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Environmental controls of soil fungal abundance and diversity in Australia's diverse ecosystems

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Abstract

Soil fungi are vital for ecosystem functioning, but an understanding of their ecology is still growing. A better appreciation of their ecological preferences and the controls on the composition and distribution of fungal communities at macroecological scales is needed. Here, we used one of the most extensive continental-scale datasets on soil fungi and modelled the relative abundance of dominant fungal phyla and community diversity in Australian soils from forests, grasslands, shrublands, woodlands, and croplands. Across these diverse ecosystems, the Ascomycota and Basidiomycota dominate Australian soils, and fungal diversity declines as climates become more arid. Climate and the water balance exert dominant control on soil fungal abundance and diversity, mediated by interactions between ecosystem type, the ensuing vegetation and edaphic factors, such as organic matter, clay and iron-oxide mineralogy, pH and nutrients. Soil organic matter and mineralogy, represented by

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absorptions of visible–near-infrared (vis–NIR) radiation, helped to improve characterisation of the abiotic controls on soil fungi. This better representation of edaphic factors improved the predictability of the models by up to 40 %. Our findings contribute to the understanding of fungal ecology at a macroecological scale. They help to appreciate better the links between fungi, soil and the environment, which underpin ecosystem stability and resilience and have implications for developing strategies for preservation, adaptation and mitigation of global change.

Keywords: soil fungi, fungal diversity, macroecology, water balance, modelling, biogeography

1. Introduction

Soil fungi are decomposers, mutualists, plant symbionts and pathogens. They drive the cycling of all essential nutrients, which affect soil functions and their ability to provide ecosystem services (Větrovský et al., 2019; Delgado-Baquerizo et al., 2016; Li et al., 2019). For example, fungi are some of the decomposers of soil organic matter, including lignin and ligno-cellulose, which are often resistant to bacterial decomposition. They do this by producing a wide variety of extra-hyphal enzymes that work to release carbon and nutrients into the soil solution. Fungi also contribute to carbon sequestration and thus act as crucial regulators of the soil carbon balance (Treseder and Lennon, 2015; Nicolas et al., 2019).

Mycorrhizal fungi form mutualistic associations with more than 90% of land plants. These associations enhance nutrient uptake, protect plants against pathogens and toxic elements, improve resistance to biotic and abiotic

stresses and mediate interactions with the soil microbiome, including nitrogen fixation and hormone production (Baum et al., 2015). Importantly, fungi, unlike any other soil microbes, can form extensive networks that physically connect plant species to facilitate community-level nutrient exchange (Frac et al., 2018). Fungal exudates also promote the formation of soil aggregates, thereby improving soil structure and supporting plant growth, especially under environmental stress (Lehmann et al., 2017).

Given the involvement of fungi in soil functions, their critical role in soil ecosystems, and concern over the growing loss of biodiversity make it increasingly necessary to improve understanding of soil fungal communities across different habitats and at different scales. Research that attempts to elucidate the soil and environmental controls on fungal community abundance and diversity have shown that climate and soil physicochemical properties play essential roles (Fierer et al., 2009; Maestre et al., 2015; Větrovský et al., 2019; Delgado-Baquerizo et al., 2018; Tedersoo et al., 2014; Sernachavez et al., 2013; Siciliano et al., 2014; Ramirez et al., 2020). However, comprehensive datasets on soil fungi are few and often limited to at most a few hundred soil samples for global-scale studies (Fierer et al., 2009; Tedersoo et al., 2014; Maestre et al., 2015).

Soil microbiological surveys are practically and methodologically challenging, particularly over large scales. Therefore, datasets are few, sparse and often underrepresent regional, biome and larger (country-, continental- and global-) scales (Tedersoo et al., 2014; Větrovský et al., 2019). Consequently, studies often report only two-way relationships rather than multi-property interactions (Andrew et al., 2018), or responses along environmental

gradients (Maestre et al., 2015; Delgado-Baquerizo et al., 2018), which tend to over-emphasis the relationship of the fungal communities with the contrasting environmental property (*e.g.*, precipitation). But, the response of soil fungi to climatic, edaphic and other environmental controls is complex. Therefore, we need to simultaneously consider the interactive effects of different climates, ecosystem types, and soil conditions to evaluate their combined impact on the composition, abundance, and diversity of fungal communities.

Changes in soil fungi and community diversity from ongoing environmental and anthropogenic change will have significant impacts on ecosystem resilience and function (Sernachavez et al., 2013; Tedersoo et al., 2014). Yet, responses of the dominant soil fungi and diversity to climate, edaphic, and other environmental factors at macroecological scales are not well-understood (Maestre et al., 2015; Delgado-Baquerizo et al., 2018; Sheik et al., 2011). The importance of ecosystem type in controlling microbial communities was emphasised by Szoboszlay et al. (2017) and Terrat et al. (2017), but we know little about the ecological preferences of soil-inhabiting fungi over large scales. The predicted increased drying and desertification of most semi-arid and arid regions in Australia and globally (Huang et al., 2016) will have profound and lasting consequences on soil microbial functioning and ecosystem sustainability (Pointing and Belnap, 2012). However, the effects of aridification on fungal species and the diversity of their communities are poorly understood (Maestre et al., 2015; Delgado-Baquerizo et al., 2018; Sheik et al., 2011). Gaining an understanding of fungal ecology is essential because fungi play a vital role in our environment.

