

Microbial communities are associated with indicators of soil surface condition across a continental gradient

Jingyi Ding^{a,b,*}, Samantha Kay Travers^b, David John Eldridge^b

^a State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China

^b Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

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ABSTRACT

Soil microbes support multiple ecosystem functions in woody biomes and are regulated by both plant communities and soil properties. While most microbes reside in the uppermost soil layer, we have a poor understanding of how the condition of the soil surface affects soil microbes across different woody biomes. This knowledge is important because it could provide a cost-effective means of predicting the extent to which different soil surface types could be useful predictors of microbial communities in soil health monitoring programs. We collected data on soil bacterial and fungal communities, and 13 soil surface indicators and grazing intensity at 173 sites in eastern Australia along a climatic gradient (humid to arid) varying in tree cover. Our aim was to investigate potential relationships among the condition of the soil surface and soil microbes in forests and non-forests using linear regressions, correlations and structural equation modelling. We found that both bacterial and fungal richness were closely associated with measures of soil surface condition, particularly in forests. Greater microbial diversity was related to enhanced plant structure and richness, and lower litter characteristics in both ecosystems. In forests, these relationships were enhanced by higher temperatures or suppressed by greater tree richness. Bacterial and fungal communities responded differently to changes in soil surface attributes in forests, with winners (e.g., Proteobacteria) and losers (e.g., Cyanobacteria) among bacterial phyla, but consistent responses across fungal phyla. Our study provides empirical evidence of significant relationships among microbes and indicators of soil surface condition. This finding advances our understanding of plant-soil interactions, and indicates the possibility of using field-based soil surface attributes as potential cost-effective, practical, yet informative indicators to monitor changes in microbial richness and composition in forests and non-forests (open woodlands, shrublands).

1. Introduction

Woody plants cover nearly half of Earth's land surface, account for most of the aboveground productivity, and form a variety of terrestrial biomes such as forests, woodlands and shrublands (Moran and Ostrom, 2005; Pan et al., 2011). Soils in woody biomes harbor a remarkable diversity of microorganisms (Bardgett and Van Der Putten, 2014), among which, bacteria and fungi account for the largest proportion of microbial biomass, maintaining the integrity of soil food webs and essential soil functions (e.g., nutrient cycling, plant productivity, organic matter decomposition; Delgado-Baquerizo et al., 2020). Bacterial and fungal communities are known to be regulated by multiple biotic and abiotic factors, ranging from soil properties (e.g., soil pH,

carbon availability; Fierer and Jackson, 2006; Tedersoo et al., 2014) to plant traits (e.g., leaf nitrogen, root exudates; Orwin et al., 2010; López-Angulo et al., 2020). Microbial communities are most abundant in the uppermost soil surface layers where they are associated with high levels of organic matter and where micro-scale differences in morphology provide markedly different habitats and niches (Fierer et al., 2003). Despite this, we have a very poor understanding of how the condition of the soil surface, the thin boundary (uppermost ~2 cm) that connects aboveground plants and belowground soil biomes, affects soil microbial communities. The soil surface facilitates the mass/energy exchange between aboveground woody plants and belowground soil biomes, determines the resistance of soils to disturbances and is closely associated with soil multifunctionality (Maestre and Puche, 2009; Eldridge et al.,

* Corresponding author at: State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.

E-mail address: jyd@mail.bnu.edu.cn (J. Ding).

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2020a). However, global environmental changes, such as extreme drought and deforestation, cause substantial declines in woody species (Maestre et al., 2015; Pires et al., 2018), and undermine soil surface condition by reducing litter cover and weakening soil stability (Le Bissonnais et al., 2005; Ding and Eldridge, 2020a). This in turn increases the vulnerability of soil biomes to predicted environmental changes. Identifying the relationship between soil surface condition and soil microbes in woody ecosystems can allow us to improve our ability to predict changes in microbial communities under changing climatic and human-induced conditions. This could prove useful for developing conservation strategies for soil biomes by maintaining the health of the soil surface.

Soil surface attributes, such as roughness, biocrust morphology, groundstorey plants and litter, have been used as proxies of soil hydrological function, nutrient cycling and soil stability (Maestre and Puche, 2009; Eldridge and Delgado-Baquerizo, 2018a), functions that are closely related to, or depend upon, the dynamics of soil microbes. For example, soil roughness and crust stability define the capacity of soils to resist erosion (e.g., wind, runoff, rain splash), and therefore likely reflect the quality of the surface to provide niches for microbes under harsh conditions (Le Bissonnais et al., 2005; Chilton et al., 2018). Biocrusts can mitigate the negative effects of climate change on soil microbes and affect the bacterial-to-fungal ratio by altering recalcitrant carbon sources (Delgado-Baquerizo et al., 2018a). Groundstorey plants and litter buffer soils against fluctuations in climate (Fetcher et al., 1985), and determine the quantity and quality of substrate inputs (e.g., root exudates, litter), thus have the capacity to alter microbial composition (Aneja et al., 2006; De Vries et al., 2012). Additionally, herbivore dung deposited on the soil surface can alter functional groups of microbes (Eldridge and Delgado-Baquerizo, 2018b) and simplify soil food web structure (Wang et al., 2020). Recent studies suggest that both soil surface attributes and soil microbial diversity are correlated with the provision of multiple soil functions (e.g., nutrient cycling, carbon sequestration; Delgado-Baquerizo et al., 2020; Eldridge et al., 2020a), but empirical support for the relationship between soil surface condition and soil microbes is limited. If consistent and unambiguous relationships among soil surface condition and microbes were established, soil surface assessments could become a useful indicator of changes in soil microbial communities across terrestrial ecosystems (Manning et al., 2018).

The relationship between soil surface condition and soil microbes might vary with different microbial communities (e.g., bacteria, fungi) due to differences in their niche preferences and adaptation to environmental changes (Liu et al., 2020). For example, bacteria are constrained by soil environments such as pH and carbon availability, and prefer stable soils (Fierer and Jackson, 2006). Fungi, however, are affected mainly by plant traits (e.g., roots, recalcitrant carbon components) and are more tolerant to drying conditions (Austin et al., 2004; Tedersoo et al., 2014). Furthermore, such a relationship might also vary among vegetation assemblages due to differences in abiotic environments, plant species, and soil surface coverage (De Deyn et al., 2008; Maestre and Puche, 2009; Maestre et al., 2015). For example, soil surfaces in mesic forests are generally covered by dense litter produced by fast-growing trees, whereas soil surfaces in arid shrublands are typically colonized by biocrusts and subject to pronounced dryness, with low litter input from the long-lived xeric plants (Reich and Cornelissen, 2014; Legay et al., 2016). Such differences in soil environments and substrate quality would select for distinct microbial communities, which would interact in different ways with soil surface attributes (Orwin et al., 2010; De Vries et al., 2012). Current studies of soil microbes have generally been restricted to specific climatic regions or systems with the same vegetation assemblage (e.g., temperature grasslands, drylands; Bezemer et al., 2006; Maestre et al., 2015), and empirical evidence across extensive woody cover gradients from mesic to arid areas is lacking. It is largely unknown, therefore, whether soil surface-microbial relationships are consistent across different woody biomes. Our study aims to test this across an extensive climatic gradient.

