Climate and plants regulate the spatial variation in soil multifunctionality across a climatic gradient

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A B S T R A C T

A patchy distribution of soil resources is a characteristic of most natural terrestrial biomes, potentially resulting in spatial variation in multiple soil functions (soil multifunctionality). However, less is known about how soil multifunctionality and its spatial variability respond to increasing dryness across extensive climatic gradients, making it difficult to predict changes in ecosystem functions under climate change scenarios. We surveyed 150 sites along a 1500 km climatic gradient in eastern Australia, from humid forests to arid shrublands, to explore the spatial variation in soil multifunctionality with increasing aridity. We assessed four functional groups (carbon stocks, organic matter decomposition, plant structure, soil stability) of multifunctionality and average (net) multifunctionality across four vegetation patch types (tree, shrub, grass and unvegetated open interspaces). We then used average dissimilarity across these four patches as our measure of spatial variability. Our results showed that 1) net soil multifunctionality remained unchanged as aridity increased, because increases in soil stability and plant structure compensated for reductions in carbon stocks and organic matter decomposition; 2) the response of soil multifunctionality to increasing aridity differed among vegetation patch types, with the greatest increases in plant structure and reductions in carbon stocks in the open, but with marginal changes beneath trees; 3) variation in soil multifunctionality increased with increasing aridity and was driven by changes in climate (aridity, rainfall seasonality), soil (pH, sand) and to a lesser extent, variation in plant size, with impacts varying with the target functional group. Our study provides empirical evidence that soils can sustain an average level of multifunctionality across the climatic gradient by regulating the trade-offs between nutrient cycling and soil stability. Furthermore, our results demonstrate that forecasted increases in aridity will increase the spatial variation in soil multifunctionality and enhance the dominance of biocrusts, which would be critical for stabilizing soils under drier global climates.

1. Introduction

Soil is critical for sustaining life on Earth, supporting key ecosystem processes (e.g., nutrient cycling, hydrological cycle) and harbouring a large proportion of global biodiversity (e.g., microbe, micro-, meso- and macrofauna; Eldridge et al., 2020; Guerra et al., 2020). A patchy distribution of soil resources is a characteristic of many terrestrial ecosystems (Ben-David et al., 2011; García-Palacios et al., 2012; Lozano et al., 2013), particularly in drier environments, where the landscape is organised into a mosaic of resource-rich vegetated and resource-poor unvegetated patches (Ludwig and Tongway, 1995). This spatial variability in soil resources is regulated by the interactions among multiple biotic and abiotic processes (Garner and Steinberger, 1989; D'Odorico et al., 2007; Allington and Valone, 2014; Ochoa-Hueso et al., 2018) and

is likely to lead to a variable pattern of multiple soil functions (soil multifunctionality; Manning et al., 2018) across the landscape (Durán et al., 2018). Forecasted shifts in climate such as increasing dryness and fluctuating rainfall would further alter the spatial variability in soil multifunctionality by changing plant cover, microbial activity and landscape connectivity (Okin et al., 2015; Huang et al., 2017; Berdugo et al., 2020). Although differences in soil properties are known to affect multiple soil functions (soil multifunctionality) simultaneously (Zheng et al., 2019), we still have a relatively poor understanding of how soil multifunctionality and its spatial variability respond to increasing dryness, particularly across large climatic gradients (e.g., humid to arid areas). This is because most studies to date have tended to focus on a single climate regime (e.g., tropical ecosystems, drylands; Durán et al., 2018; Singh, et al., 2018) or narrow climatic ranges (e.g., altitudinal

gradient; Martinez-Almoyna et al., 2019). This lack of empirical data makes it difficult to predict how potential changes in climate would affect the spatial distribution of multiple soil functions. This makes it harder to manage soils sustainably under different climate change scenarios (Doran, 2002; Huang et al., 2017).

Spatial variation in soil multifunctionality arises potentially from variation in soil and vegetation as environments change (Durán et al., 2018; Zheng et al., 2019). Shifts in aridity and rainfall seasonality can alter variability in soil multifunctionality by influencing soil properties (e.g., soil texture, pH) *via* physical processes such as wind erosion, aeolian deposition, rock weathering and soil leaching (Delgado-Baquerizo et al., 2013; Berdugo et al., 2020). Furthermore, changes in climate can also affect the variability in soil functions among different vegetation patch types (e.g., woody patches, grass patches, open interspaces) by altering plant structure, species composition and vegetation patterns (Meron et al., 2004; Durán et al., 2018; Singh et al., 2018). Variation in plant structure (e.g., crown size and root architecture) is likely to affect the spatial variation in nutrient cycling as structural attributes are positively associated with the ability of plants to accumulate resources (Fry et al., 2018; Teixeira et al., 2020). For example, more soil resources such as moisture, carbon and nitrogen are concentrated at the soil surface around larger woody patches than grass patches. This is because trees have a greater ability to scavenge resources due to their larger canopies and better developed root systems (Belsky et al., 1989; Ochoa-Hueso et al., 2018). Additionally, variation in species composition among vegetation patches can affect multifunctionality by influencing ecological interactions (e.g., plant-plant and plant-microbe interactions). For example, spatial homogenization of plant diversity reduces ecosystem multifunctionality by reducing the dissimilarity in species composition and selecting for a particular soil microbial community (Hautier et al., 2018; Singh et al., 2018; Valencia et al., 2018). Furthermore, variation in vegetation patterns among patch types can also enhance the variability in soil functions at the landscape scale by affecting source-sink dynamics such as runon-runoff processes (Maestre and Cortina, 2004; Saco et al., 2007; Garibotti et al., 2018). To date, however, there are few empirical tests of the direct and indirect effects of climate, soil and plants on the spatial variation in soil multifunctionality, either among different vegetation patch types, or along extensive climatic gradients (though see the global dryland study by Durán et al., 2018). It remains unclear, therefore, whether shifts in abiotic environments (e.g., climate, soil) or variation in plants (i.e., biotic factors) are the major driver of the spatial variation in soil multifunctionality under predicted hotter and drier climates.