Considering the importance of climatic and edaphic factors on soil fungi

at a macroecological scale, we pose two hypotheses. First, climate and the water balance significantly influence fungal community diversity and structure in Australian ecosystems. Improved knowledge of how climate affects soil fungal communities and their interaction with other edaphic and environmental controls is essential for managing and mitigating the effects of ongoing global climate change and for maintaining the stability and functioning of ecosystems. Second, soil visible–near infrared (vis–NIR) spectroscopy, which provides integrated measures of the soil's mineral-organic composition (Viscarra Rossel et al., 2016), can be used to explain the diversity and composition of soil fungal communities. The frequencies recorded in the vis–NIR spectrum encode information on the soil's minerals, organic compounds and water. Broad absorptions at wavelengths smaller than 1000 nm can result from chromophores and iron oxides; narrow, well-defined absorptions near 1400 and 1900 nm are due to hydroxyl bonds and water; absorptions near 2200 nm arise from clay minerals; organic matter absorbs at various wavelengths throughout the vis–NIR spectrum. Spectroscopy also provides information on soil particle size and thus information on the soil matrix (Viscarra Rossel et al., 2016). Hence vis–NIR spectra can be used to estimate functional soil physicochemical (Viscarra Rossel et al., 2006; Shi et al., 2015) and biological properties (Yang et al., 2019).

Here, we apply machine learning and structural equation modelling to a DNA-based continental-scale characterisation of soil fungi to test our hypotheses. Thus, we aim to: (i) determine the interactive effects of climatic, edaphic and other environmental factors on the distribution, relative abundance and diversity of soil fungi in forests, grasslands, shrublands, wood-

lands, and croplands, which extend across arid, semi-arid, semi-humid and humid climates across Australia, and (ii) supplement the representation of edaphic factors in the modelling with soil visible–near-infrared (vis–NIR) spectra since the frequencies recorded in the vis–NIR range (400–2500 nm) encode information on the soil's iron oxides, clay minerals, organic matter, water and particle size (Viscarra Rossel et al., 2016).

Materials and Methods

Soil samples, laboratory analyses and datasets

We used 577 soil samples from the Biomes of Australian Soil Environments (BASE) project (Bissett et al., 2016). The soil samples were collected from a diverse array of plant communities as described by (Bissett et al., 2016). They originated from two soil layers (0–0.1 m and 0.2–0.3 m) and covered four representative Australian ecosystems comprising forests, grasslands, shrublands, woodlands, and croplands (Fig. 1). Each sample was divided into sub-samples for DNA sequencing, and physicochemical and spectroscopic analyses (see below). The subsamples for physicochemical and spectroscopic analyses were air-dried and crushed to a particle size of $\leq$2 mm.

Fungal abundance and diversity

The soil DNA extraction and sequencing are described in detail in (Bissett et al., 2016). Briefly, all soil DNA was extracted in triplicate according to the methods used by the Earth Microbiome Project[1]. Sequencing was performed

[1]http://www.Earthmicrobiome.Org/emp-standard-protocols/dna-extraction-protocol/

using an Illumina MiSEQ, as described in detail by the BASE protocols[2]. In summary, amplicons targeting the fungal ITS region were prepared and sequenced for each sample. The ITS amplicons were sequenced using 300 bp paired end sequencing. ITS1 regions were extracted using ITSx (Bengtsson-Palme et al., 2013). Sequences comprising full and partial ITS1 regions were passed to the Operational Taxonomic Units (OTU) picking and assigning workflow (Bissett et al., 2016).

The selection and assignment of OTU followed guidelines described in the BASE protocols[3] and in (Bissett et al., 2016), which are based on the most current version of UNITE database (version 8.2, updated 15-01-2020) for molecular identification of fungi (Nilsson et al., 2018). We used the final sample-by-OTU data matrix and annotated taxonomy file for the analyses of fungal diversity and composition.

In total, there were more than 60 million quality sequences across the samples, with 11,090–2,177,737 sequences per sample (mean 107,310). Sequences clustered into 202,200 OTUs at 97% similarity, with an average of 666 OTUs per sample. We removed the bias that results from unbalanced sequencing by re-sampling each sample at a depth of 11 000 sequences, which represents the median number of sequences in the samples. At this depth, rarefaction curves for all 577 samples were starting to level (Supplementary Fig. S1). Community diversity was then calculated with the abundance-based coverage estimator (ACE) index (Lozupone and Knight, 2008) from the resampled sample-by-OTU matrix. The relative abundance of fungal

[2]https://ccgapps.Com.Au/bpa-metadata/base/information

[3]https://ccgapps.com.au/bpa-metadata/base/information

taxa at the phylum, class and genus level was then determined using the ratio of sequences classified at individual taxa to the rarefied number of sequences for each sample. We performed the resampling and computation of the ACE index with functions of the RAM library in the R software (R Core Team, 2020)

Soil physicochemical properties

The soil properties analysed in the BASE project (Bissett et al., 2016) include total organic carbon, ammonium, nitrate, phosphorus, potassium, sulphur, pH, electrical conductivity, exchangeable cations (aluminium, sodium, magnesium, calcium), available trace elements (zinc, manganese, iron, copper, boron) and texture (sand, silt and clay) (Supplementary Table S1).