We conducted a field survey at 173 sites along an extensive tree cover gradient spanning over humid, dry subhumid, semiarid and arid areas in eastern Australia to determine the relationship between soil surface attributes (13 surface indicators and grazing intensity) and the richness and composition of soil microbial communities (i.e., bacteria, fungi) in forests (tree cover > 10%; FAO, 2000) and non-forests (tree cover ≤ 10%). We had three hypotheses. First, we hypothesized that soil surface attributes indicative of soil surface health would be positively related to microbial richness (Fig. 1), with greater litter (litter cover, incorporation), plant structure (groundstorey plants, biocrusts) and soil stability (crust stability, surface roughness) associated with greater bacterial and fungal richness (Eldridge et al., 2020a). Second, we expected that this relationship would differ between bacterial and fungal communities (Fig. 1a) due to differences in their ecological niches (Liu et al., 2020). Finally, we expected that the nature of the relationship would vary with forested and non-forested systems (Fig. 1b) due to differences in climate regimes, plant communities and soil surface coverage (Maestre and Puche, 2009; Eldridge and Delgado-Baquerizo, 2018a).

2. Material and methods

2.1. Study area

This study was conducted along a 1500 km tree cover gradient in eastern Australia from east coasts to the dry interior, covering humid, dry sub-humid, semiarid and arid zones (29.0°S to 35.1°S, 140.7°E to 151.4°E; Fig. 1c). Aridity was determined as $1 - \text{precipitation/potential evapotranspiration}$ (United Nations Environment Programme, 1992), and were obtained from Consortium for Spatial Information (CGIAR-CSI) for the 1950–2000 period (Zomer et al., 2008). Average annual rainfall ranged from 1299 mm to 184 mm, changing from summer dominant in the north and east, uniform in the centre, to predominantly winter dominant in the south-west (Bureau of Meteorology, 2019; <https://www.worldclim.org/>). Average annual temperature varied from 13 °C to 21 °C along the gradient, with data derived from the WorldClim Version 2 averaged across 1970–2000 in 30 s resolution (~1km²) (<https://www.worldclim.org/>). The texture of topsoil (0–5 cm), based on field assessment, ranged from loams near the coast to clay loams in the semiarid and to loamy sands in the arid areas. Soils were generally acidic near the coast (pH 5.1 ± 0.6 ; mean \pm SD) and tended to be calcareous in arid areas (pH 7.5 ± 0.8). Vegetation communities across the gradient were highly variable, ranging from coastal forests, to semiarid woodlands and arid shrublands. Tree species were dominated by Eucalypts in humid (*Corymbia gummifera*, *Eucalyptus piperita*) and dry subhumid (*Eucalyptus punctata*, *Eucalyptus maculata*) areas, *Callitris* and *Eucalyptus* spp. in semiarid areas (*Callitris glaucophylla*, *Eucalyptus populnea*, *Eucalyptus largiflorens*), and *Eucalyptus* and *Acacia* spp. in arid areas (*Eucalyptus populnea*, *Acacia aneura*).

2.2. Field survey

We surveyed 173 sites along the gradient of tree cover, ranging from 0.6% to 80% coverage during 2015–2016 and 2018–2019. These sites were divided into forested (i.e., tree cover > 10%; 102 sites; FAO, 2000) and non-forested systems (i.e., tree cover ≤ 10%; 71 sites), with forested sites located in humid (24%), dry subhumid (22%) and semiarid (54%) areas, and non-forested sites mainly distributed in semiarid (54%) and arid (39%) areas (Fig. S1 in Appendix S1). To control for the confounding effects of climatic variability (i.e., rainfall variability, temperature variability), we sampled sites characterized by low rainfall and temperature variability (coefficient of variation, CV < 30%; calculated using monthly climatic data from WorldClim Version 2) and avoid sampling seasons with extreme weather events. Disturbance regimes and land management (e.g., cropping, clearing; Veatch et al., 2015; Xi et al., 2019) have been shown to affect soil microbes. Therefore, to avoid