To fill this knowledge gap, we undertook a field survey at 150 sites along an extensive climatic gradient from humid to arid areas in eastern Australia to 1) determine how the spatial variation in soil multifunctionality (net multifunctionality, carbon stocks, organic matter decomposition, plant structure, soil stability) responds to increasing aridity, and 2) evaluate the relative importance of climate, soil and plants as drivers. Specifically, we had three hypotheses. First, we expected that the response of spatial variation in soil multifunctionality to increasing aridity would vary with the target functional group because different soil attributes such as nutrients, crust stability and plant cover respond differently to dryness (Delgado-Baquerizo et al., 2013; Ding and Eldridge, 2020). Second, we predicted that increases in aridity and rainfall seasonality would increase the spatial variation in soil multifunctionality directly and indirectly by altering the variation in plant size, richness, and density among vegetation patch types (Durán et al., 2018). Third, we expected that the relative importance of biotic (plants) and abiotic (climate, soil) drivers on the spatial variation in soil multifunctionality would differ among different functional groups, with nutrient cycling (i.e., decomposition and carbon sequestration) more likely to be driven by biotic factors (e.g., plant structure; Ochoa-Hueso et al., 2018), with soil stability more likely to be regulated by abiotic factors (e.g., climate, soil; Eldridge et al., 2020).

2. Material and methods

2.1. Study area

This study was conducted along an extensive climatic gradient in eastern Australia from the eastern coast to the dry interior, covering humid, dry subhumid, semiarid and arid zones (29.0°S to 35.1°S, 140.7°E to 151.4°E; Fig. 1). Aridity (unitless) was determined as 1 – (precipitation/potential evapotranspiration) (United Nations Environment Programme, 1992) with data obtained from the Consortium for Spatial Information (CGIAR-CSI) averaged over 1950–2000 (Zomer et al., 2008) (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). Average annual rainfall ranged from 1299 mm to 184 mm, changing from summer dominance in the north and east, uniform in the centre, to predominantly winter dominance in the south-west, with the lowest rainfall in the north-west (Bureau of Meteorology, 2019). Average annual temperature varied from 13 °C to 21 °C along the gradient, and soil textures ranged from loams near the coast to clay loams in the semiarid areas and to loamy sands at the arid areas. Climatic variables, such as amount of precipitation (mm), mean annual temperature (°C) and rainfall seasonality (%) were derived from the WorldClim Version 1.4 averaged across 1970–2000 with 30 s resolution (https://www.worldclim.org/).

2.2. Field survey

The 150 sites were sampled at regular intervals of aridity (e.g., 0.007 aridity difference among sites, on average) along the gradient, covering various biomes (e.g., coastal forests, semiarid woodlands, arid shrublands). Species composition varied markedly along the gradient. Tree species were dominated by *Eucalyptus* spp. 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*). Midstorey (shrub) species were dominated by *Leptospermum*, *Persoonia*, *Melaleuca* and *Pultenaea* spp. in humid and dry subhumid areas, and *Dodonaea*, *Eremophila*, *Atriplex*, and *Maireana* spp. in semiarid and arid areas. Groundstorey (graminoids) species were dominated by *Lomandra*, *Aristida*, *Dianella* spp. in humid and dry subhumid areas, and *Enteropogon*, *Austrostipa*, *Triodia* spp. in semiarid and arid areas. Disturbance regimes and extensive grazing by herbivores have been shown to regulate the spatial variation in soil functions (Eldridge et al., 2019). Therefore, to avoid confounding effects of overgrazing, fire and land management on the spatial variation in soil multifunctionality, we chose to sample in protected areas that had not been burned for at least 50 years (e.g., national parks, nature reserves, parkland, state forests) where grazing is maintained at a low level, predominantly by kangaroos. Sites were selected under certain aridity levels within these protected areas, where the spatial distribution of plants and species composition can represent the dominate vegetation patterns of the landscape.

Data were collected between February 2018 and August 2019. At each site, defined as an area of about 300 m by 300 m, we randomly established a 100 m transect and measured the canopy diameter (m) of trees and shrubs along the transect, and basal diameter (m) of 50 perennial grasses to obtain the average size (i.e., canopy coverage of trees and shrubs and plant basal coverage of grasses, m²) for each plant growth form at the site level. We also recorded plant density and species richness of trees, shrubs and grasses at each site as measures of plant abundance and diversity for each plant growth form.

