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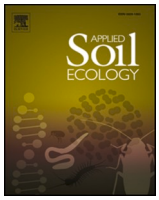

Drivers of soil biodiversity vary with organism type along an extensive aridity gradient

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ABSTRACT

Soils harbor a diverse range of biodiversity, including microbes and soil animals, which are crucial in supporting ecosystem functions. Despite the well-known effects of biotic and abiotic factors on soil biodiversity, their relative importance on different soil organisms remains less known, reducing our ability to maintain multiple soil communities under environmental changes. We sampled 150 sites from humid to arid areas in eastern Australia to explore the direct and indirect effect of climate (aridity, temperature), soil properties (pH, texture, infiltrability), plants (woody structure and plant richness) and soil surface attributes (litter, biocrusts, surface morphology) on overall soil biodiversity and the richness of bacteria, fungi, invertebrates and protists. We found that the relative importance of biotic and abiotic attributes varied with soil organisms and specific phylum, with bacterial richness related to soil pH, total plant richness and surface stability, fungal richness associated with litter, invertebrate richness related to aridity and total plant richness, and protist richness associated with soil pH. Larger tree canopies, greater tree spacing and increasing aridity either suppressed (bacteria, fungi, protists) or enhanced (invertebrates) richness indirectly by either exacerbating the negative effect of litter depth and soil pH, or promoting the positive effect of groundstorey foliage cover. Our study provides empirical evidence of how different soil organisms respond to environmental changes, indicating trade-offs among soil communities with no single environmental condition can maximum soil biodiversity. Moreover, our results highlight that increasing dryness would results in fewer bacterial and invertebrate species, potentially leading to declines in soil biodiversity and ecosystem functions under the predicted hotter and drier climate.

1. Introduction

Soils harbor a large proportion of global biodiversity, ranging from microscopic bacteria, fungi and protists to larger organisms such as earthworms and soil-inhabiting vertebrates (Van Der Heijden et al., 2008; Tedersoo et al., 2014). These soil organisms play important roles in ecological processes such as organic matter decomposition, nutrient cycling and biomass production, supporting multiple services and a myriad of functions simultaneously (multifunctionality; Delgado-Baquerizo et al., 2020). The biogeography of communities and their environmental drivers are among the classical ecological questions (Grisebach, 1894) and studies have explored how belowground soil microbes, invertebrates and protists are distributed at regional and global scales (Fierer and Jackson, 2006; Chen et al., 2015; Oliverio et al., 2020). Previous research has indicated that soil biodiversity is affected by a combination of biotic and abiotic factors ranging from large-scale shifts in climates to small-scale variation in soils (pH, moisture, available carbon; Fierer and Jackson, 2006; Oliverio et al., 2020), and from perennial vascular plants (Legay et al., 2014; Eisenhauer, 2016) to biological soil crusts (Delgado-Baquerizo et al., 2018). However, changes in global climates such as increasing dryness and more fluctuating rainfall could substantially alter soil environments and affect the composition of soil communities, posing challenges for global biodiversity and terrestrial functions (Pires et al., 2018; Huang et al., 2016), thereby compromising the supply of ecosystem services on which human livelihoods depend. Thus, identifying the key biotic and abiotic drivers of different soil organisms (bacteria, fungi, invertebrates, protists) along extensive climatic gradients is a global priority if we are to predict how soil communities will respond to changing environmental conditions.

The response of soil organisms to changes in biotic and abiotic attributes would be expected to vary depending on their niche preferences

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and adaptation strategies (Delgado-Baquerizo et al., 2020). For example, bacteria are constrained by soil characteristics such as pH and carbon availability, preferring the biofilms around stable and fine-textured soils (Fierer and Jackson, 2006; Dequiedt et al., 2011). Fungi, however, are regulated more by differences in plant functional traits, and are more tolerant of drying soils (Tedersoo et al., 2014; López-Angulo et al., 2020). Protists, as the key consumers in the soil food web, generally vary with large-scale shifts in precipitation and temperature (Oliverio et al., 2020), whereas soil invertebrates (mites, nematodes) are more sensitive to changes in soil moisture (Sylvain et al., 2014). Moreover, different soil organisms play different roles in soil processes (Delgado-Baquerizo et al., 2020; Van Der Heijden et al., 2008) and they are likely to show clearly-defined responses to changes in environmental conditions. For example, fungal communities regulate nutrient cycling through their association with plant roots (Powell and Rillig, 2018) whereas larger soil invertebrates stimulate soil nutrient fluxes either by vertical movement (Dowdy, 1944) or by predation on soil microorganisms (Hättenschwiler and Gasser, 2005). Previous studies of soil biodiversity, however, have been largely restricted to soil microbes (bacteria, fungi) and a relatively narrow set of biomes (temperate forests, grasslands, drylands; Thoms et al., 2010; Legay et al., 2014; Maestre et al., 2015). This more nuanced approach has tended to limit our ability to identify the key environmental drivers of different soil organisms across a broad climatic envelope.

Biotic and abiotic factors can interact and regulate soil biodiversity simultaneously. For example, soil properties (pH, moisture and texture) can affect soil biodiversity through their effects on plant communities, which are known to maintain soil biomes by concentrating resources (fertile islands; Ochoa-Hueso et al., 2018) or by buffering the effects of climatic variability (Fetcher et al., 1985). Soils and plants can also affect soil biodiversity indirectly by changing conditions at the immediate surface (e.g., litter, biocrusts and soil morphology, Tongway and Hindley, 2004), which are closely related to the resistance of soils to disturbances and soil multifunctionality (Aneja et al., 2006; Eldridge et al., 2020). However, the relative importance of biotic and abiotic drivers is highly debated, and a number of studies has suggested that it is highly variable, depending on ecosystem (temperate, arid biomes; Thoms et al., 2010; Maestre et al., 2015) and organism type (bacteria, fungi; Rousk et al., 2009). Therefore, empirical evidence of the interactions among biotic and abiotic factors and their roles in soil communities is needed if we are to improve our understanding of how multiple soil organisms might change under changing environmental conditions.