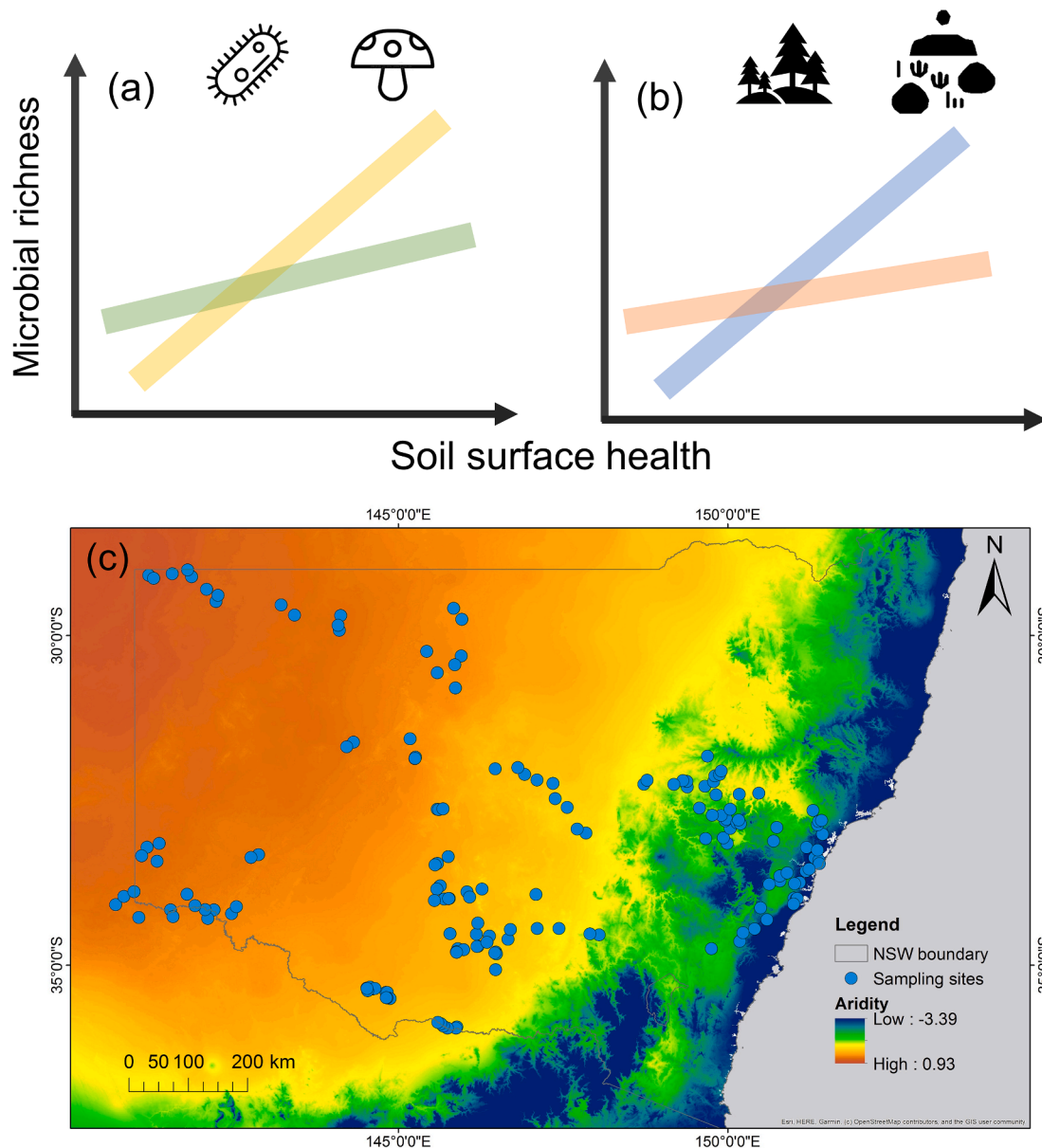


Fig. 1. (a-b) Diagram of hypotheses and (c) location of the 173 sampling sites in relation to aridity across eastern Australia. We expected that greater soil surface health would be positively related to microbial richness, and such relationships would differ among (a) microbial communities (bacteria and fungi), and (b) eco-systems (forests and non-forests).

confounding effects of these external factors on microbial richness, we chose to sample in protected areas (e.g., national parks, nature reserves, parklands, state forests) that had not burned for at least 50 years. At each site, we established a 100 m transect (i.e., belt transects), and recorded all tree species along the transect to obtain tree richness. Transect widths varied from 10 m wide at densely timbered sites to 40 m in sparse arid woodland, in order to sample at least 30 trees at each site. We measured the canopy width of each tree and recorded tree density to obtain tree canopy cover (%) at each site.

We measured the soil surface indicators (13 attributes) under two replicate dominant tree patches at each site within small circular quadrat (64 cm diameter) using a variant of the Soil Surface Condition module of Landscape Function Analysis (LFA; Tongway and Hindley, 2004; Eldridge et al., 2020a). Within each quadrat, we surveyed (1) surface roughness, (2) crust resistance, (3) crust brokenness, (4) crust stability, (5) surface integrity, (6) cover of deposited material, (7) the cover of biocrusts, (8) basal cover, (9) foliage cover, (10) plant richness,

(11) litter cover, (12) litter depth, (13) litter incorporation (See details and measurements for each attribute in Table S1 in Appendix S2). We also measured grazing intensity at each site by counting the dung of different herbivores within the quadrats and converting counts to dry mass of dung per herbivore type per hectare (kg per ha) using algorithms relating dung counts to dung mass for different herbivores (Eldridge et al., 2017a).

2.3. Soil properties and microbe analysis

A composite sample consisting of five soil cores (0–10 cm depth) was collected under the dominant trees, and samples bulked at the site level. About 5 g of soil was frozen below -20°C for soil microbe analyses and other soils were air dried to assess soil pH (1:5 soil water extract) using SMARTCHEM-Lab multi-parameter laboratory analyser (TPS Pty Ltd, Brendale, Australia). Due to the lack of continuous data on soil texture, we derived the site-level surface layer (0–5 cm) soil clay content from

the Soil and Landscape Grid of Australia database (3 arc second) to account for the variation in soil texture across the 173 sites along the extensive tree cover gradient.

We used DNeasy PowerSoil Kit (Qiagen, Hilden, Germany) to extract the microbial genomic DNA from defrosted soil samples (0.25 g) according to the manufacturer's instructions. Amplicons targeting the bacterial 16S rRNA gene (341F-805R) (Herlemann et al., 2011) and the eukaryotic 18S rRNA gene (Euk1391f/EukBr) (Ihrmark et al., 2012) were sequenced at the Next-Generation Sequencing Facility, University of Western Sydney (Sydney, Australia) on the Illumina MiSeq platform using Illumina MiSeq 2x 301 bp (16S, 18S) paired end sequencing. DNA extraction and sequencing was conducted in 2016 and 2020. The maximum expected error was set as 1.0 for the merged reads filtering using USEARCH (Edgar, 2010). zOTUs (denoised sequences) were gained by denoising (error-correction) the amplicon reads using unoise3 (Edgar, 2016). Representative sequences were annotated against the Silva database (Quast et al., 2013) in QIIME (Caporaso et al., 2010) using UCLUST (Edgar, 2010). We further categorized soil microbes into functional groups. The functional prediction tools for bacteria (e.g., PICRUSt, PICRUSt2, Tax4Fun or FAPROTAX) were originally developed for non-environmental samples. Their performance on short amplicons (e.g., soil microbes in our study), however, rarely provide sufficient taxonomic discrimination at the genus level (Sun et al., 2020). We use therefore only fungal functional predictions based on FUNGuild Version 1.0 (Nguyen et al., 2016), which are more widely used in soil research and more reliable. The OTU abundance tables were rarefied to an even number of sequences per sample. We used species richness (i.e., number of phylotypes or zOTUs) as a measure of microbial richness. Species richness is the most used and the simplest metric of biodiversity (Gotelli, and Colwell, 2011; Delgado-Baquerizo et al., 2020), and is the major predictor of ecosystem functions in both forests and drylands (Maestre et al., 2012; Chisholm et al., 2013). It can effectively represent the role of species diversity in ecological processes and help generate findings that can be widely applicable. We also assessed the relative abundance of the major phyla for bacteria and fungi in each site.