2.3. Soil surface condition assessment

We assessed a range of soil attributes (i.e., measures of soil surface condition and soil chemical properties; Table 1) at each site in dominant
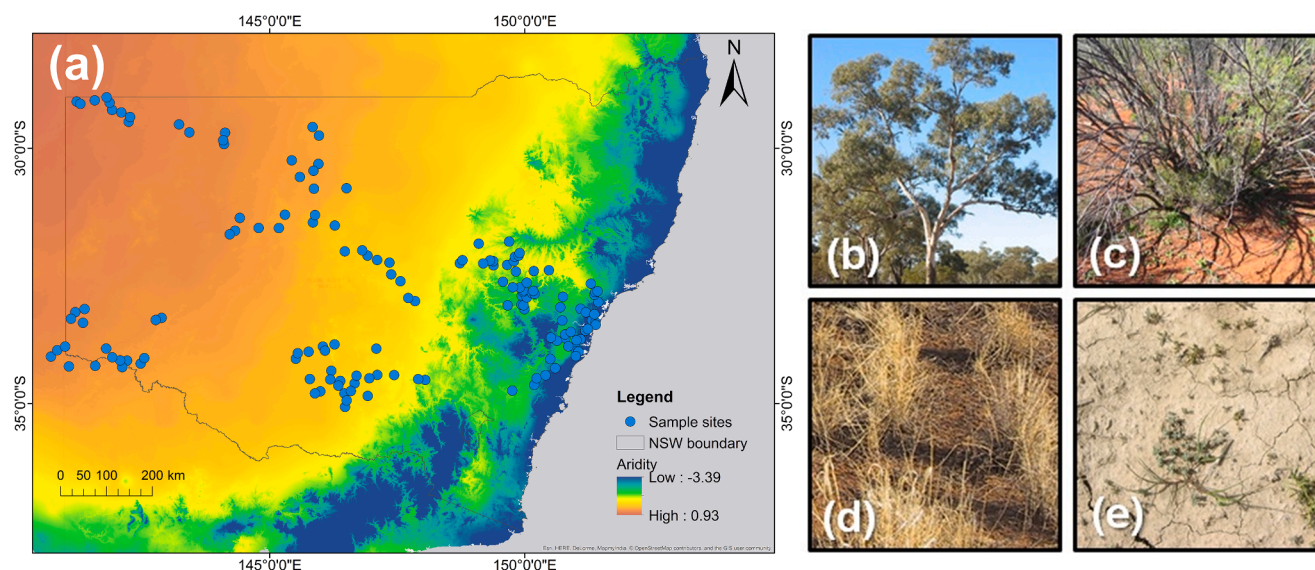
Fig. 1. Location of (a) sampling sites along the climatic gradient in eastern Australia and representative images of (b) tree patch, (c) shrub patch, (d) grass patch and (e) the open interspace.

Table 1
. Ecological attributes within each soil functional group.

Overall	Functional groups	Attributes	Function role	Measurement
Net soil multifunctionality	Plant structure	Foliage cover	Plant coverage	Soil surface condition
		Plant basal cover	Plant coverage	Soil surface condition
		Plant richness	Plant diversity	Soil surface condition
		Biocrust cover	Soil surface coverage	Soil surface condition
	Carbon stocks	Litter cover	Carbon pools	Soil surface condition
		Litter incorporation	Carbon cycling	Soil surface condition
		Litter depth	Carbon pools	Soil surface condition
		Labile carbon	Available carbon	Soil chemical analysis
	Soil stability	Surface brokenness	Stability of soil against erosion	Soil surface condition
		Soil integrity	Stability of soil against erosion	Soil surface condition
		Deposited material	Stability of soil against erosion	Soil surface condition
		Surface roughness	Soil microtopography	Soil surface condition
		Soil resistance	Stability of soil against erosion	Soil surface condition
		Crust stability	Stability of soil against erosion	Soil surface condition
	Organic matter decomposition	Enzyme BG	Sugar (C) degradation	Soil chemical analysis
		Enzyme CB	Cellulose (C) degradation	Soil chemical analysis
		Enzyme NAG	Chitin (N) degradation	Soil chemical analysis
		Enzyme PHOS	Phosphorus (P) mineralization	Soil chemical analysis

tree, shrub, and grass patches, and in open interspaces (bare, unvegetated). We used a field-based protocol (Tongway and Hindley, 2004; Landscape Function Analysis, hereafter "LFA") to assess the characteristics of the soil surface using soil surface indices. This field-based soil surface condition assessment is a simplified, cost-effective and practical suite of indices to measure *in situ* soil functions. It has been widely used as the proxy of hydrological function, nutrient cycling and soil stability (Maestre and Puche, 2009; Eldridge and Delgado-Baquerizo, 2018), and is closely correlated with soil multifunctionality across global drylands (Eldridge et al., 2020). For each of the four vegetation patch types (tree, shrub, grass, open), we used circular quadrat (64 cm diameter) to survey the 13 soil surface condition indices (Table S1 in Appendix S1). We sampled two replicates of each vegetation patch type and averaged the values of each attribute. In addition, we also measured soil sand content at the surface layer (0–10 cm devoid of organic material) under each vegetation patch type based on categorical values of soil texture using the bolus method (Northcote 1979), 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 = clayey sand). Grazing intensity was assessed at each site by counting the dung of different herbivores within the quadrats and converting the counts to mass of dung for each

herbivore type (kg ha^{-1}) using algorithms relating dung counts to dung mass (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. Thus, there could have been seasonal changes in some attributes such as litter or plant cover. 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 single temporal measurement was unlikely to affect our soil multifunctionality indices.

2.4. Soil chemical analysis

A composite sample consisting of five soil cores (0–10 cm depth) was collected under each of the dominant trees, shrubs, perennial grasses and in the open area within the same quadrats where we measured soil surface condition, and samples bulked at the site level for each patch type. We examined soil pH (1:5 soil water extract) using SMARTCHEM-Lab multi-parameter laboratory analyser (TPS Pty Ltd, Brendale,

Australia). Soil labile carbon was examined using KMnO$_4$ solution following the Weil et al. (2003) method and measured at 550 nm wavelength (UV mini-1240, Shimadzu, Japan). The activity of four enzymes was tested in this study: β-glucosidase (BG) for carbon cycling; cellobiosidase (CB) for cellulose decomposition; N-acetyl-β-glucosaminidase (NAG) for nitrogen cycling and phosphatase (PHOS) for phosphate cycling. Enzyme activities (nmol g^{-1} dry soil^{-1}h^{-1}) were measured using 1 g of soil, as described in reference (Bell et al., 2013) at 365 nm excitation wavelength and 450 nm of emission wavelength in the microplate reader (CLARIOstar, BMG Labtech, Germany).