To fill this knowledge gap, we conducted a field survey in which we derived soil biodiversity data from 150 sites along an extensive aridity gradient (1500 km) from humid to arid areas in eastern Australia. Our overall aim was to explore the impacts of climate (aridity, temperature), soil properties (pH, texture, infiltrability), plants (woody structure and richness) and soil surface attributes (e.g., litter, biocrusts, surface morphology) on overall soil biodiversity and the richness of different groups; bacteria, fungi, invertebrates and protists. We had two hypotheses. First, we predicted that the relative effects of biotic (e.g., plants, biocrusts, litter) and abiotic (e.g., climate, soil pH, soil integrity) factors on soil biodiversity would vary with soil organisms due to differences in their physiology and optimal ecological niches (Delgado-Baquerizo et al., 2020). For example, variation in bacteria and invertebrates might relate predominately to abiotic factors such as climate or soil pH that restrict their activity (Fierer and Jackson, 2006; Tajik et al., 2019), while changes in fungal communities would be closely associated with biotic factors such as overstorey and groundstorey plants via plant-fungal associations (López-Angulo et al., 2020). Second, we expected that abiotic factors such as climate and soil properties would affect soil biodiversity both directly, and indirectly, through their effects on biotic factors such as plant communities and the conditions of soil surface, because changes in abiotic conditions largely affect biomass production and litter deposition, which further influence the microclimate and stability of soil biomes (Fetcher et al., 1985; Delgado-Baquerizo et al., 2018).

2. Material and methods

2.1. Study area

This study was conducted along an extensive 1500 km aridity gradient in eastern Australia from the east coast 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. S1 in Appendix S1). Aridity was determined as 1 - (precipitation/potential evapotranspiration) (United Nations Environment Programme, 1992), and aridity data 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, with the lowest rainfall in the north-west (Bureau of Meteorology, 2019; https://www.worldclim.org/). Average annual temperature varied from 13 °C to 21 °C along the gradient. Climatic variables, such as rainfall and mean annual temperature were derived from the WorldClim Version 2 averaged across 1970–2000 with 30 s resolution (https://www.worldclim.org/). Soil textures ranged from loams near the coast to clay loams in semiarid areas and to loamy sands at the arid areas. Soils were generally acidic near the coast (pH 5.1 ± 0.6; electrical conductivity [EC] 0.06 ± 0.04 dS m^{-1}; mean ± SD) and tended to calcareous and slightly saline in arid areas (pH 7.5 ± 0.8; EC 0.12 ± 0.13 dS m^{-1}).

2.2. Field survey

We surveyed 150 sites at regular intervals along the aridity gradient in humid (n = 30 sites), dry subhumid (n = 30 sites), semiarid (n = 60 sites), and arid (n = 30 sites) zones. The gradient covers various woody biomes (i.e., forests, woodlands, shrublands) with tree density ranging from 720.6 ± 60.0 ha^{-1} in mesic areas to 146.9 ± 11.2 ha^{-1} in arid areas. Vegetation communities across the gradient were dominated by woody plants, with a highly variable species composition. The overstorey tree layer was dominated by *Eucalyptus* spp., *Callitris* spp. and *Acacia* spp., midstorey shrub layer dominated by *Leptospermum* spp., *Dodonaea* spp. and *Eremophila* spp., and understorey grass layer dominated by *Lomandra* spp., *Aristida* spp., *Stipa* spp. and *Enteropogon* spp. Disturbance regimes and land use management (e.g., grazing, cropping, land clearing) have been shown to affect soil organisms. Therefore, to avoid potentially confounding effects of overgrazing, fire and land management on soil biodiversity, we chose to sample in protected areas that had not been burned for at least 50 years (e.g., national parks, nature reserves, parklands, state forests) where grazing is maintained at a low level, predominately by kangaroos.

Data were collected between February 2018 and August 2019. At each site, we measured attributes related to woody plant structure along a 100 m long transect, with transect width adjusted from 10 m to 40 m in order to capture at least 30 trees at each site. To ensure that the sampling regime captured differences in plant structure, we focused on surveying mature trees (i.e., tree height > 4 m). For each tree, we measured six attributes: (1) plant height (m); (2) height of the first branch (m); (3) canopy diameter (m); (4) stem diameter at breast height (DBH, cm); (5) branching number (i.e., number of branches from the main stem, after Borchert and Slade, 1981); (6) the spatial position (i.e., x- and y-coordinates in relation to the transect) for each tree. Height was measured using a Haglöf ECII-D electronic clinometer (ASICS Crop., Sweden). Canopy depth (%) was calculated as the proportion of the canopy (plant height minus height to the first branch) to the plant height. Nearest distance between neighbours was calculated based on the spatial position of the target tree to its nearest neighbour. We calculated basal cover (m^2 ha^{-1}) and canopy coverage (%) at the site-level as the measures of basal and canopy cover of woody plants for each site. At each site, tree

density, tree richness and the total plant richness (includes trees, shrubs, grasses, vines) were recorded as indicators of abundance and diversity.