2.4. Statistical analysis

We fitted linear and nonlinear (log transformed soil surface attributes) relationships between soil surface attributes (13 soil surface indicators and grazing intensity), and microbial (i.e., bacterial and fungal) richness for forests and non-forests to explore whether microbial richness varies with changes in soil surface attributes. After comparing the AIC of these two types of models (Table S2 in Appendix S3), we retained the simple linear relationship (microbial richness ~ soil surface attributes; Table S3 in Appendix S3) to ensure that the results were comparable across all the models based on the same model structure. However, the significant linear relationships between microbial richness and soil surface condition detected in our study have limited application for predicting microbial richness using soil surface attributes such as foliage cover, biocrust cover, basal cover and grazing intensity due to their skewed data distributions. We undertook further Spearman correlation analyses between soil surface attributes and the relative abundance of different bacterial and fungal phyla for forests and non-forests, respectively. Correlation analyses were conducted in SPSS 26.0 (IBM, Chicago, IL), linear regressions fitted in R 3.4.1 version (R Core Team, 2018) and figures created using the 'ggplot2' package (Wickham, 2016).

We then used Structural Equation Modelling (SEM; Grace, 2006) to explore the impact of climate (aridity, temperature), soil (pH, clay), tree attributes (canopy cover, tree richness) and soil surface condition on bacterial richness and fungal richness in forests and non-forests, respectively. After excluding colinear soil surface attributes based on the variance inflation factor test (i.e., crust brokenness and litter cover were excluded), we used random forest to select the major soil surface attributes. We ran random forest analyses for bacterial richness and fungal richness respectively, with the raw values of soil surface

attributes as predictors (Fig. S2 in Appendix S4). To ensure that the effects of soil surface attributes were comparable between the SEMs for bacteria and fungi, we selected predictors that were significant ($P < 0.05$) or at least marginally significant ($P = 0.06$ for biocrust cover for fungal richness) for both bacterial richness and fungal richness based on random forests (Table S4 in Appendix S4). Finally, we identified five soil surface attributes as key predictors of microbial richness: litter depth, deposited material, foliage cover, groundstorey plant richness and biocrust cover. Structural equation modelling allowed us to test our hypothesized relationships among predictors and microbial richness based on an *a priori* model (see Fig. S3 in Appendix S5) that constructs pathways among model terms based on prior knowledge (Table S5 in Appendix S5). Our *a priori* model predicted that climate would affect soil properties and tree attributes, and these factors would affect microbial richness directly or indirectly by influencing soil surface attributes. Models with low χ^2 and Root Mean Error of Approximation (RMSEA < 0.05), and high Goodness of Fit Index (GFI) and R^2 were selected as the best fit model for our data. In addition, we calculated the standardized total effects to show the total effect of each variable. Random forest was performed in the 'rfPermute' package (Archer, 2016) in R 3.4.1 version (R Core Team, 2018) and SEM was performed using SPSS AMOS 22 (IBM, Chicago, IL, USA) software.

3. Results

3.1. Soil surface attributes are related to microbial richness in both forests and non-forests

Bacterial and fungal richness showed a similar, significant response to changes in soil surface attributes in forests (Fig. 2). Greater microbial richness was associated with greater soil stability (e.g., surface roughness, crust resistance, crust stability), plant structure (e.g., biocrust cover, foliage cover and richness) and deposited material (i.e., amount of material moved during erosion), but lower surface integrity and litter. By comparison, in non-forests, only around half of the soil surface attributes changed significantly with microbial richness, with no relationship between microbial richness and soil stability, surface integrity and grazing intensity (Fig. 3).

Different microbial phyla had contrasting relationships with soil surface attributes. In forests, the relative abundance of Actinobacteria, Proteobacteria, Acidobacteria, Verrucomicrobia, and Zygomycota was positively related to litter cover, depth and incorporation, and surface integrity, but negatively related to grazing intensity, deposited material and measures of soil stability and plant structure (Fig. 4). Conversely, the relative abundance of Chloroflexi, Planctomycetes, Gemmatimonadetes, Cyanobacteria, Firmicutes, Ascomycota, Basidiomycota and most fungal functional groups had opposite relationships with these soil surface attributes. In contrast, there were 80% fewer significant associations among soil surface attributes and microbial phyla in non-forests than forests (Fig. 4). For example, the relative abundance of Proteobacteria, Acidobacteria, Gemmatimonadetes, Firmicutes and Basidiomycota was associated mainly with litter, and only the relative abundance of dung saprotrophs was positively related to plant structure and grazing intensity.

3.2. Climate, soil and trees are associated with microbial richness via soil surface attributes

Microbial richness was correlated with different soil surface attributes in forests and non-forests (Fig. 5), with increasing microbial richness associated with greater biocrust cover, plant richness and deposited material in forests, but greater plant richness and foliage cover in non-forests. Climate, soil and tree attributes affected microbes in different ways in forests and non-forests through their relationship with various soil surface attributes. For example, greater tree richness reduced bacterial richness directly in non-forests and indirectly in