2.5. Soil multifunctionality calculation

The multifunctionality index is a widely used approach that provides a measure of the simultaneous performance of multiple ecosystem processes and services (Maestre et al., 2012; Byrnes et al., 2014), enabling us to link ecological processes with ecosystem functioning at the landscape scale (Manning et al., 2018). We collected data on 18 attributes related to soil nutrients and the structure and morphology of the soil surface, and these variables were classified into four functional groups that reflect different ecological processes related to soils (Table 1). They are carbon stocks (litter cover, litter incorporation, litter depth, labile carbon), organic matter decomposition (enzymes BG, CB, NAG, PHOS), plant structure (foliage cover, plant basal cover, plant richness, biocrust cover), and soil stability (surface brokenness, soil integrity, deposited material, surface roughness, soil resistance, crust stability). To obtain quantitative multifunctionality indices, we standardized (z-transformed) the values of these 18 attributes. These standardized attributes within each functional group were then averaged to obtain a multifunctionality index for each functional group and the net soil multifunctionality index was calculated by averaging the values of all 18 standardized attributes. Multifunctionality index at the site i (M_i) is calculated as

$$M_i = \sum_{j=1}^{n} \left(\frac{x_{ij} - \overline{x}_j}{\sigma_j} \right) \bigg/ n$$

where x_{ij} is the raw value of a given soil attribute j that included within each functional group (e.g., "Attributes" in Table 1) at the site i. $\overline{x}_j$ and σ_j are the mean and standard deviation of soil attributes j, respectively. n is the number of soil attributes included within each functional group.

This averaging approach is widely used in studies of multifunctionality, and provides an easily interpretable measure of the ability of soils to sustain multiple functions simultaneously (Manning et al., 2018). To assess the spatial variation in soil multifunctionality at the site level, we calculated a dissimilarity index (Bray-Curtis dissimilarity, unitless) between vegetation patch types based on the matrix of soil attributes (raw values) within each functional group, and used average dissimilarity across these four patches as a measure of spatial variability at each site. The Bray-Curtis dissimilarity between vegetation patch type j and k at each site (D_{jk}) is calculated as

$$D_{jk} = \sum_{i=1}^{n} |x_{ij} - x_{ik}| \bigg/ \sum_{i=1}^{n} (x_{ij} + x_{ik})$$

where x_{ij} and x_{ik} refer to the raw value of soil attributes i in vegetation patch type j and k at each site. n is the number of soil attributes included within each functional group.

2.6. Statistical analysis

We first evaluated how soil multifunctionality (i.e., the net multifunctionality and the four functional groups) changed with increasing aridity in each patch type using linear regression. We then assessed whether the changing magnitude differed among vegetation patch types by comparing differences in slopes using Tukey's HSD test. Linear

regression was also used to explore how the spatial variation in soil multifunctionality (i.e., the dissimilarity of soil multifunctionality among vegetation patch types) changed with increasing aridity. Linear regressions were fitted in R 3.4.1 version (R Core Team, 2018). The dissimilarity index was calculated using the 'vegan' package (Oksanen et al., 2010), and figures created with 'ggplot2' packages (Wickham, 2016).

We used Structural Equation Modelling (SEM; Grace, 2006) to explore the major biotic (coefficient of variation of plant size, plant density and plant richness among vegetation patch types; average grazing intensity at the site level) and abiotic (aridity, rainfall seasonality, soil sand, soil pH) drivers of the spatial variation (i.e., dissimilarity index) in soil multifunctionality for the average (net) and four functional groups of soil multifunctionality. All the abiotic drivers were derived at the site level. As both pH and sand content were collected at a microsite level (e.g., different vegetation patch types), we used the relative cover of woody and open areas to derive a site-level value for each of these attributes. Such a scaling process has been used previously to assess multifunctionality of global drylands (Eldridge et al., 2020). Structural equation modelling allowed us to test hypothesized relationships among predictors and the spatial variation in soil multifunctionality based on an *a priori* model (see Fig. S1 in Appendix S2) that constructs pathways among model terms based on *prior* knowledge (Table S2 in Appendix S2). Our *a priori* model predicted that both climate variables and soil properties would affect grazing intensity and the variation in plants (e. g., coefficient of variation in plant size, plant density and plant richness among different vegetation patch types), with all these factors would have direct effect on the spatial variation in soil multifunctionality. 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 variables to show the total effect of each variable. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

3. Results

3.1. Soil multifunctionality varies with target function and vegetation patch type

Net soil multifunctionality was generally unchanged across the climatic gradient, with carbon stocks and organic matter decomposition declining, but soil stability and plant structure increasing, with increasing aridity (Fig. 2; Table S3 in Appendix S3). Ecological attributes associated with each functional group also varied in their response to increasing aridity (Figs. S2-S5 in Appendix S4). For example, as aridity increased, increases in plant structure resulted from greater biocrust cover but lower plant richness (Fig. S2 in Appendix S4), while increases in soil stability resulted from greater surface roughness and crust stability but reduced cover of deposited material (Fig. S4 in Appendix S4). Similarly, as aridity increased, declines in labile carbon, and the cover, depth and incorporation of litter led to reduced carbon stocks (Fig. S3 in Appendix S4). Reductions in enzymes (phosphatase) accounted for less organic matter decomposition (Fig. S5 in Appendix S4).