We measured the condition of the soil surface under two replicates of the dominant tree patches at each site within small circular quadrats (64 cm diameter) using a variant of the Soil Surface Condition module of the Landscape Function Analysis procedure (LFA; Eldridge et al., 2020; Tongway and Hindley, 2004). Within each quadrat, we surveyed (1) the cover of biocrusts, including cyanobacteria, fungi, lichens, and mosses, (2) crust stability (the stability of surface soil aggregates assessed using the Slake Test; 0 = not applicable, 1 = very unstable, 2 = unstable, 3 = moderately stable, 4 = very stable), (3) crust brokenness (extent to which the soil crust is broken; 0 = no crust, 1 = extensively broken, 2 = moderately broken, 3 = slightly broken, 4 = intact crust), (4) soil integrity (100 minus the cover of erosional features; 1 $\geq$ 50%, 2 = 20–50%, 3 = 10–25%, 4 $\leq$ 10%; percentages present the cover of eroded soil surface), (5) groundstorey foliage cover (projected foliage cover on the quadrat; %), (6) groundstorey plant richness (total number of groundstorey vascular plants), (7) litter cover (0–100%), (8) litter depth (mm), (9) soil sand content (soil texture) based on categorical values of soil texture with higher values representing greater sand content (1 = silty to heavy clay, 2 = sandy clay loam to sandy clay, 3 = sandy to silty loam, 4 = sand to clayey sand); (10) vertebrate herbivore grazing intensity. Grazing intensity at each site was assessed by counting the dung of different herbivores within the quadrats and converting counts to dry mass of dung per herbivore type per hectare using algorithms relating dung counts to dung mass for different herbivores (Eldridge et al., 2017).

We acknowledge that our measurements were conducted at one point in time with sites surveyed at different time of the year. Therefore, there could potentially be seasonal changes in some attributes such as litter or plant cover, which might further affect soil biodiversity. However, our gradient was dominated by evergreen woody plants (e.g., *Eucalyptus* and *Acacia* spp.), and rainfall was the major driver of their litter fall rather than phenology (Travers and Eldridge, 2013). Additionally, our gradient was located in an area of relatively uniform seasonal rainfall, and within a period of generally lower rainfall, with less temporal variation in groundstorey plants and litter, and therefore the one-point-time measurements are unlikely to have influence on our soil biodiversity.

2.3. Soil properties and soil biodiversity assessment

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 for each patch type. About 5 g of soil was frozen below −20 °C for assessing soil biodiversity, and other soils were air or oven dried (<35 °C) to assess soil physical and chemical properties. We used a laboratory-derived index of infiltrability as our measure of soil infiltration based on the syringe method (Mills et al., 2006). We examined soil EC (salinity) and pH (1:5 soil water extract) using SMARTCHEM-Lab multi-parameter laboratory analyser (TPS Pty Ltd., Brendale, Australia).

The DNeasy PowerSoil Kit (Qiagen, Hilden, Germany) was used 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 2 × 301 bp (16 s, 18 s) paired end sequencing. The maximum of 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). For 18S data, the Protist Ribosomal Reference database (PR2, https://pr2-database.org/) was used as well. Trophic mode of fungal OTUs that were assigned to taxa was then inferred using FUNGuild (version 1.0; Nguyen et al., 2016). The OTU abundance tables were rarefied to a same number of sequences per sample (10,000 for bacteria, 2068 for fungi, 317 for invertebrates, 1031 for protists; the minimum number of sequences for a soil sample). Some sites are discarded due to the low reads yield, which results in 146 sites for bacteria, 145 sites for fungi, 126 sites for invertebrates and 143 sites for protists included in further analysis. We used two different metrics of diversity; (1) the richness (i.e., number of phylotypes or zOTUs) within each of the four soil organisms (bacteria, fungi, invertebrates, protists) examined independently, and (2) overall soil biodiversity (a multidiversity index), a measure of the richness of highly connected soil species within ecological networks, as a proxy of soil biodiversity. To obtain an overall soil biodiversity index (multidiversity index), we first standardized the richness of each soil community between 0 and 1 [rawRichness-min(rawRichness) / (max(rawRichness) − min(rawRichness))] and then calculated their average value. This multidiversity index is widely used and accepted in the current biodiversity–function literature (Delgado-Baquerizo et al., 2020). The standardization and averaging calculation can account for the influence of environmental conditions on the raw richness of each soil community across our extensive climatic gradient, allowing the comparison of soil biodiversity among sites. This approach also ensures that the richness of each soil organism contributes equally to this multidiversity index while maintaining the relative differences in diversity among different soil organisms in the index.

2.4. Statistical analysis

To assess changes in species composition along the aridity gradient, we calculated the relative abundance of soil phyla at each site for bacteria, fungi, invertebrates and protists, and calculated the proportion of major phyla by climatic zones (humid, dry subhumid, semiarid, arid), with any phyla with a relative abundance <2% grouped into “others”. We conducted a Pearson correlation analysis among the 27 environmental attributes measured (climate variables, soil properties, plant attributes and soil surface attributes; Table S1 in Appendix S2) and the richness of soil organisms and the relative abundance of dominate soil phyla to test the presence of linear relationships between specific environmental attributes and soil biodiversity measures rather than using these environmental attributes to predict or model variation in soil biodiversity. In the correlation analysis, we only included soil phyla that account for the majority proportion of each soil organism group (98% of bacteria, 68% fungi, 94% of invertebrates, 80% of protists).

