REGULAR ARTICLE

The fertile island effect varies with aridity and plant patch type across an extensive continental gradient

Jingyi Ding · David J. Eldridge

Abstract

Aims Perennial plants play important roles in maintaining ecosystem functions by forming fertile islands beneath their canopies. Little is known about how the fertile island effect varies among different patch types and across climatic gradients, or what drives the strength of its effect.

Methods We assessed biotic (plants, biocrusts, litter) and abiotic (soil infiltrability, labile carbon, enzymes) fertile island effects beneath three plant patch types (tree, shrub and grass patches), and collected data on biotic (canopy size, grazing intensity) and abiotic (soil texture, electrical conductivity and pH) drivers at 150 sites along an extensive aridity gradient in eastern Australia.

Results The fertile island effect was generally apparent beneath trees, shrubs and grasses, with biotic (plants) and abiotic (soils) attributes regulated differently by plant canopy size. The fertile island effect intensified with increasing aridity, with the greatest litter and soil resources accumulated beneath trees.

Conclusions Our study provides evidence of the fertile island effect across the whole spectrum of the aridity gradient, with the effect depending on the target attribute and plant patch type. Forecasted increases in aridity will likely strengthen the fertile island effect beneath trees, reinforcing the importance of trees in drier environments to support critical ecosystem functions and services.

Keywords Climate gradient · Fertile patch · Plant canopy · Plant-soil feedbacks · Relative interaction index · Soil properties

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Introduction

Perennial plants are major biotic components of terrestrial ecosystems, driving important ecological processes, providing multiple critical ecosystem services, and supporting human livelihoods (Chapin et al. 2011). Perennial plants stabilize the soil with well-developed root systems, drive nutrient cycles *via* rhizosphere mining, and provide resources and shelter for countless biota, including humans (Chapin et al. 2011; Garner and Steinberger 1989). The effects of perennial plants on soils and ecosystem functions have been studied extensively in drylands, particularly the feedbacks between discrete vegetation patches and heterogenous resources. These feedbacks enhance both biotic (e.g. plant species, litter, microbial activity) and abiotic resources (e.g. nutrients, moisture, infiltration) beneath vegetation, leading to the development of so-called fertile islands or islands of fertility (de Soyza et al. 1997; Ravi et al. 2007;

Schlesinger and Pilmanis 1998). Potential mechanisms supporting the fertile island effect involve both biotic and abiotic processes. Abiotic processes that redistribute resources to the vegetation patches include the trapping of aeolian sediments (de Soyza et al. 1997), funneling of nutrient-rich stem flow (Martinez-Meza and Whitford 1996), and redistribution of runoff from bare interspaces (Daryanto et al. 2013). Biotic processes can promote the formation of fertile islands by either enhancing resource accumulation and biotic activities beneath vegetation (e.g. root sequestration of nutrients, nitrogen fixation, and harboring diverse microbe communities; Li et al. 2017; Ochoa-Hueso et al. 2018), or by increasing the differences between vegetated and unvegetated patches *via* animal activities (e.g. herbivory by insects and overgrazing by livestock; Allington and Valone 2014; Cai et al. 2020; Duval and Whitford 2008).

Although the fertile island effect appears to be most strongly apparent in drylands (Ochoa-Hueso et al. 2018; Ravi et al. 2007), it widely occurs in different environments such as coastal wetlands, semiarid woodlands and deserts (Dunham 1991; Garcia-Moya and McKell 1970; Ochoa-Hueso et al. 2018; Rong et al. 2016; Ward et al. 2018). However, we know relatively little about how it might vary across various environments along extensive climatic gradients, and whether any effects might differ among different perennial patch types (e.g. trees compared with shrubs or grasses). Continental shifts in climate, such as increasing aridity, are likely to influence the magnitude of the fertile island effect by altering resource availability and transfer processes (Berdugo et al. 2020; Garner and Steinberger 1989; Ravi et al. 2007). For example, increasing aridity can cause abrupt reductions in resources (e.g. plant productivity, soil fertility and microbial abundance; Berdugo et al. 2020), alter patterns of water availability by changing runoff-infiltration relationships, and increase the heterogeneity of vegetation distribution (Meron et al. 2004), strengthening the contrast between vegetated and unvegetated patches.

The magnitude of the fertile island effect is likely complicated by variations in perennial patch types along climatic gradients (Ochoa-Hueso et al. 2018). For example, patches dominated by shrubs or trees may strengthen the fertile island effect more than grass patches due to their larger crowns and deeper root systems, which are more effective at trapping sediments and scavenging resources, respectively (Li et al. 2017; Val et al. 2020; Ward et al. 2018). Plant-plant interactions also vary with perennial patches along climatic

gradients (Callaway and Walker 1997; Michalet et al. 2014), with trees often suppressing groundstorey vegetation through resource competition in mesic areas, but more likely to act as nurse plants for understorey protégé species in drier areas as water stress intensifies (Dohn et al. 2013). Despite the generally acknowledged importance of fertile islands in drylands (Ochoa-Hueso et al. 2018; Ravi et al. 2007), empirical evidence across broader climatic regions spanning gradients from humid to arid areas is lacking, and it remains largely unknown whether broad subcontinental scale effects exist.