Soil visible–near-infrared spectra

We measured the diffuse reflectance spectra of all air-dried $\leq$ 2 mm soil samples with the Labspec® vis–NIR spectrometer (Malvern Panalytical, Boulder, Colorado, USA) following the protocols described in (Viscarra Rossel et al., 2016). The spectrometer has a spectral range from 350 to 2500 nm. Because of a low signal-to-noise at the start and end of each spectrum, for our analysis, we retained spectra in the range between 380 and 2450 nm. The measurements were made with its high intensity contact probe (PaNalytic, Boulder, Colorado, USA), and a Spectralon® white reference panel was used for calibration once every 10 measurements. We converted the vis–NIR reflectance spectra (R) to apparent absorbance (A) using $A = \log_{10}(1/R)$. The spectra were then pre-processed with a Savitzky-Golay filter and first derivative (Savitzky and Golay, 1964) to remove baseline

effects and to enhance the signal. Absorptions at wavelengths smaller than 1000 nm can result from chromophores and iron oxides; narrow, well-defined absorptions near 1400 and 1900 nm are due to hydroxyl bonds and water; absorptions near 2200 nm arise from clay minerals; organic matter absorbs at various wavelengths throughout the vis–NIR spectrum. We selected only the most relevant wavelengths for further analyses, using the Boruta variable selection algorithm (Kursa et al., 2010).

Climatic and other environmental datasets

We assembled a set of readily available environmental variables that represent climate, terrain, vegetation and parent material. To represent climate, we used data on mean annual temperature (MAT), mean annual precipitation (MAP), solar radiation, and evapotranspiration (Xu and Hutchinson, 2011) and the Prescott index (PI) (Prescott, 1950). We used the PI, which is calculated as the ratio of precipitation to evapotranspiration, as a measure of water balance, and an inverse proxy for aridity, *i.e.*, decreasing values of PI represent increasingly arid environments.

A digital elevation model (DEM) from the 3-arc second shuttle radar topographic mission (SRTM) and derived terrain attributes (Gallant et al., 2011) were used to capture functional landscape characteristics. To represent vegetation, we used data on net primary productivity (NPP) (Haverd et al., 2013), and on the fraction of photosynthetically active radiation intercepted by the sunlit canopy of the evergreen (Fpar-e) and woody (Fpar-r) vegetation (Donohue et al., 2009). To represent parent material, we used gamma radiometrics, which comprises data on potassium, uranium, and thorium (Minty et al., 2009). Supplementary Table S1 lists these data and their

main characteristics.

Controls on the relative abundance and diversity of fungi in Australia

To determine the controls on the relative abundance and diversity of soil fungi, we modelled the data using a conceptual state-factor model similar to that described by (Jenny, 1994). In our model, the soil state (*i.e.* fungal abundance and diversity) is a function of climatic, edaphic, biotic, and other environmental controls. To proxy the factors in the model, we used the set of climatic, soil, vis–NIR, vegetation, terrain and environmental variables, described above (and listed in Supplementary Table S1). The function that we used to relate soil fungal abundance and diversity to those variables is the machine-learning method CUBIST (Quinlan, 1992).

Machine learning with CUBIST

CUBIST is a piece-wise linear regression tree (Quinlan, 1992) that uses recursive **if-then** partitioning of the predictor variable space and partitions the data into subsets that are more similar with respect to the predictors in the data. When the conditions in each rule are satisfied, piecewise linear least squares regressions are used to predict the response within each partition. The advantage of having conditions in the rules is that they enable the models to capture the non-linearity in different parts of the predictor variable space, leading to smaller, more interpretable trees with robust predictability. The method has been used for different applications (Viscarra Rossel et al., 2019; Liang et al., 2019; Viscarra Rossel and Bui, 2016).

After centering and scaling the variables, we used a grid search approach (Hastie et al., 2005) for optimising the CUBIST hyper-parameters, which in-

clude the number of rules in the model, an extrapolation factor, the ensemble of rule-based models, called 'committee models' and the number of nearest neighbouring observations to use (Quinlan, 1992). The optimisation results in a tuple of hyperparameters that yields an optimal model with the smallest root-mean-squared-error (RMSE). To assess the models of fungal relative abundance and diversity we report the coefficient of determination (R^2), which expresses the proportion of the variance that is explained by the independent variables in the model. For the interested reader, we detail our implementation of CUBIST and the hyperparameter optimisation in the Supplementary Information linked to this article.

To determine the controls, we report the relative importance of the variables, which we measured by calculating the frequency that each individual variable is used in the conditions and linear models of CUBIST. For this, we used the varImp function of the caret library (Kuhn et al., 2008) in the software R.

To determine the contribution of the selected vis–NIR data in the modelling, we set up additional the state-factor models, as above, but excluded the vis–NIR data from the predictor set.

Characterising the interactions between variables that control the relative abundance and diversity of fungi in Australia

To test our hypotheses and to evaluate the direct and indirect effects of the controls on fungal abundance and diversity we established an a priori model (Supplementary Fig. S2) based on the results from CUBIST and our understanding of Australian ecology. We used structural-equation modelling (see below) to study the interactions and developed a model (Supplementary

Fig. S2) with five latent variables that represent water balance (measured with the PI), ecosystem type (Fig. 1a), above-ground biomass (measured with NPP), the mineral and organic composition of the soil (measured with the vis–NIR spectra) and soil condition and fertility (measured with soil pH, organic carbon, nitrogen, phosphorus, exchangeable ions).

Structural-equation modelling (SEM)

SEM is an extension of factor analysis and is a methodology designed primarily to test substantive theory from empirical data. It allows a partitioning of the associations among multiple variables included in the model as well as the separation of their direct and indirect effects, which can suggest causal relationships (Grace, 2006; Murdoch et al., 2019). Essentially, SEM is a system of linear equations among a set of predictor variables (or constructs) and the responses. It is composed of two parts: a structural part, linking the constructs to each other, and a measurement part, linking those constructs to the observed responses. We used maximum-likelihood to fit the SEM model (Grace, 2006) and the Chi-square test and RMSE to assess the goodness of fit (Schermelleh-Engel et al., 2003). Further details on our implementation are provided in the Supplementary Information. We displayed the SEMs in visual form using path diagrams and calculated the standardised total effects of each variable on fungal abundance and diversity by summing all direct and indirect pathways. The SEM was performed using the `sem` function from `lavaan` package in R.