Among soil properties, we only included four soil physical and chemical attributes (pH, EC, texture, infiltrability) and did not include either soil carbon or soil nutrients (nitrogen, phosphorus) because soil fertility (soil carbon and nutrients) and soil biodiversity interactively affect each other in ecosystem processes (Delgado-Baquerizo et al., 2017), thus there is no one-way cause-effect relationship. For the selection of predictors, we first carried out a variance inflation factor (VIF) test on the 27 environmental attributes and excluded four attributes that were highly collinear (Tables S1, S2 in Appendix S2). We then used random forest analyses to select key predictors from the 23 environmental attributes using soil biodiversity as the response variable. We ranked attributes by their explained variance (%IncMSE) and selected those that explained more than 1% of the variance as final predictors to include in the structural equation models. Rather than selecting a unique set of best predictors for each soil community, we used the same set of predictors across the four soil communities (Table S3 in Appendix S2), which enabled us to compare the relative importance of abiotic and biotic drivers among soil organisms. Finally, we identified 12 attributes as key drivers, including climate (aridity, temperature), soil properties (soil pH, soil infiltrability), soil surface attributes (groundstorey foliage cover, groundstorey plant richness, litter depth, soil integrity), and plant attributes (tree canopy cover, tree density, nearest distance to neighbouring trees, branch number of trees). We explored how soil

biodiversity (multidiversity index) changed with these 12 biotic and abiotic drivers. Linear regressions were fitted in R 3.4.1 version (R Core Team, 2018), random forest was performed in the 'rfPermute' package (Archer, 2016) and figures were created using 'ggplot2' packages (Wickham, 2016).

We used Structural Equation Modelling (SEM; Grace, 2006) to explore the 12 biotic (tree canopy cover, tree density, nearest distance to neighbouring trees, branch number of trees, groundstorey foliage cover, groundstorey plant richness, litter depth) and abiotic (aridity, temperature, soil pH, soil infiltrability, soil integrity) drivers of soil biodiversity and the richness of each soil organism. Structural equation modelling allowed us to test hypothesized relationships among predictors and soil biodiversity based on an *a priori* model (see Fig. S2 in Appendix S3) that constructs pathways among model terms based on *a priori* knowledge (Table S4 in Appendix S3). Our *a priori* model predicted that climate (aridity, temperature) would affect soil properties (soil pH, soil infiltrability), which would affect plant attributes (tree canopy cover, tree density, nearest distance to neighbouring trees, branch number of trees). These factors would also influence soil surface attributes (groundstorey foliage cover, groundstorey plant richness, litter depth, soil integrity) and all predictors would have direct effect on soil biodiversity and the richness of soil organisms. 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 of each explanatory variable to show the total effect of each variable. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

3. Results

3.1. Variation in soil biodiversity with environmental attributes

The major phyla of soil organisms varied little across the gradient (Fig. 1), with bacteria dominated by Actinobacteria (53–61%) and Proteobacteria (23–28%), fungi by Ascomycota (42–46%) and Basidiomycota (10–17%), invertebrates by Nematoda (38–43%) and Rotifera (12–16%), and protists by SAR, i.e., groups of Stramenopiles, Alveolates, and Rhizarians (45–55%). Soil biodiversity was associated with changes in soil properties and soil surface attributes (Fig. 2, Table S5 in Appendix S4), with soil biodiversity reducing with increases in soil pH and litter depth.

Relationships among soil biodiversity and environmental attributes varied with soil organisms (Fig. 3). For example, greater bacterial richness was associated with greater total plant richness, but less biocrust cover, crust stability, and low salinity or alkaline (pH) soils (Fig. 3). There were more invertebrate species in mesic areas and in soils supporting a richer plant species community and greater groundstorey foliage, but fewer fungal and protist species under deeper litter or in more alkaline soils (Fig. 3). Different soil phyla also varied, particular for bacteria and fungi (Fig. 3). For example, declines in the relative abundance of Acidobacteria were associated with taller trees with larger canopies, and more stable soils tended to harbor a greater relative abundance of Proteobacteria (Fig. 3). Declines in the relative abundance of Ectomycorrhizal fungi were associated with lower levels of sand, and reduced crust stability, while the relative abundance of Chytridiomycota, Glomeromycota and Arbuscular Mycorrhizal fungi was associated with increased grazing intensity (Fig. 3).

3.2. Direct and indirect effects of biotic and abiotic factors

Biotic and abiotic factors exerted consistent overall effects on soil organisms (Fig. 4a), with climate, soil pH and litter depth generally having negative effects on soil organisms, compared to the positive effects of soil infiltrability and groundstorey foliage cover. The relative importance of driving factors also differed among soil organisms (Fig. 4b), with bacterial and protist richness mainly explained by soil properties and soil surface attributes, fungal richness predominately explained by plant communities and soil properties, and invertebrate richness mainly explained by climate and soil surface attributes.