The magnitude of changes in soil multifunctionality with increasing aridity also differed with vegetation patch type. For example, as aridity increased, reductions in carbon stocks (e.g., litter cover, litter depth and labile carbon; Fig. 2b, Fig. S3 in Appendix S4) and increases in plant structure (e.g., biocrust cover; Fig. 2d, Fig. S2d in Appendix S4) were greatest in the unvegetated open interspaces but least under trees.

3.2. Variation in soil multifunctionality is influenced by biotic and abiotic factors

Increasing aridity was associated with a greater spatial variability in the net soil multifunctionality, carbon stocks, plant structure and soil
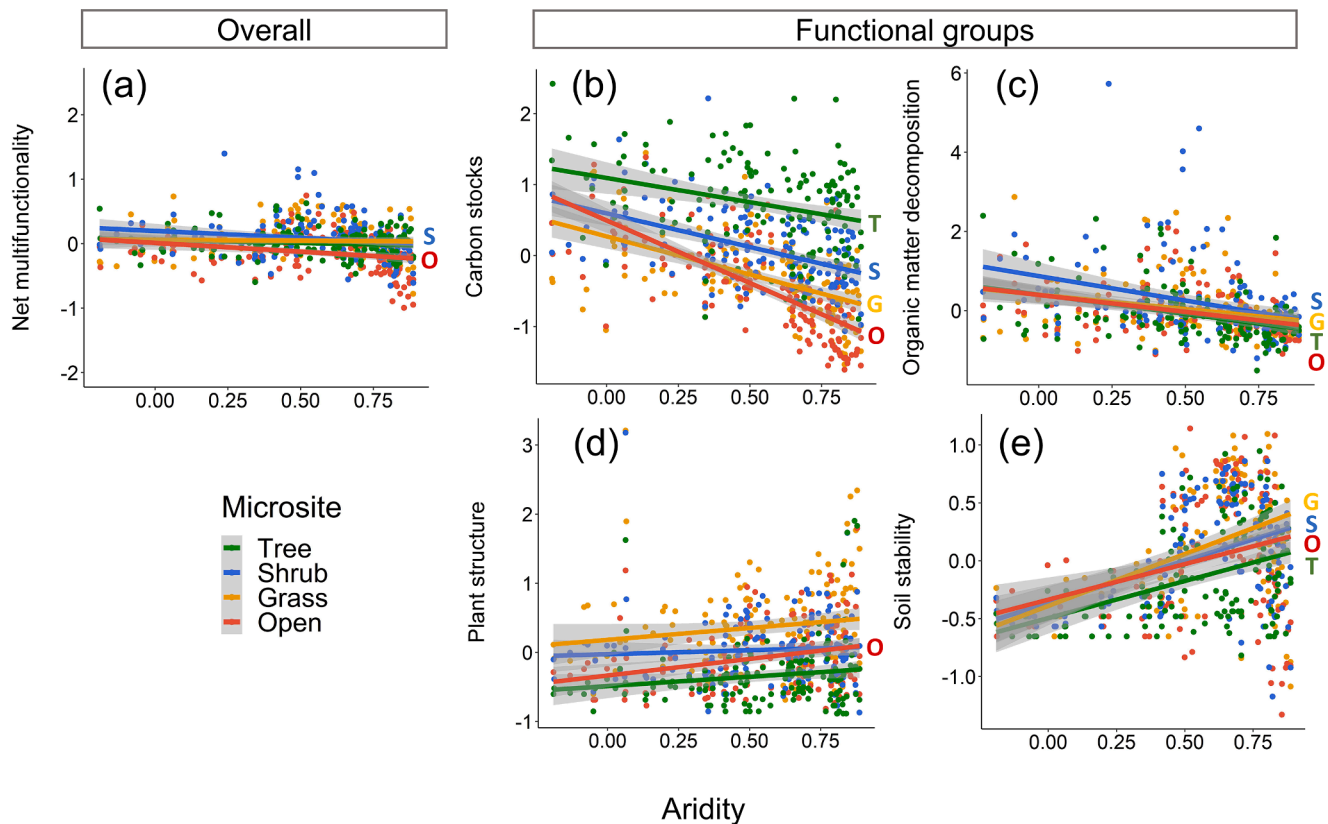
Fig. 2. Changes in (a) net multifunctionality, (b) carbon stocks, (c) organic matter decomposition, (d) plant structure and (e) soil stability with increasing aridity in tree (T), shrub (S), grass (G) and open (O) patches. Both x and y axis are unitless. Lines are fitted by linear regressions (Table S3 in Appendix S3). Different colored letters indicate significant changes in soil multifunctionality with increasing aridity for the patch type.

stability among vegetation patches, but lower spatial variability in organic matter decomposition (Fig. 3; Table S4 in Appendix S3).