Results

We analysed 577 soil samples collected from a diverse array of plant communities (Bissett et al., 2016), and covered four representative Australian ecosystems: forests, grasslands, shrublands, woodlands, and croplands (Fig. 1a).

Figure 1 near here

Fungal community composition and variation

A total of sixteen phylotypes were identified, which represented 88% of the sequences. Five phyla (> 2% of the total number of sequences) were present in most soil samples. The relative abundance of these five phyla varied across ecosystem types (Fig. 1b). The Ascomycotawere more abundant in croplands, grasslands, shrublands and woodlands, respectively, than in forest soils, while the Basidiomycota were more abundant in forests, woodlands and shrublands than in grasslands and croplands, respectively (Fig. 1b). The relative abundance of the Mortierellomycota, Glomeromycota and Mucoromycota were smaller in Australian soils. However, the Mortierellomycota were relatively more abundant in soils under cropping compared to grasses and forests, and they were least abundant in soils under woodlands and shrublands, respectively. The Glomeromycota were relatively more abundant in cropland and grassland soils and the Mucoromycota were relatively more abundant in forests, shrublands, and woodlands (Fig. 1b).

Overall, the two dominant phyla were the Ascomycota(average 43% relative abundance) and the Basidiomycota (average 37% relative abundance). The Basidiomycota tended to be more abundant in humid and dry sub-humid

environments, while the Ascomycotawere more abundant in drier, semi-arid and arid environments (Fig. 2).

Figure 2 near here

Environmental controls on the relative abundance and diversity of fungi in Australia

The CUBIST regression trees models derived with the climatic, soil, spectral, vegetation, terrain and other environmental variables explained between 40 and 65% of the variation in fungal abundance and diversity (Table 1). Inclusion of the vis–NIR spectra in the modelling, whose frequencies represent organic matter composition, iron and clay mineralogy, resulted in 5% to 40% improvement in the variance explained (Table 1).

Table 1 near here

The climatic, edaphic and environmental controls on the relative abundance of fungal phyla and diversity across Australia differed, but climate, soil properties, the organic matter of the soil and NPP were the most dominant explanatory variables. Terrain attributes and parent material were less important in the models (Fig. 3). The vis–NIR spectra, which represent the Fe-oxide and clay mineralogy as well as the organic matter in the soil, were important explanatory variables of fungal relative abundance and diversity (Fig. 3).

Figure 3 near here

The dominant controls of community diversity were total organic carbon (TOC), the Prescott Index (PI), which represent an ecosystem's water balance, nitrate-N and the mineralogy and organic matter of the soil (represented by the vis–NIR spectra) (Fig. 3). The controls on the relative abundances of Ascomycota and Basidiomycota are similar, with the water balance, soil pH and the mineral-organic composition of the soil being the most dominant (Fig. 3). Net primary productivity (NPP) and total P (TP) appear to also exert some control over the relative abundance of *Ascomycota*, while exchangeable Ca (Exc.Ca), exchangeable Al (Exc.Al) and silt content influence the Basidiomycota (Fig. 3). Climatic factors had smaller effects on the Mortierellomycota, Mucoromycota and Glomeromycota. However, the soil's mineralogy and organic matter (represented by the vis–NIR spectra), and vegetation exert control on them. Other controls on the relative abundance of Glomeromycota are soil pH, total K (TK) and Exc.Ca, and on Mortierellomycota and Mucoromycota is TP (Fig. 3).

Given that the water balance across Australia's diverse ecosystems has a dominant effect on the two most relatively abundant phyla, the Ascomycota and Basidiomycota, and community diversity, its individual effects are shown in Fig. 4. The Ascomycotawere generally more abundant in arid, semi-arid and dry sub-humid environments across the different ecosystems, while Basidiomycota were more abundant in humid environments under mainly forests (Fig. 4). More arid and semi-arid environments, largely under croplands, hosted less diverse fungal communities, and diversity increased with increasing humidity, largely under forests (Fig. 4).

Figure 4 near here

Interactive relationships between the controls on the relative abundance and diversity of fungal communities

The a priori structural equation model (SEM) that we used to study the interactive effects of the environment on soil fungi (Fig. S2) is based on our results from CUBIST (Fig. 3) and the dominant role that the water balance plays in ecosystems (Fig. 4). Thus, we parameterised the SEM with five latent variables that test the interactive effects of an ecosystem's water balance, ecosystem types, aboveground biomass, the soil's organic matter and mineral composition and soil fertility and pH, on the relative abundance and diversity of soil fungi in Australia (Supplementary Fig. S2). The SEM explained 40–55% of the variation in the relative abundances of the Ascomycota and Basidiomycota, and community diversity (Fig. 5).