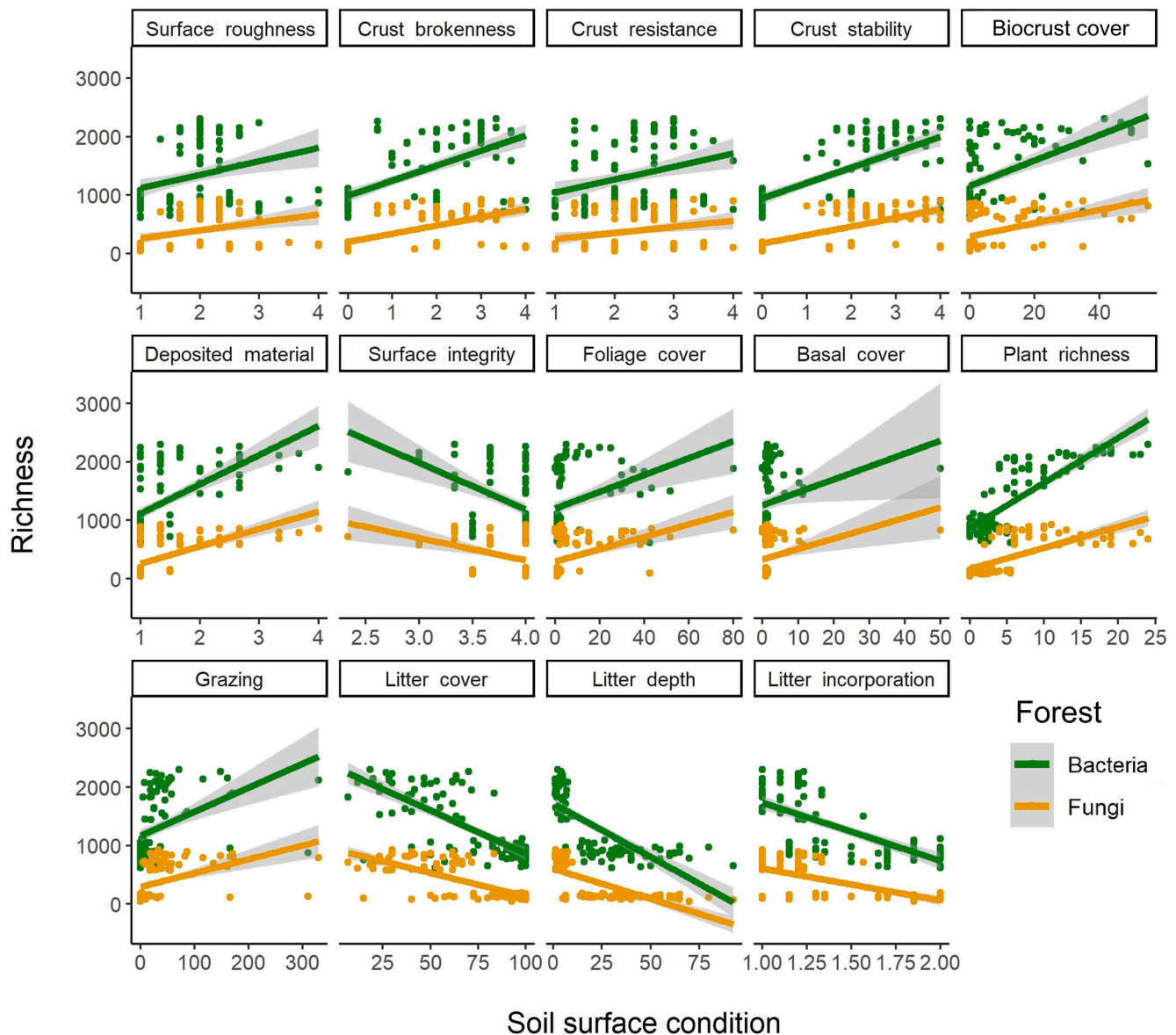


Fig. 2. Variation of microbial richness (bacterial and fungal richness) in relation to soil surface attributes (13 surface indicators and grazing intensity) in forests. All the linear relationships are significant and the shaded zone represents the 95% confidence interval. Further details on model fit are provided in Table S3 in Appendix S3.

forests through a suppressive effect on groundstorey plant richness (Fig. 5a, 5c). Similarly, increasing temperature directly reduced fungal richness in both forests and non-forests, but indirectly enhanced fungal richness in forests by promoting groundstorey plant richness (Fig. 5b, 5d). Aridity affected microbial richness predominantly indirectly by regulating soil properties. Aridity enhanced both bacterial and fungal richness in forests through its positive association with soil clay, but it reduced bacterial richness in non-forests through its positive association with soil pH.

4. Discussion

Our study provides clear empirical evidence of the close association between indicators of soil surface condition and soil microbial richness. Such a relationship varied with forested and non-forested systems and was either mitigated or enhanced by changes in temperature and tree richness. Bacterial and fungal communities also differed in their relationships with soil surface condition, with clear bacterial winners and

losers but little taxon discrimination for fungi. This study extends our understanding of how the soil surface might interact with the below-ground soil biome, highlighting the importance of protecting soil microbial communities by maintaining the health of the soil surface.

4.1. Soil surface condition is closely associated with microbial richness

Bacterial and fungal richness increased as groundstorey foliage cover, groundstorey plant richness, biocrust cover, and the cover of deposited material increased, but declined with decreasing litter (i.e., litter cover, depth or incorporation) in both forests and non-forests. Vascular plants (Fetcher et al., 1985) and biocrusts (Chilton et al., 2018) provide important habitat for soil microbes, help to buffer climatic variability (Delgado-Baquerizo et al., 2018a; Ding and Eldridge, 2021b), enhance soil moisture (Miralles et al., 2020) and protect soils against erosion (Le Bissonnais et al., 2005). A richer plant groundstorey can also provide a greater range of root types and exudates, thereby promoting a richer microbial community (Bezemer et al., 2006; Legay