The spatial variation in soil multifunctionality was regulated mainly by climate, soil properties, and to a lesser extent, variation in plant size (Figs. 4 and 5). For example, aridity was positively associated with the spatial variation in the net soil multifunctionality, and different functional groups such as carbon stocks, plant structure and soil stability, but negatively associated with the spatial variation in organic matter decomposition (Fig. 4). Greater rainfall seasonality was related to a more homogeneous distribution of organic matter decomposition and

plant structure, but a more heterogeneous distribution of net soil multifunctionality and carbon stocks (Fig. 4). Higher levels of soil pH and sand content were associated with a greater variability in net soil multifunctionality, carbon stocks and soil stability (Fig. 4). Such relationships were either enhanced or suppressed by changes in aridity and rainfall seasonality (Fig. 5). For example, increased aridity and reduced rainfall seasonality enhanced the spatial variation in net soil multifunctionality and carbon stocks by promoting the positive effect of soil pH, but reduced the spatial variation in net soil multifunctionality, carbon stocks and soil stability by suppressing the positive effect of soil
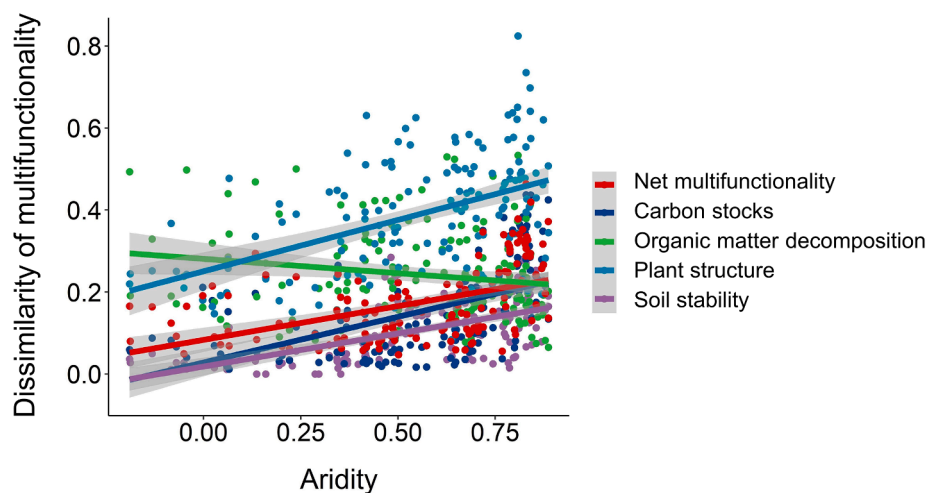

Fig. 3. Changes in the spatial variation (dissimilarity index) in soil multifunctionality with increasing aridity. Both x and y axis are unitless. Lines are fitted by linear regressions (Table S4 in Appendix S3) and are all significant.
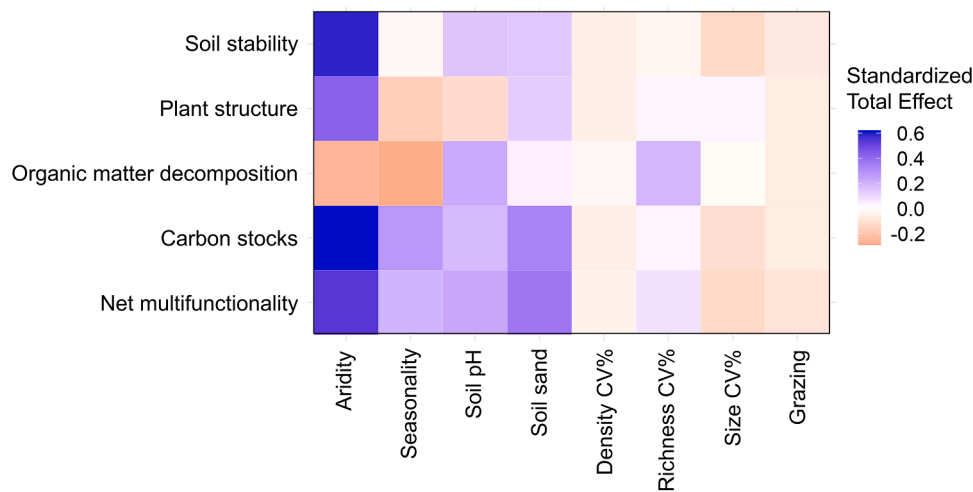
Fig. 4. Heatmap of the standardized total effects (sum of direct plus indirect effects; unitless) of driving factors derived from the structural equation modelling (Fig. 5) for the spatial variation in soil multifunctionality. CV % coefficient of variation; Seasonality, rainfall seasonality; Density CV%, variation in plant density among the four vegetation patch types; Richness CV%, variation in plant richness among the four vegetation patch types; Size CV %, variation in plant size (plant canopy coverage of trees and shrubs and plant basal coverage of grasses) among the four vegetation patch types; Grazing, grazing intensity.

sand (Fig. 5a, b, e). Among biotic drivers, a greater variation in plant size among vegetation patch types was related to a less variability in net soil multifunctionality (Fig. 5a), but there were no effects of grazing intensity on the spatial variation in soil multifunctionality (Figs. 4 and 5).

4. Discussion

4.1. Soil multifunctionality varies with functional group and vegetation patch type

We found that soils generally maintained a consistent level of net multifunctionality as dryness intensified, with reductions in nutrient cycling (e.g., carbon stocks, organic matter decomposition) compensated by increases in measures of soil surface condition (e.g., soil stability, plant structure). Such tradeoffs among functional groups might be due to changes in biotic elements covering the soil surface along the climatic gradient (Ding and Eldridge, 2020). Vascular plants are known to drive nutrient cycling by affecting organic matter and soil microbial communities (Hacker et al., 2015; Prober et al., 2015). Under intensifying dryness, reductions in plant cover and diversity reduce both organic matter input and microbial activity, retarding carbon sequestration and decomposition processes (Delgado-Baquerizo et al., 2013; Valencia et al., 2018). Conversely, more open soil niches and less plant competition in drier environments (Berdugo et al., 2020) promote a greater dominance of biocrusts (aggregations of lichens, bryophytes, bacteria and fungi; Eldridge and Greene, 1994), which play important roles in stabilizing soils, increasing hydrological functions, providing habitat for microbes, and mitigating the negative impact of climate change (Gao et al., 2017; Delgado-Baquerizo et al., 2018; Eldridge et al., 2020). Thus, as dryness intensifies, increases in the cover of biocrusts at the expense of vascular plants result in few changes in net soil multifunctionality under drier climates.