Figure 5 near here

As expected, ecosystem type has a direct effect on relative abundances of fungal phyla, but the effect is relatively small (Fig. 5). Generally, the water balance indirectly affects the relative abundance of the two phyla and diversity through its action on ecosystem type, vegetation, the mineral and organic composition of the soil and via its regulation of soil nutrients and pH (Fig. 5). The effect of the water balance on ecosystem type is strong; however, the effect of ecosystem type on the relative abundances of the two phyla and community diversity is relatively weak and insignificant, respectively (Fig. 5). The total effect of water balance on the Ascomycotais strong and negative, but positive on the Basidiomycota, which is consistent with our observation

in Fig. 4. The effect is via its influence on soil fertility, pH and the organic and mineral composition of the soil. A more humid environment (that is less arid) with more weathered mineralogy and higher organic matter turnover can result in more acidic soil, and vice versa. Soil pH and organic matter show a positive effect on *Ascomycota*, but negative effect on Basidiomycota (Fig. 5). Total phosphorus affects the relative abundance of the *Ascomycota*, while the effect of exchangeable calcium was negative on the Basidiomycota (Fig. 5). The water balance in ecosystems had a positive effect on fungal diversity through its regulation of above-ground biomass, soil organic matter and consequently, soil carbon, available nitrogen and pH (Fig. 5). More humid environments are conducive to the production of more biomass, larger rates of mineralisation and organic matter turnover, leading to more fertile soils with more organic carbon and nitrogen.

Wavelengths that represent clay minerals (Viscarra Rossel, 2011) were directly associated with the water balance, likely via their effect on soil texture (type) and the soil's water holding capacity. Clay minerals had direct but opposite effects on the relative abundances of Ascomycota and Basidiomycota, and with Fe-oxides (Viscarra Rossel et al., 2010b), had direct and positive effects on fungal diversity. The wavelengths corresponding to soil organic matter and its functional groups (Viscarra Rossel and Hicks, 2015) were also directly associated with the water balance and overall had positive effects on the relative abundance of Ascomycota and Basidiomycota. In contrast, its effect on diversity was negative (Fig. 5).

Discussion

Soil fungal communities in Australia's ecosystems

Our results show that in the ecosystems sampled, the Ascomycota and Basidiomycota, respectively, are the most dominant fungi in Australian soils. Their dominance over the continental scale may be due to the abundance of wind-dispersed spores, their functional attributes as common mycorrhizal organisms and their habits. Our results show that ecosystem type has a significant direct effect on the relative abundances of Ascomycota and Basidiomycota, indicating clear environmental preferences. The ecosystem type has an insignificant (direct) effect on community diversity. More Basidiomycota tend to inhabit native forests, shrublands and woodlands, possibly because of the symbiotic relationship between mycobionts and the roots of woody plants that are dominant in native ecosystems. More Ascomycota tend to inhabit croplands and grasslands in Australia. Their endophytic lifestyles play a crucial role in agriculture because of their effect on the habitat adaptation of plants. They can help to improve plant performance and plant protection against biotic and abiotic stresses. Although less abundant, the Mucoromycota tended to prefer forest, shrublands and woodlands, while the Mortierellomycota and Glomeromycota were more abundant in croplands and grasslands. Members of the Glomeromycota form endomycorrhizae with the roots of roughly 70% of the world's plants, including many crops, in which they help improve plant nutrient uptake and productivity (Brundrett and Tedersoo, 2018). The dominance of the Ascomycota and Basidiomycota in Australian soils might suggest that they are better equipped to use existing resources and withstand environmental stresses than the other identified

species.

Aridity controls soil fungi in Australia

Climate is an important factor controlling fungal community composition and diversity over larger scales (Maestre et al., 2015; Tedersoo et al., 2014; Delgado-Baquerizo et al., 2018). We found that climate, particularly the water balance, also indirectly controls the relative abundance of the two dominant phyla and community diversity via its strong effect on ecosystem type, the ensuing vegetation and soil. The climate and water balance effects were opposite on the Ascomycota and Basidiomycota. The Basidiomycota tend to prefer more humid environments, while the Ascomycota showed a clear preference for drier environments. Unlike other similar studies that report only minor effects of edaphic properties on soil fungi (Maestre et al., 2015; Tedersoo et al., 2014), we found that an ecosystem's water balance indirectly affects the relative abundance of these two dominant phyla and community diversity via their influence on edaphic characteristics. Soil organic matter directly affects the relative abundance of the two dominant phyla studied, but it inversely affects community diversity, possibly because the addition of labile substrates provides a readily available source of carbon and other nutrients for microbial growth. Reducing the type of carbon available to microorganisms will tend to homogenise microbial communities (Ramirez et al., 2020; Murphy et al., 2011). We also found that soil pH has a dominant and opposite effect on the relative abundance of Ascomycota and Basidiomycota, most of which are saprophytes. Although most fungi do not require specific soil pH ranges for colonisation, habitation and growth (Rousk et al., 2009), some basophilic or acidophilic fungi are sensitive to changes in pH (Gai et al.,

2006). Compared to other fungi, saprophytes are more susceptible to soil pH (Kivlin and Hawkes, 2016).

vis–NIR spectra are useful edaphic controls on soil fungi

Soil organic matter, iron-oxides and clay mineralogy, measured by vis–NIR spectra, were important controls of the relative abundance of the Ascomycota and Basidiomycota and community diversity. They markedly improved the explanatory power of the models. Overall, our models explained 40–64% of the variation in the relative abundance and diversity of fungi in Australian soil. The soil information contained in the spectra provided additional and relevant information on the functional groups of different forms of organic matter (Viscarra Rossel and Hicks, 2015), clay minerals (Viscarra Rossel, 2011) and Fe-oxides (Viscarra Rossel et al., 2010b), which supply elements (*e.g.* iron, calcium, magnesium) needed for fungal growth (Müller, 2015). The quantity and the quality of organic matter are both important for microbial growth and activity (Baldock et al., 1992). Thus, models with the spectra as additional explanatory variables were markedly better (by up to 40%) than models based solely on soil properties and environmental covariates. Hence, compared to other large-scale studies, on average, our models explained around 20% more of the variation in community diversity and around 10% more of the variation in relative phyla abundance (Tedersoo et al., 2014; Větrovský et al., 2019). Although vis–NIR spectra successfully explained bacterial abundance and diversity (Zornoza et al., 2008; Yang et al., 2019), we found no published research that uses soil spectra as explanatory variables of soil fungi.