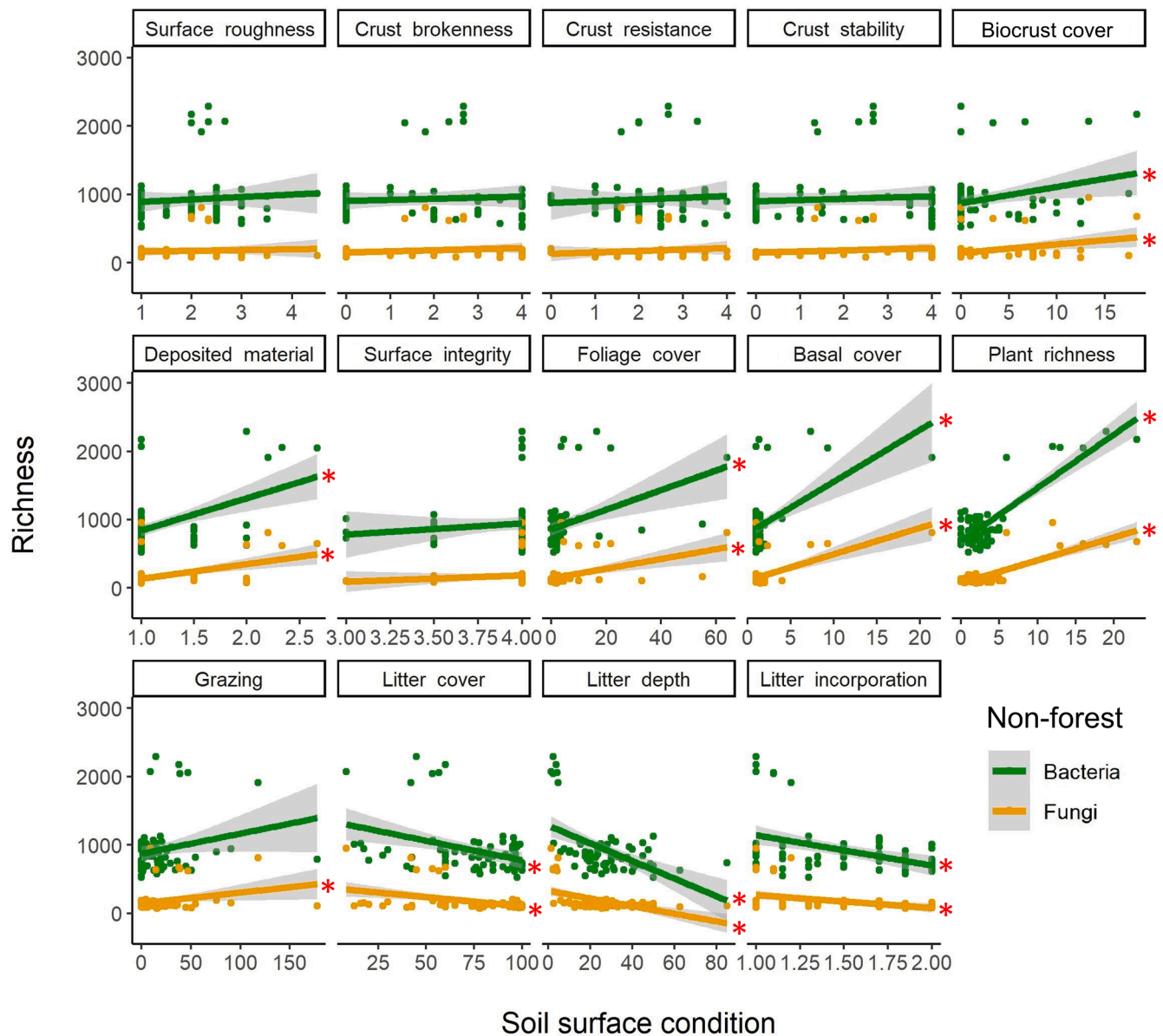


Fig. 3. Variation of microbial richness (bacterial and fungal richness) in relation to soil surface attributes (13 surface indicators and grazing intensity) in non-forests. Significant relationships are indicated by red *, and the shaded zone represents the 95% confidence interval. Further details on model fit are provided in Table S3 in Appendix S3.

et al., 2014). Unexpectedly, we detected a negative relationship between litter and microbial richness, possibly due to the creation of homogenized anaerobic conditions by oxidizing bacteria and dense litter cover under trees (Tiedje et al., 1984; Bardgett and Van Der Putten, 2014). Furthermore, eucalypts (dominated 69% of our study sites) are known to be allelopathic by releasing phenolic acids and volatile oils from their decomposing leaves, potentially suppressing belowground microbial communities (Zhang and Fu, 2009). Contrary to the general view of the negative effect of erosion, we found that low surface integrity and greater cover of deposited material, attributes of historic erosion, were associated with greater microbial richness. Water and wind erosion can deposit fine particles with associated nutrients and pioneering microorganisms, which would likely enhance niche heterogeneity and enrich microbial species pool (Li et al., 2015; Ma et al., 2017).

Microbial richness was related to grazing intensity and our measure of soil stability (i.e., crust brokenness, resistance and stability), but only in forests. Soil stability relates closely to crust development stage (Miralles et al., 2020), with more developed, later stage biocrusts (e.g.,

mosses) characterized by higher stability (Gao et al., 2020) and greater microbial species (Chilton et al., 2018). Such a relationship was pronounced only in forests, possibly because soil surfaces in forested systems are dominated by dense litter (Krishna and Mohan, 2017). Thus, greater soil stability might play a more important role in harboring microbes and mitigating the impact of erosion (Seitz et al., 2017). Contrary to the well-known detrimental effects of overgrazing (Wang et al., 2020), we detected a positive relationship between grazing intensity and microbial richness in forests. This is possibly a consequence of different herbivore guilds across forested and non-forested systems, with kangaroos (*Macropus* spp.) dominating in forests but both kangaroos and livestock dominating in more open (non-forest) communities. Kangaroos are thought to exert a less suppression effect on soil surface (Eldridge et al., 2017b; Eldridge et al., 2020b), and a higher grazing intensity might promote microbial richness by suppressing the dominant microbial phylum and releasing subordinate microbial taxon from competition exclusion (Eldridge et al., 2017b).