After accounting for the effects of other factors in our models, soil

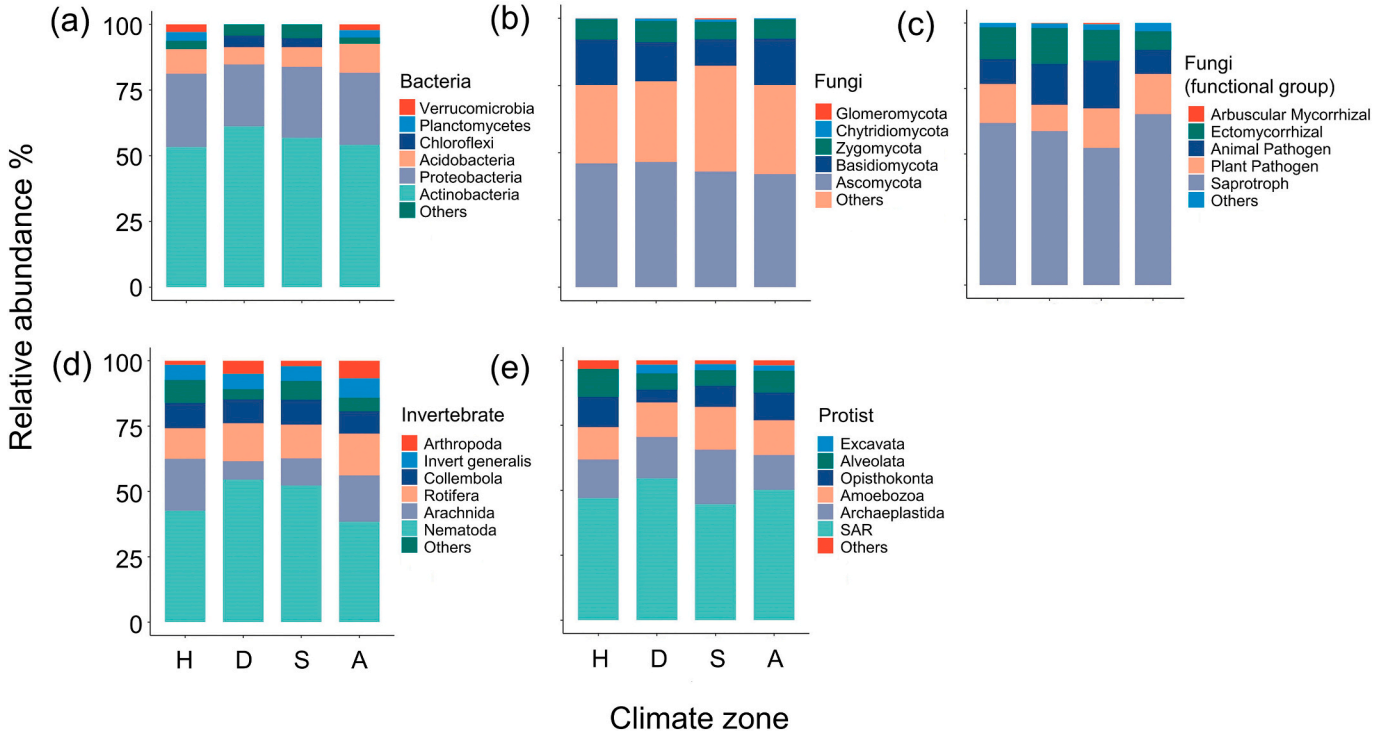

Fig. 1. Relative abundance of the major soil phyla across the four climatic zones. H, humid; D, dry subhumid; S, semiarid; A, arid. The SAR protist group contains Stramenopiles, Alveolates, and Rhizarians.

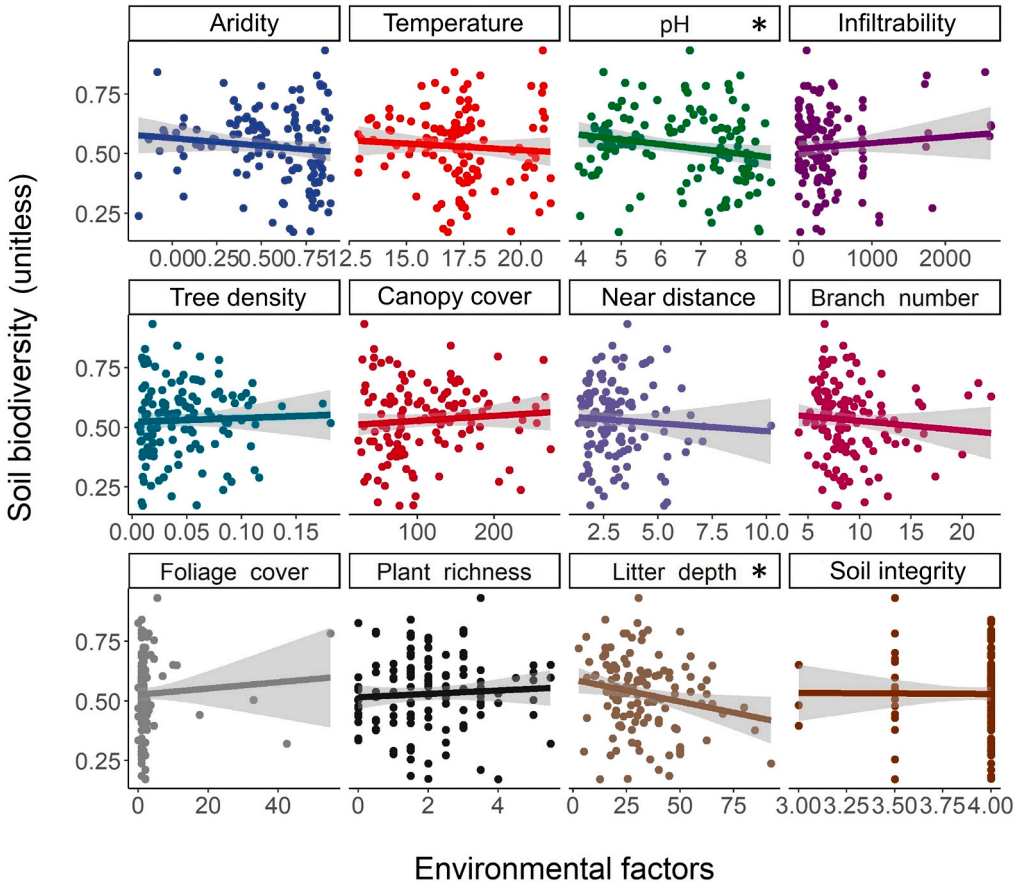

Fig. 2. Variation in overall soil biodiversity (multidiversity index) with changes in climate (aridity, mean annual temperature), soil (soil pH and infiltrability), plant communities (tree density, tree canopy cover, nearest distance to neighbouring trees, the number of tree branches), and soil surface attributes (groundstorey foliage cover, groundstorey plant richness, litter depth and soil integrity). * indicates significant linear relationships ($P < 0.05$) for soil pH and litter depth.