The data used

We used one of the most extensive and inclusive continental-scale datasets on soil fungi and, for the first time, used climatic, edaphic and other environmental data in combination with vis–NIR spectra to help explain the variation and distribution of dominant fungi and community diversity in Australian soils, and to elucidate their interactive controls. The dataset covers all of Australia, its four most extensive ecosystems and climates (Bissett et al., 2016). We obtained 60 million sequences across all samples, an average of 107,310 sequences and 666 OTUs per sample, mainly resulting in saturated rarefaction curves (Supplementary Fig. S1), which indicates an adequate representation of the most common species in those soils. Thus, although we have likely underestimated the actual diversity of soil fungi, the dataset and methodology that we used are suitable for the research presented.

Future considerations

Here, we focused on modelling the relative abundance of the dominant soil fungal phyla and community diversity in Australia's main ecosystems with a wide range of environmental covariates, including vis–NIR spectra, to ascertain their environmental controls and interactions. But, we acknowledge that the BASE dataset (Bissett et al., 2016) has a limited representation of the highly diverse tropical ecosystems in northern Queensland, which restricted the number of fungal taxa characteristics of those biomes. Future research should include samples of soils from tropical regions in Australia to identify common and, therefore, potentially functionally significant members of the soil mycobiome. An expanded sampling campaign would also improve the modelling. It could help to resolve the effects of those environmental factors

on different fungal ecological guilds to understand better the importance of fungal adaptation, migration and acclimatisation to global change and to test whether fungi can track changes in climate (Bidartondo et al., 2018).

Our results indicate the potential for developing more rapid and cost-efficient methods to estimate the relative abundance and diversity of soil fungi. Therefore, our findings could also guide methodological development towards more rapid and cost-efficient characterisation of soil fungi. Although such estimates might not be as precise as sequencing technologies, spectroscopic measurements integratively characterise the soil's mineral and organic composition. They are also inexpensive so that one can make many measurements across space and in time. Such an approach might complement molecular techniques for the assessment, characterisation and improved understanding of soil fungal communities and their associated functions (Hart et al., 2020).

Final remarks

Disentangling the interactive environmental controls of soil fungi and their diversity to understand their distributions over large scales better is an important goal in fungal ecology: soil fungi are among the most ecologically relevant organisms. The research presented here improves understanding of the links and interactions between the dominant soil fungi, their diversity, and soil, plants and other environment properties at a macroecological scale. In addition, it helps to explain what the environmental controls of soil fungi are and their interactions across Australia's diverse ecosystems and climates. Exploring such interactive effects is essential for understanding ecosystem stability and resilience and for developing management strategies to conserve

these organisms and their functions, including the adaptation and mitigation of global change. Our findings might serve as a baseline against which to monitor possible shifts in the dominant soil fungi in Australia, which we need for developing strategies to preserve soil microbial diversity and functionality.

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Author contributions

RAVR conceived the study and with YY performed the bioinformatics, machine learning and SEM analysis. AB performed the workflow to pick OTUs and assign read abundance to a Sample-by-OTU matrix. RAVR wrote and edited the manuscript with input from YY. AB, TB, KD, PN, SL provided input to the writing and editing of different sections of the manuscript. RAVR and YY revised the manuscript with input from all authors.

Conflict of interest statement

The authors declare no competing financial interests.

Data availability

The BASE data are available online at DOI: 10.1186/s13742-016-0126-5. The spectra are deposited at DOI: 10.5281/zenodo.6265730

Code availability

The scripts used in this study are available from the corresponding author upon reasonable request.

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Tables

Table 1: The coefficient of determination (R^2) of models for fungal abundance and diversity derived by a 10-fold cross-validation using all data (n = 577). The last column indicates the % improvement in the models by additionally including the vis–NIR spectra.

Fungal phyla and diversity	Model without the vis–NIR variables	Model with the vis–NIR variables	% improvement
Ascomycota	0.42	0.50	19
Basidiomycota	0.51	0.60	18
Mortierellomycota	0.60	0.63	5
Glomeromycota	0.31	0.40	29
Mucoromycota	0.59	0.64	8
Diversity	0.30	0.42	40

Figures

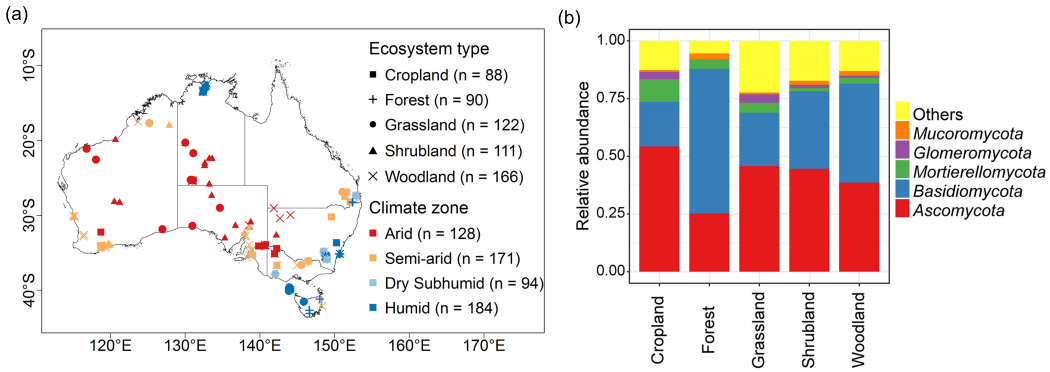

Figure 1: (a) Sample locations across Australia and the range of Australian ecosystem types and climate zones. (b) Relative abundances of dominant soil fungal phylotypes in five major Australian ecosystem types.