Importantly, our results demonstrate the importance of vegetation patch type in defining the magnitude of changes in soil multifunctionality, with substantial changes in the open interspaces but only slight changes beneath trees. Different patches of biotic components (e.g., trees, shrubs, grasses, biocrusts in the open) vary in their capacity to modify ecological processes (Breshears et al., 1997; Ochoa-Hueso et al., 2018). For example, trees characterized by tall stems, large crowns and strongly developed root systems, have a greater ability to ameliorate environmental stresses (Belsky et al., 1989) and are more resistant to climatic shifts (e.g., water deficiency, extreme temperature; Hodgkinson, 1992). By comparison, soils in open patches are relatively sensitive to dryness as they are less shielded by a wide and dense canopy (Belsky et al., 1989), resulting in rapid reductions in nutrient cycling (e.g., litter, labile carbon), but greatest increases in biocrusts cover due to less

competition from sparse vascular plants (Havrilla et al., 2019).

4.2. Spatial variation in soil multifunctionality is regulated by climate, soil and plant size

We found that net soil multifunctionality became more variable as aridity increased, suggesting a greater degree of landscape patchiness and more variable functions under drier climates. However, different functional groups of soil multifunctionality differed in their responses, with carbon stocks, plant structure and soil stability becoming more variable, but organic matter decomposition becoming more homogeneous, as aridity increased. These different responses of spatial variation in soil multifunctionality were associated with different biotic (variation in plant size) and abiotic (climate, soil) drivers.

Aridity was the major abiotic factor regulating the spatial variation in soil multifunctionality. As moisture availability declines with increasing aridity, enhanced resource concentration from unvegetated open interspaces to vegetated patches (Garner and Steinberger, 1989; Saco et al., 2007) leads to a more heterogeneous distribution of plant cover (Caballero et al., 2008), biocrusts (Eldridge and Greene, 1994) and litter (Carrera and Bertiller, 2013). However, changes in organic matter decomposition became less variable among patches, probably due to weakened decomposition across arid landscapes (Delgado-Baquerizo et al. 2013). Apart from the reduced enzyme activity in all vegetation patches with increasing aridity (Fig. S5 in Appendix S4), a lower plant richness in drier areas (Fig. S6 in Appendix S5) is likely to further reduce microbial activity (Maestre et al., 2012; Prober et al., 2015), suppressing decomposition processes across vegetation patch types (Garcia-Pausas and Paterson, 2011). Aridity and rainfall seasonality also indirectly affected the spatial variation in soil multifunctionality by modulating the positive effect of soil pH and sand content. A greater soil sand content is often associated with sparser plant coverage in the open interspaces as less moisture is retained in sandy soils (Schlesinger et al., 1990; Felde et al., 2018; Ding and Eldridge, 2020), thus exacerbating the differences in carbon stocks and soil stability between vegetated and unvegetated patches. Such an effect would be expected to intensify under highly varied rainfall where the water supply for plant growth is less stable (Noy-Meir, 1973). Additionally, high levels of soil pH can affect carbon stocks by constraining bacterial diversity and inhibiting the ability of mycorrhizal fungi to colonize plant roots (Aggangan et al., 1996; Fierer and Jackson, 2006). This would exacerbate the differences in soil microbial communities beneath vegetation patches and in the open interspaces (Ochoa-Hueso et al., 2018), and such an effect would become stronger as soil leaching process further weakens with increasing aridity.