biodiversity was only directly associated with soil surface attributes (litter depth) (Fig. 5). Biotic and abiotic factors were also influential through their indirect effects on soil properties or soil surface attributes. Increasing tree canopy size reduced soil biodiversity and fungal richness indirectly by exacerbating the negative effects of litter depth, and such an effect was mitigated by increasing aridity or temperature (Fig. 5, Fig. S3b in Appendix S5). Greater tree spacing increased invertebrate richness by promoting groundstorey foliage cover, and such an effect was exacerbated by higher levels of aridity or temperature (Fig. S3c in Appendix S5). Aridity indirectly suppressed the richness of bacteria and protists by increasing the negative effect of soil pH (Fig. S3a, d in Appendix S5). By comparison, temperature indirectly promoted invertebrate richness by enhancing the positive effect of groundstorey foliage cover (Fig. S3c in Appendix S5).

4. Discussion

Our study demonstrates that the relative importance of biotic (plant communities, biocrusts, litter) and abiotic (climate, soil, surface stability) attributes in regulating soil biodiversity varies with soil organism type and specific soil phylum. Moreover, aridity and tree canopy also influenced the richness of soil organisms indirectly through their effects on soil pH, litter depth or groundstorey foliage cover. This study broadens our understanding of the key environmental factors driving different soil organisms at a sub-continental scale, and highlights the need to implement multiple restoration strategies to ensure the persistence of diverse soil communities.

4.1. Soil organisms differ in their association with biotic and abiotic attributes

Consistent with previous findings at small spatial scales (Aggangan et al., 1996; Aneja et al., 2006), we found that soil biodiversity was predominately associated with plant communities (total plant richness), soil properties (pH, EC) and surface condition (litter) across a large sub-continental gradient (Appendix S4). Aboveground and belowground communities are known to be positively coupled through the input of organic matter and symbiotic fungal associations (Kardol and Wardle, 2010). Richer plant species can provide a broad spectrum of litter and root exudates that are critical for supporting a diverse community of soil organisms (Hättenschwiler et al., 2005; Eisenhauer, 2016) and for promoting multiple soil functions simultaneously (Yuan et al., 2020). Soil pH is one of the key abiotic factors regulating soil biomes, with highly acidic or alkaline soils constraining the distribution of microorganisms (Aggangan et al., 1996; Fierer and Jackson, 2006). Despite the well-known positive effect of litter on microbial communities (Fanin and Bertrand, 2016), we detected a negative relationship between litter depth and soil biodiversity. This was likely due to the creation of anaerobic conditions within thick litter beneath trees, leading to the selection of anaerobic specialist fauna and therefore reductions in the belowground species pool (Tiedje et al., 1984).

However, the relationship between soil biodiversity and environmental attributes differed among soil organisms and specific phyla. For example, bacterial richness was associated predominately with soil pH, plant communities and soil stability, with Acidobacteria negatively associated with taller and wider trees, and Proteobacteria positively related to more stabilized biocrusts. Acidobacteria, which adopt a more