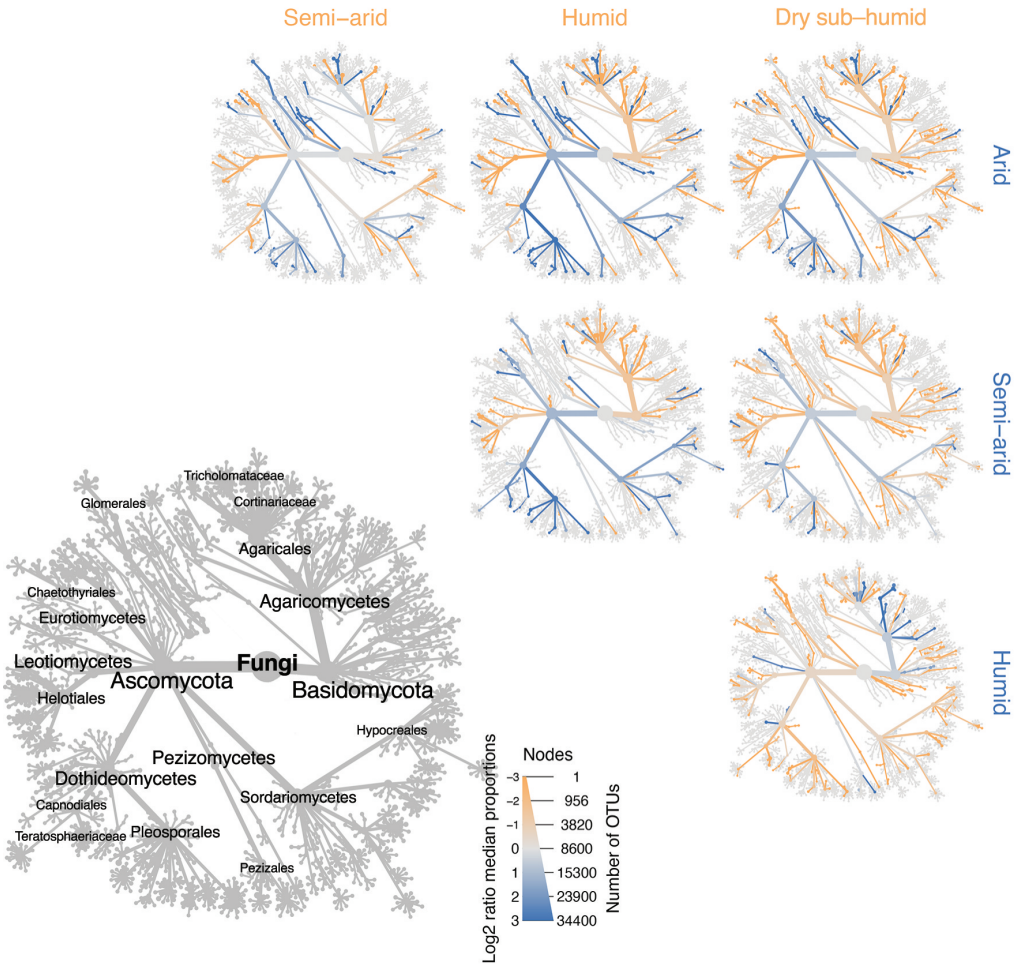

Figure 2: Taxonomic tree for the phyla Ascomycota and Basidiomycota. The grey tree on the lower left provides a key for the unlabelled, coloured tree matrix. Each of the smaller (coloured) trees represent a comparison between climate zones. A taxon coloured orange is more abundant in the climate zone depicted in the columns and a taxon coloured blue is more abundant in the climate zone of the rows. For example, the Ascomycotaare generally more abundant in the arid and semi-arid zones, while the Basidiomycota are geberally more abundant in the humid zone. The tree was drawn using the `metacoder` library in R (Foster et al., 2017) by first filtering out rare and unclassified and unknown taxa.