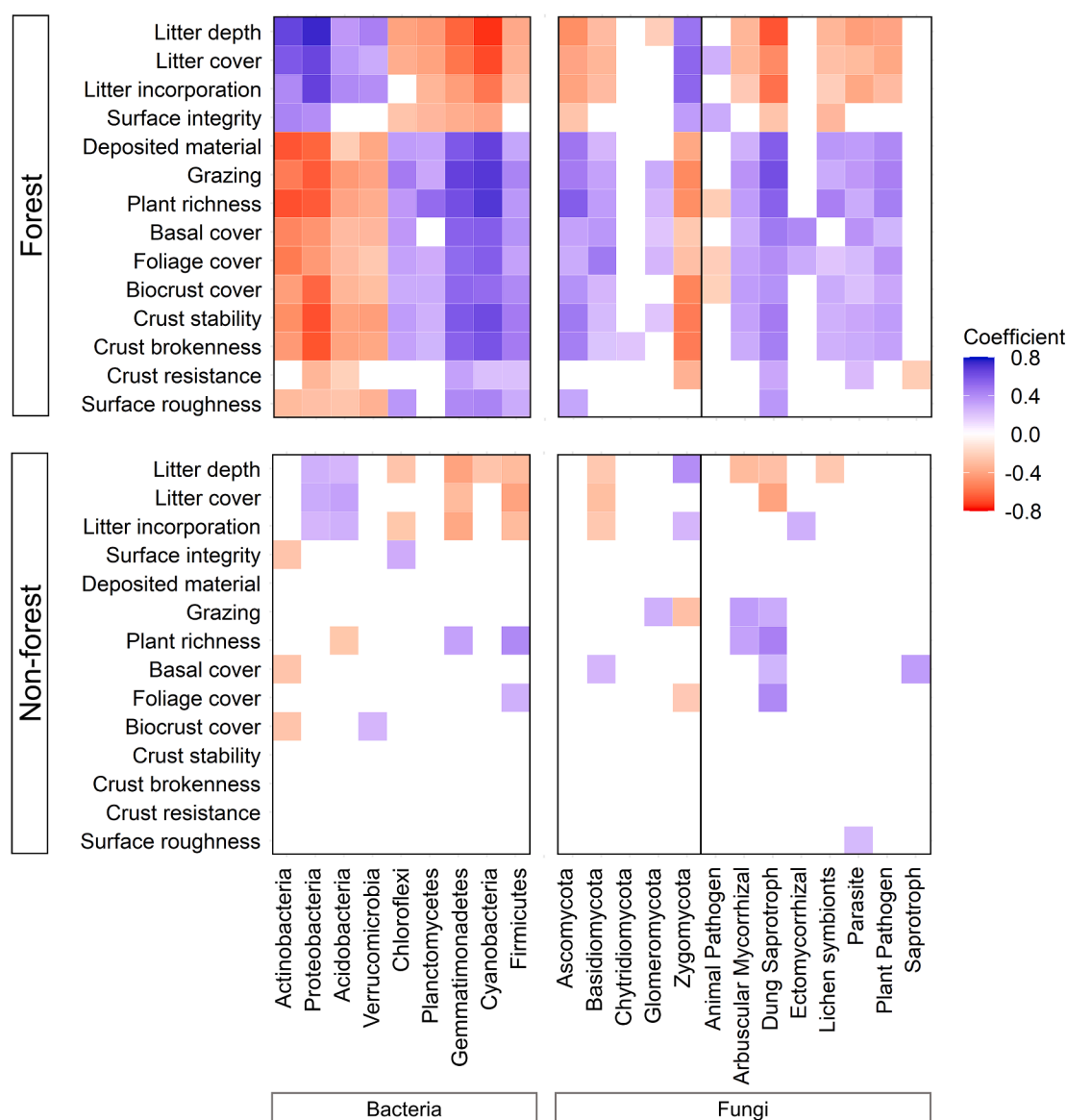


Fig. 4. Heatmap of Spearman correlations between the relative abundance of microbial phyla and soil surface attributes (13 surface indicators and grazing intensity) in forests and non-forests. Only significant ($P < 0.05$) correlations are shown.

4.2. Varied association among bacterial and fungal phyla and soil surface attributes

Despite similar responses in bacterial and fungal richness, we found marked differences at the phylum level, particularly for bacterial phyla. For example, the abundance of Cyanobacteria was associated positively with soil stability but negatively with litter input. Cyanobacteria are early pioneers of biocrusts (Chilton et al., 2018), which promote soil stabilization, but are likely to be suppressed by greater litter due to light deprivation and niche competition (Ding and Eldridge, 2020a). Conversely, Actinobacteria, Acidobacteria and Proteobacteria, the dominant bacterial phyla in drylands (Delgado-Baquerizo et al., 2018b), are metabolically active in decomposing litter due to their broad array of genes capable of catabolizing recalcitrant organic compounds such as lignin, chitin and cellulose (Battistuzzi and Hedges, 2009; Delgado-Baquerizo et al., 2020). Unlike Cyanobacteria, these common bacterial phyla might be more abundant in less stable soils due to their high tolerance of environmental harshness (e.g., Actinobacteria; Battistuzzi and Hedges, 2009) and their ability to thrive in oligotrophic (carbon-poor) environments (e.g., Acidobacteria; Ramin and Allison, 2019).

Apart from phylum Zygomycota, fungal phyla generally showed a consistent response to changes in soil surface attributes in forests. Arbuscular mycorrhizal fungi, for example, are biotrophs that depend on plant hosts for their carbon supply (da Silva et al., 2020), thus explaining its positive relationship with groundstorey foliage cover and plant richness rather than litter. By comparison, Zygomycota have generally fast-growing copiotrophic lifestyles that depend on a high carbon input (Chigineva et al., 2009); hence having greater positive association with litter. However, there were only a few significant relationships (15%) in non-forested systems, with bacterial and fungal phyla associated mainly with litter. The most parsimonious explanation relates to the disproportionate contribution of soil surface attributes to soil microbes in non-forests. Soil surfaces in non-forests (open woodlands, savannas, grasslands, shrublands) are dominated by biocrusts, with relatively lower litter inputs (Ding and Eldridge, 2020a). Hence, increases in litter in non-forested systems would likely induce significant increases in substrate suitability for bacteria and fungi (Aneja et al., 2006). Similarly, litter also buffers soils against fluctuations in climate and mitigates temperature stress on microbes, a situation that is critical in non-forests due to the paucity of canopy shading (Fanin et al., 2014).