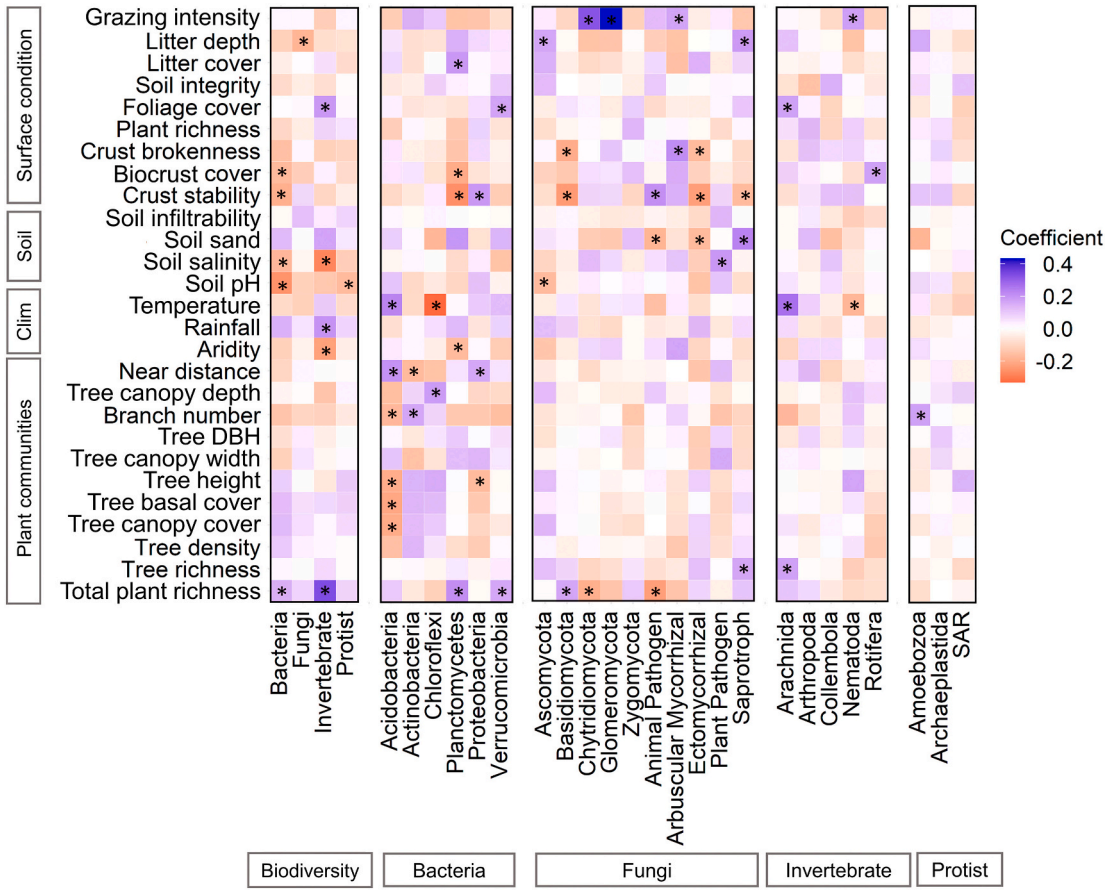

Fig. 3. Correlation among environmental variables, and the richness of soil organisms and the relative abundance of major soil phyla. * indicates significant correlation coefficient ($P < 0.05$). Clim: climate; DBH: stem diameter at breast height of trees; Branch number: the number of tree branches; Near distance: nearest distance to neighbouring tree; Foliage cover: groundstorey foliage cover; Plant richness: groundstorey plant richness; SAR: groups of Stramenopiles, Alveolates, and Rhizarians.

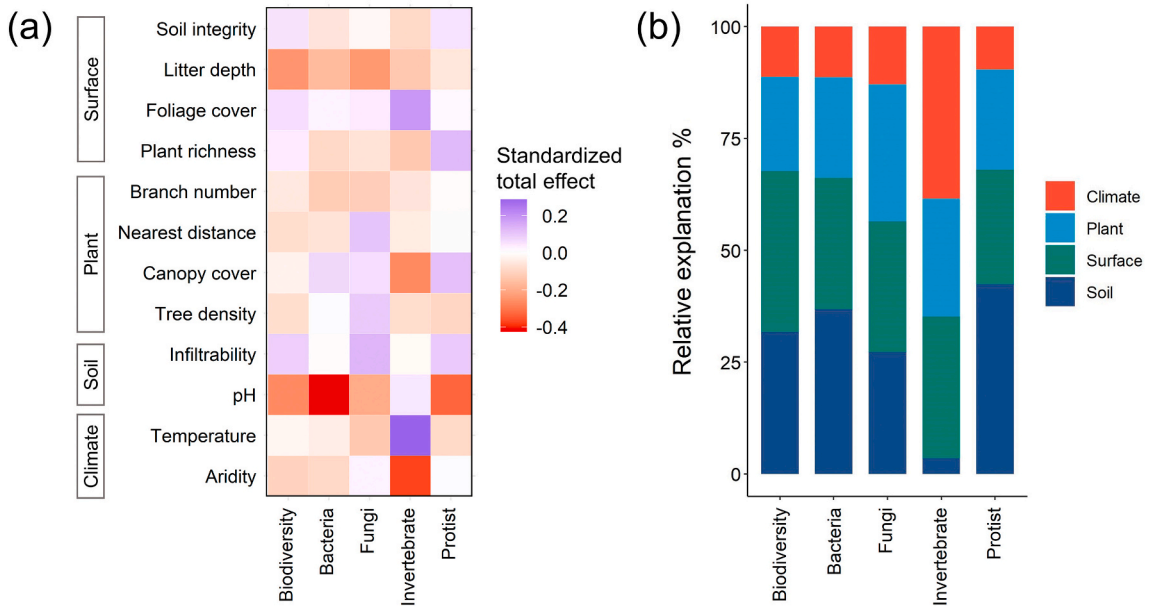

Fig. 4. (a) Heatmap of the standardized total effect (sum of direct and indirect effects) derived from the structural equation model and (b) the relative explanation of climate (Climate), soil properties (Soil), plant communities (Plant), and soil surface attributes (Surface) based on the absolute value of standardized total effect for the overall soil biodiversity (Biodiversity) and the richness of four soil organisms.

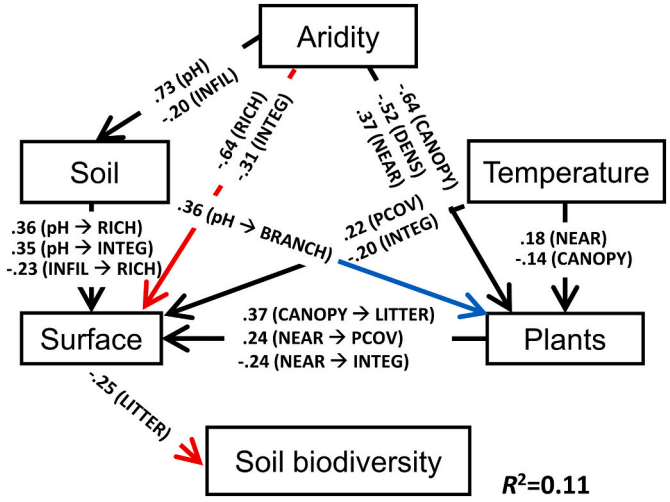

Fig. 5. Structural equation modelling assessing the indirect and direct effects of climate (aridity, temperature), soil (pH, infiltrability [INFIL]), plant communities (tree density [DENS], tree canopy cover [CANOPY], nearest distance to neighbouring trees [NEAR], branch number [BRANCH]), and soil surface attributes (groundstorey plant foliage cover [PCOV], groundstorey plant richness [RICH], litter depth [LITTER], soil integrity [INTEG]) on the overall soil biodiversity. 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: $\chi^2 = 2.87$, df = 3, $P = 0.41$, $R^2 = 0.11$, root mean error of approximation (RMSEA) < 0.01, Bollen-Stine $= 0.35$ (2000 bootstrap). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