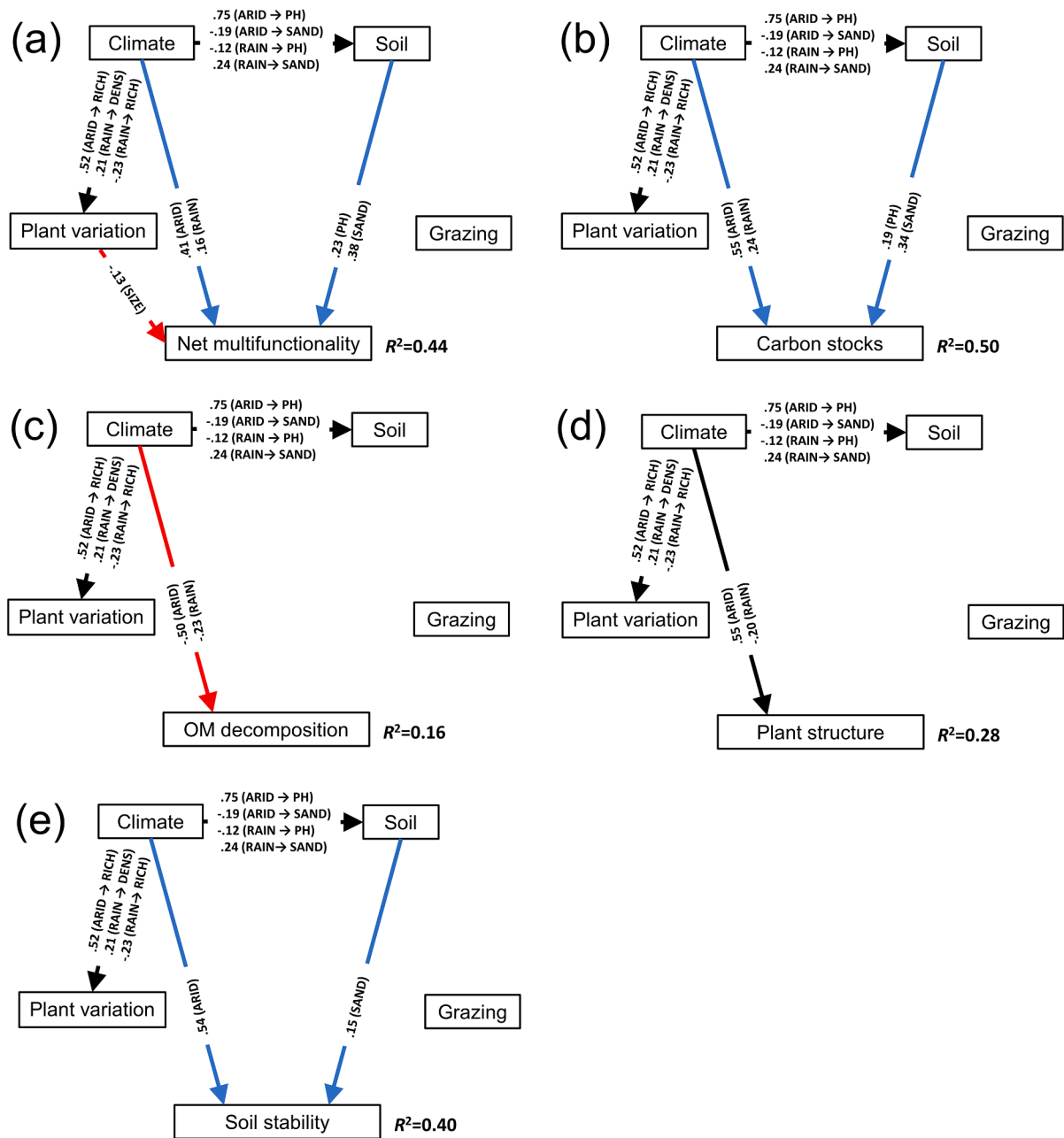Plant size is known to be positively related to the ability of plants to

Fig. 5. Structural equation modelling of assessing the direct and indirect effects of Climate (aridity [ARID], rainfall seasonality [RAIN]), Soil (soil pH [PH], soil sand [SAND]), Plant variation (coefficient variation in plant density [DENS], plant size [SIZE] and plant richness [RICH] among the four vegetation patch types), Grazing (grazing intensity) on the spatial variation (dissimilarity index) in soil multifunctionality. Plant size is the plant canopy coverage of trees and shrubs and plant basal coverage of grasses. Model fit: (a) Net multifunctionality $\chi^2 = 5.77$, df $= 5$, $P = 0.33$, $R^2 = 0.44$, root mean error of approximation (RMSEA) $= 0.03$; (b) Carbon stocks $\chi^2 = 5.77$, df $= 5$, $P = 0.33$, $R^2 = 0.50$, root mean error of approximation (RMSEA) $= 0.03$; (c) Organic matter (OM) decomposition $\chi^2 = 5.77$, df $= 5$, $P = 0.33$, $R^2 = 0.16$, root mean error of approximation (RMSEA) $= 0.03$; (d) Plant structure $\chi^2 = 5.77$, df $= 5$, $P = 0.33$, $R^2 = 0.28$, root mean error of approximation (RMSEA) $= 0.03$; (e) Soil stability $\chi^2 = 5.77$, df $= 5$, $P = 0.33$, $R^2 = 0.40$, root mean error of approximation (RMSEA) $= 0.03$.

enhance most functions simultaneously (Ochoa-Hueso et al., 2018; Ward et al., 2018). In our study, however, the variation in plant size was negatively related to the spatial variation in net soil multifunctionality. The most parsimonious explanation relates to a greater similarity in plant size among plant growth forms (trees, shrubs, grasses), but a greater contrast between vegetated and unvegetated patches as environments become drier. Resource distribution is relatively homogeneous in humid areas due to the large overlap among adjacent patches (e.g., large woody plants, small grasses; D'Odorico et al., 2007). Although such differences tend to contract in arid areas due to environmental filtering (Berdugo et al., 2020), the greater contrast between

vegetated and open patches reinforces resource redistribution (Okin et al., 2015), resulting in a more heterogeneous net soil multifunctionality. Although grazing is often regarded as an important stimulant for soil heterogeneity in drier regions (Allington and Valone, 2014; Eldridge et al., 2019), we did not detect any effects of grazing intensity, indicating that low grazing by native herbivores (i.e., kangaroos) may not play an important role in affecting variation in soil multifunctionality across the landscape.

5. Conclusions

Our study provides empirical evidence that net levels of soil multi-functionality remains largely unchanged across the climatic gradient, though the relative importance of different functional groups (e.g., carbon stocks, soil stability) varied. As dryness intensifies, soil multi-functionality, particularly nutrient cycling (e.g., carbon stocks), will become more variable, which could alter the symmetry of resource competition, potentially resulting in more varied plant communities across the landscape (García-Palacios et al., 2012). In addition, we demonstrate that shifts in climate (i.e., aridity, rainfall seasonality), soil properties (i.e., pH, sand) and to a lesser extent variation in plant size, exert different effects on the spatial variation in soil multifunctionality, indicating that no single environmental conditions can optimise all soil functions. Furthermore, the predicted increases in aridity would result in a sparser plant cover and lower microbial activity, but a greater dominance of biocrusts, which can buffer negative impacts of global climate change and stabilize the surfaces of soils where biological activity is concentrated.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105233.

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