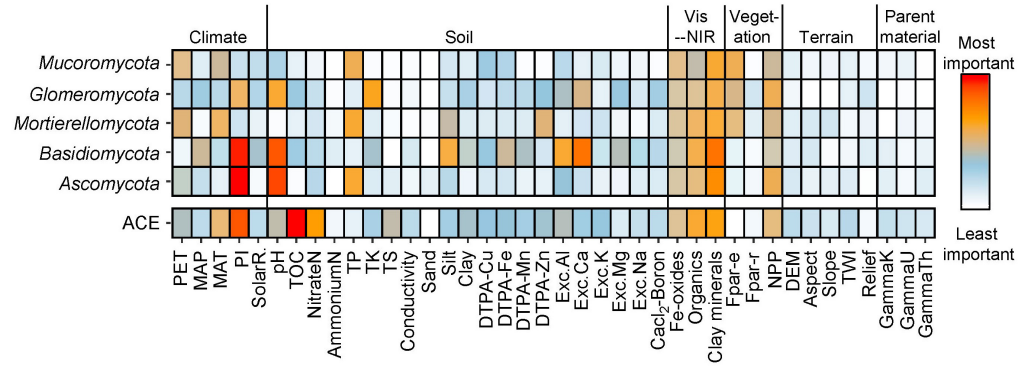

Figure 3: Important controls on the relative abundance of fungal phyla and diversity of soil fungi in Australia, described by the variable importance of the CUBIST models (n = 577). Diversity is measured with the abundance-based coverage estimator (ACE) index (Lozupone and Knight, 2008). The vis–NIR wavelengths were aggregated to represent Fe-oxides, clay mineral, and organics (Viscarra Rossel et al., 2010a; Viscarra Rossel, 2011; Viscarra Rossel and Hicks, 2015).

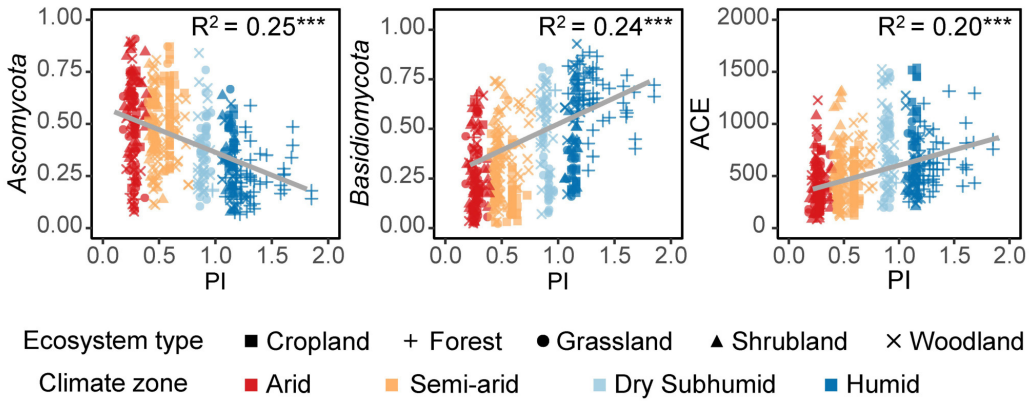

Figure 4: Relationship between the Prescott index, which represents water balance, and the relative abundance of the most dominant fungal phyla and diversity, measured with the ACE index. Significance level was shown with $^{***}P \leq 0.001$.

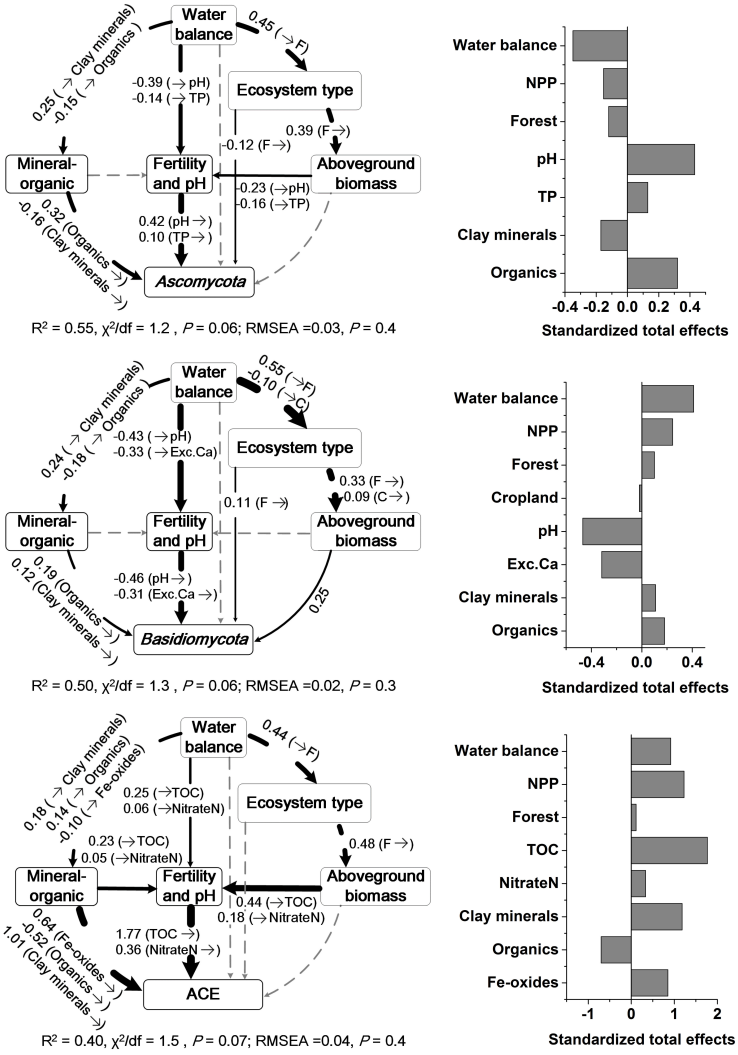

Figure 5: Path diagrams of the effects of water balance, ecosystem type (C = Cropland; F = Forest), above-ground biomass, the mineral and organic composition of soil, and soil pH and fertility, on the relative abundance and diversity of soil fungi in Australia. Solid and dotted lines indicate significant and insignificant paths respectively ($P < 0.05$). Line width is proportional to the strength of path coefficients. Numbers are the standardized effects, and negative effects are indicated by minus signs. The standardized total effects are the sum of direct and indirect effects from each predictor on a particular response.