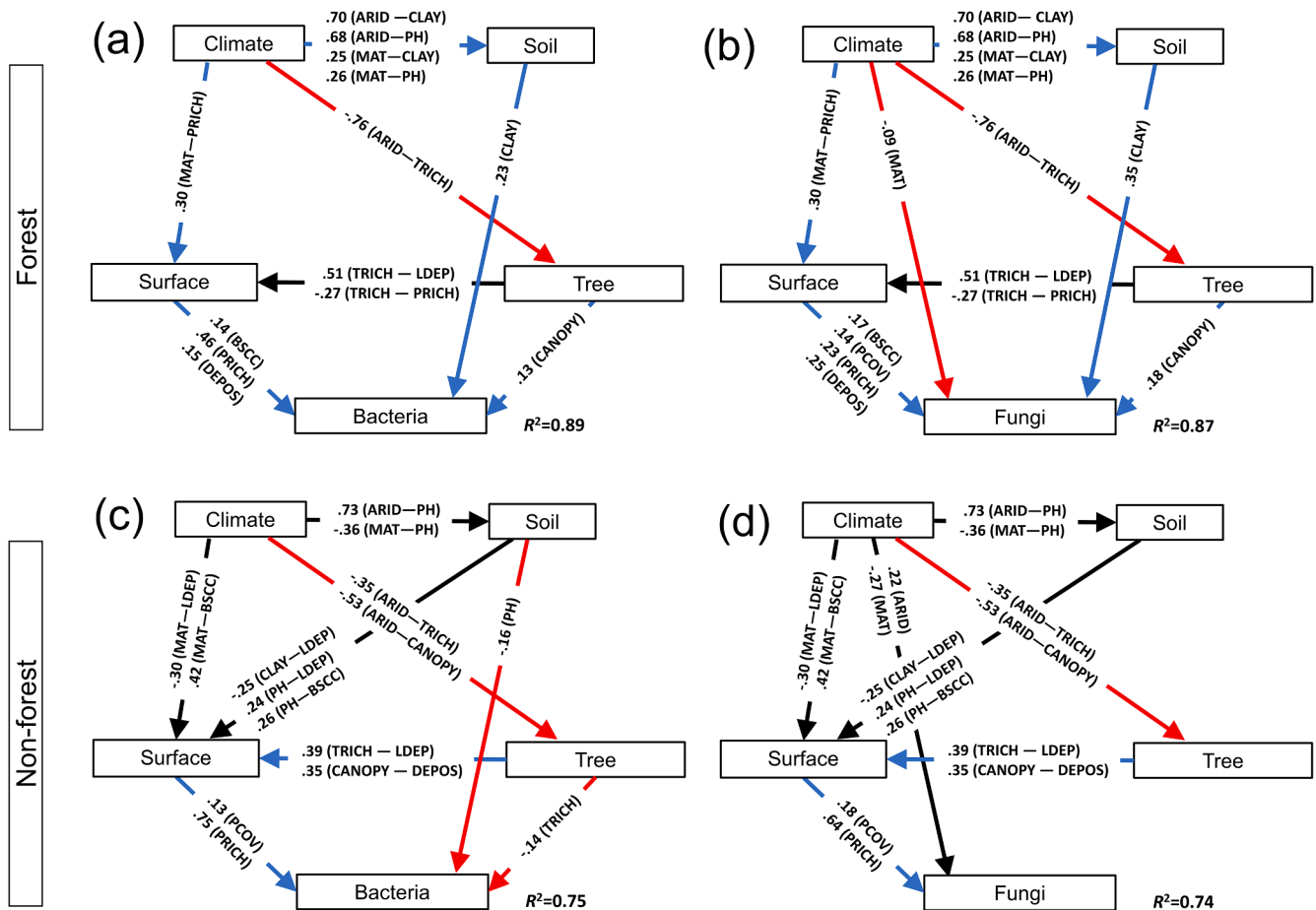


Fig. 5. Structural equation models depicting the direct and indirect effects of climate (aridity, temperature), soil (pH, clay), tree attributes (tree richness, canopy cover), and soil surface attributes (biocrust cover, plant richness, foliage cover, deposited material, litter depth) on microbial richness (bacterial richness, fungal richness) in forests and non-forests. ARID, aridity; MAT, mean annual temperature; PH, soil pH; CLAY, soil clay content; TRICH, tree richness; CANOPY, tree canopy cover; BSCC, biocrust cover; PRICH, plant richness of groundstorey plants; PCOV, foliage cover of groundstorey plants; DEPOS, deposited material cover; LDEP, litter depth. Standardized path coefficients, adjacent to the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Pathways are significant negative (red unbroken line), significant positive (blue unbroken line) or mixed significant negative and significant positive (black unbroken lines). Non-significant pathways were not shown in the models. Model fit: (a) bacteria in forest $\chi^2 = 0.06$, $df = 1$, $P = 0.82$, $R^2 = 0.89$, root mean error of approximation (RMSEA) = 0, Bollen-Stine = 0.82 (2000 bootstrap); (b) fungi in forest $\chi^2 = 0.06$, $df = 1$, $P = 0.82$, $R^2 = 0.87$, root mean error of approximation (RMSEA) = 0, Bollen-Stine = 0.82 (2000 bootstrap); (c) bacteria in non-forest $\chi^2 = 1.76$, $df = 1$, $P = 0.19$, $R^2 = 0.75$, root mean error of approximation (RMSEA) = 0.10, Bollen-Stine = 0.31 (2000 bootstrap); (d) fungi in non-forest $\chi^2 = 1.76$, $df = 1$, $P = 0.19$, $R^2 = 0.74$, root mean error of approximation (RMSEA) = 0.10, Bollen-Stine = 0.31 (2000 bootstrap).

4.3. Climate and trees affect microbial richness through their effects on soil surface attributes

The positive effect of soil surface condition, such as groundstorey plant richness, was either enhanced by temperature or mitigated by increasing tree richness in forests. Higher temperature can stimulate the potential germination of plants and therefore enhance nitrogen supply (Roberts et al., 1988), promoting a more diverse groundstorey composition (Steinbauer et al., 2018), and a greater variety of niche and substrates for soil microbes. A more diverse tree community, however, is likely to exclude groundstorey plants through 1) intense competition for resources such as water and nutrients (Munzbergova and Ward, 2002), 2) reduced light penetration, and 3) suppression of plant germination via litter burial (Barbier et al., 2008), resulting in fewer belowground microbial taxa. We found that a richer assemblage of tree species was also negatively associated with bacterial richness in non-forests. Despite the expected wider range of litter qualities with richer tree species, trees in non-forests such as semiarid woodlands are characterized by high resource-use efficiency (Reich and Cornelissen, 2014). The low levels of nutrients and high levels of recalcitrant carbon in their litter would

select for distinct bacterial communities such as those with oligotrophic lifestyles rather than a wide range of microbial species (Wardle et al., 2004; Legay et al., 2014). This adverse effect of richer trees on soil microbes suggests that global forest restoration projects (e.g., Plant-for-Planet and A Trillion Tree projects; Bastin et al., 2019) that aim to mitigate climate change by planting different tree species may possibly compromise ecosystem functions such as soil carbon sequestration and nutrient cycling.

Aridity affected bacterial richness indirectly by either enhancing the positive effect of soil clay in forests or by exacerbating the negative effect of soil pH in non-forests. In forests, increasing dryness would reduce the proportion of fine particles that are dispersed by runoff (Garner and Steinberger, 1989) and result in higher soil clay content which is positively related to soil organic carbon, nutrient availability and water retention, that are crucial drivers of microbial richness (Hansel et al., 2008). Higher soil pH in non-forested systems is known to suppress microbial activity and reduce bacterial diversity (Fierer and Jackson, 2006), and this effect has been shown to intensify as sites become drier due to weakened soil leaching (Ding and Eldridge, 2021b). However, we detected a positive association between aridity and fungal richness in

non-forests. Fungi are generally more tolerant of dryness than bacteria (Austin et al., 2004), and the abundance of fungal phyla is more likely to increase in low productivity systems where plants produce low quality litter (Wardle et al., 2004; Orwin et al., 2010), resulting in a richer fungal community in drier environments.

5. Conclusions

Our study provides new insights into the potential utility of measurements of soil surface condition as proxies for soil microbial richness and composition in different woody-dominated ecosystems. We also demonstrate the close association between all the 13 soil surface indicators and grazing intensity, and soil microbes, particularly in forests. Our results provide support for the notion that soil surface morphology and structure are useful, simple, cost-effective and practical indicators of changes in soil microbes, which are cryptic and difficult to monitor in the field (*sensu* Eldridge et al., 2020a). Furthermore, we highlight the fact that increased tree richness potentially has negative impacts on soil microbial richness in forests due to its association with the suppression of groundstorey plant richness, which indicates that aboveground and belowground diversity are not always positively coupled (De Deyn and Van der Putten, 2005). It demonstrates that trade-offs in ecosystem functions may occur in forests due to negative associations between tree species and soil microbes (e.g., bacteria). However, the extent to which these changes in microbial communities will translate to altered functional effects on ecosystems is unknown. Consequently, agencies tasked with reforestation programs need to be cognizant of the potential long-term impacts of widespread tree plantings in areas that might not be sustainable and might compromise the role of soil microbes in maintaining ecosystem function.

Author contributions

JD, DE and ST conceived the ideas, designed the research and collected the data. JD performed the statistical analyses. JD wrote the manuscript draft and, DE and ST critically revised the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data statement

Data are available via the Figshare repository (<https://doi.org/10.6084/m9.figshare.14129438.v1>).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2021.115439>.

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