were found to be universal predictors (via Random Forest analyses) of multiple plant attributes including plant community attributes (cover and richness) and traits (SLA index, N fixation and leaf N).

Table S1 *P*-values associated to the relative contribution of the different predictors used to model the richness and community composition of bacteria and fungi in Australia and England

Methods S1 Supplementary methods.

Methods S2 Extended discussion on particular microbial phylotypes associated with particular plant functional traits.

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