conservative life strategy (oligotrophs) with a high capacity to decompose recalcitrant organic compounds (Lee et al., 2008), are more abundant in oligotrophic (resource-poor) environments (Wang et al., 2021) where resources are insufficient to support large-stature trees. Proteobacteria are the dominant bacterial phylum in dry soils where biocrusts predominate, and are also the most common microorganisms that assimilate nitrogen in early successional biocrusts (Pepe-Ranney et al., 2016), thus promoting crust stabilization. By comparison, the relative abundance of Ectomycorrhizal fungi declined with increasing crust stability. Ectomycorrhizal fungi are biotrophs, and they rely heavily on host plants as their main carbon source (Shah et al., 2016). Vascular plants are known to compete strongly with biocrusts for soil niches, light and resources (Ding and Eldridge, 2020), thus explaining the negative relationship between Ectomycorrhizal fungi and crust stability in our study. Notwithstanding this observation, we detected a positive association between grazing intensity and Arbuscular Mycorrhizal fungi. Although intensive grazing is expected to suppress microbes by reducing carbon availability (Van Der Heyde et al., 2017), light grazing by native herbivores in our study could increase the carbon exudation from plant roots, potentially promoting fungal communities (Eom et al., 2001). We found that mesic areas supported a richer community of soil invertebrates (particular Arachnida) likely due to a stimulation of animal activity in wetter soils (Tajik et al., 2019). There were also more invertebrate species in soils with a greater total plant richness or groundstorey cover. Richer plant species and greater foliage cover can provide diverse substrate (root exudates, litter) and complex habitat for a variety of invertebrate species (Mueller et al., 2016), which in turn, enhance litter incorporation, make more nutrients available for plants, and protect plants from pests (Lavelle et al., 2006).

4.2. Climate and plants affect soil biodiversity via soil and surface attributes

In addition to direct associations, we found that climate and plants also affected soil organisms indirectly by influencing either soil properties or conditions of soil surface. For example, increasing tree canopy cover reduced soil biodiversity indirectly by exacerbating the negative effect of litter depth. Trees are the major carbon sink in woody biomes, with denser litter produced by a greater canopy coverage (Keenan and Williams, 2018). Despite the fact that litter is the key substrate for soil microbes, dense litter might result in a habitat that is more homogeneous than thinly distributed litter, thus reducing the variety of niches (Eisenhauer, 2016; Hautier et al., 2018). Further, thick litter can create environments of low oxygen concentration, which narrows soil niches (Tiedje et al., 1984), resulting in lower species richness. However, such a suppressive effect was mitigated by increasing dryness, where trees become sparser, more conservative in resource usage, and produce low quantity of litter with high levels of recalcitrant organic matter (Legay et al., 2016).

Changes in climate such as increasing aridity and temperature, generally had negative effects on the richness of soil organisms in our study, reinforcing the notion that drier climates would lead to belowground biodiversity loss (Maestre et al., 2015). Variation in climate can also influence soil biodiversity through its indirect effect on biotic and abiotic attributes. For example, aridity suppressed the richness of bacteria and protists by exacerbating the negative effects of soil pH. Soil pH is known to be the fundamental constraint on soil microorganisms, with alkaline soils (pH > 7.5) reducing bacterial diversity and limiting the ability of mycorrhizal fungi to colonize plant roots (Aggangan et al., 1996; Fierer and Jackson, 2006). Soil pH is also an important constraint on soil protists (Dupont et al., 2016) by regulating bacterial communities that protists feed on (Fierer and Jackson, 2006; Schulz et al., 2019), with increasing pH reducing bacterial abundance and thus limiting the composition of protist communities (Saleem et al., 2013). Such an adverse effect intensified with increasing aridity due to weakened soil leaching, which is typical of water-limited systems (Maestre et al., 2016). By comparison, increasing temperature promoted the richness of invertebrate, indirectly, by enhancing the positive effect of groundstorey foliage cover. Higher temperature is often associated with higher plant productivity, and can promote the germination of groundstorey plant species, thereby supporting greater soil invertebrates by increasing the input of organic matter and the availability of soil resources (Brown et al., 2004).

5. Conclusions

Our study provides empirical evidence of the biotic and abiotic drivers of soil bacteria, fungi, invertebrates and protists at the subcontinental scale, providing support for the response of different soil organisms to environmental changes. We demonstrate that the relative importance of biotic (plants, biocrusts, litter) and abiotic (climate, soil, surface stability) drivers varies with the target organism, with bacterial richness related to soil pH, total plant richness and surface stability, fungal richness associated with litter, invertebrate richness related to total plant richness and aridity, and protist richness associated with soil pH. This indicates that different soil organisms have their own optimal environments, with tradeoffs among different soil communities, and therefore, no single environmental condition that maximizes the total spectrum of soil biodiversity. Furthermore, our results highlight the fact that increasing aridity is likely to reduce the diversity of soil organisms such as bacteria and invertebrates directly or indirectly by influencing soil pH. This suggests that there will be potential loss of soil biodiversity and its attendant functions (e.g., decomposition, nutrient cycling) under predicted increases in global temperatures and reduced rainfall (Huang et al., 2016).

CRediT authorship contribution statement

JD and DJE conceived the ideas, designed the research and collected the data. JD performed the statistical analyses and wrote the manuscript draft. DJE 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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Availability of data and material

Data used in the study is available via the Figshare repository (https://doi.org/10.6084/m9.figshare.14865258.v1).

Appendix A. Supplementary data

Supplementary material to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104271.

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