Herein, we report on a study where we used an extensive gradient from mesic coastal forests to arid shrublands to examine whether the magnitude of the biotic and abiotic fertile island effect varied with increasing aridity under multiple, morphologically distinct perennial patch types (tree, shrub and grass patches). Rather than merely focussing on soil fertility, we explored the broad fertile island effect by evaluating the differences among plant patches and open interspaces in a wide range of biotic (plants, biocrusts, litter) and abiotic (soil infiltrability, labile carbon, enzymes) properties of soils as measures of the biotic and abiotic fertile island effect, respectively. We had two hypotheses (Fig. 1). First, we expected a strengthening of the effect with increasing aridity because reductions in water availability would result in greater resource concentration by plants and fauna than dispersal by physical processes such as aeolian transport or soil leaching (Garner and Steinberger 1989). Second, we predicted that the fertile island effect would vary with perennial patch type, with a stronger enhancement of resources beneath trees than the other patch types. Because canopy size is known to influence the efficiency of resource concentration (Li et al. 2017), trees characterized by larger canopies would have a greater capacity to moderate temperature extremes, accumulate resources (e.g. intercept rainfall, trap aeolian particles and seeds) and support abundant and diverse microbial communities (Val et al. 2020; Ward et al. 2018), than shrubs and grasses.

Methods

Study area

We conducted a field survey along an extensive aridity gradient (1500 km) in eastern Australia (aridity ranges

Fig. 1 Hypothesized relationship between the relative fertile island effect and increasing aridity (solid pink line), and separate relationships for trees, shrubs, and grasses (broken lines)
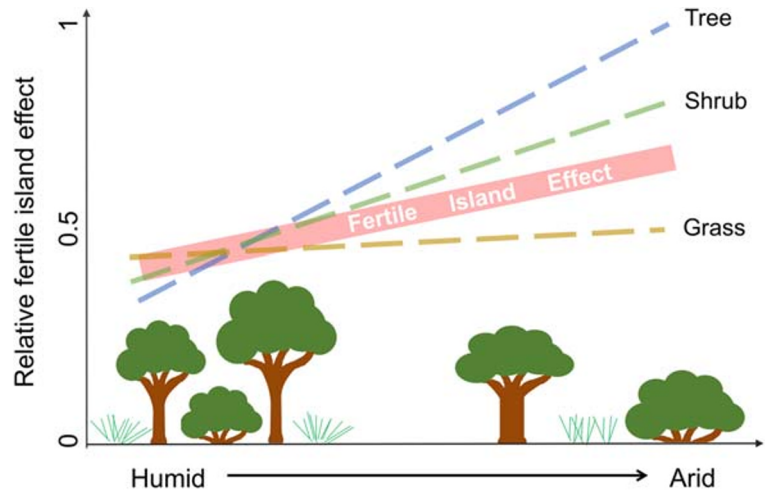
from − 0.2 to 0.9), from the east coast to the dry interior (Fig. S1 in Appendix S1). Aridity was determined as 1 − (precipitation/potential evapotranspiration) (UNEP 1992), with data obtained from the Consortium for Spatial Information (CGIAR-CSI) averaged over 1950–2000 (Zomer et al. 2008) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database). Average annual temperature varied from 13 °C to 21 °C and average annual rainfall from 184 to 1299 mm. Rainfall was summer dominant in the north-east, uniform in the centre, and predominantly winter dominant in the south-west (Bureau of Meteorology 2019). Soil texture ranged from loams in humid areas to clayey sands in arid areas. Soils were generally acidic near the coast (pH 5.1 ± 0.6; electrical conductivity [EC] 0.06 ± 0.04 dS/m; mean ± SD) and tended to calcareous and slightly saline in arid areas (pH 7.5 ± 0.8; EC 0.12 ± 0.13 dS/m). Vegetation communities across the gradient were highly variable, ranging from coastal forests, to semiarid woodlands and arid shrublands. 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 *Entropogon*, *Austrostipa*, *Triodia* spp. in semiarid and arid areas.

Sites were selected at regular intervals along the aridity gradient in places where vegetation communities were dominated by perennial plant species (trees, shrubs and perennial grasses). We sampled 150 sites in total in the humid (n = 30 sites), dry sub-humid (n = 30 sites), semiarid (n = 60 sites), and arid (n = 30 sites) zones, covering the wide spectrum of climatic environments and various biomes (i.e. forests, woodlands, shrublands). To avoid confounding potential effects of overgrazing, fire history or past land management practices such as clearing or timber removal, we restricted our sampling to areas that had been unburned in the last 50 years, and where grazing was at relatively low levels and dominated by native macropods (kangaroos). Consequently, most sampling was carried out in national parks, conservation reserves, parklands and state forests.

Field survey

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 ran a 100 metre transect and selected one of each of three plant patch types that represented the dominant tree, shrub and grass at that site (i.e. tree patch, shrub patch, grass patch) and representative open (bare, unvegetated) patches at the beginning and the middle of the transect, respectively, with two replicates of each patch type sampled. Open patches were devoid of perennial plants but may have supported annual plants, litter or biocrusts (biological soil crusts; Eldridge 1999). Beneath each perennial patch, and in the

open, we characterized the condition of soil surface within small circular quadrat (64 cm diameter) using a variant of the Soil Surface Condition module of Landscape Function Analysis (LFA; Eldridge et al. 2020; Tongway and Hindley 2004). In each quadrat, we measured: (1) plant cover (projected foliage cover of groundstorey perennial and annual plants in the quadrat, 0-100%); (2) plant richness (all plants); (3) litter cover (0-100%); (4) litter depth (mm); (5) biocrust cover (0-100%, including cyanobacteria, fungi, lichens, and bryophytes); (6) soil sand content at the surface layer (0–10 cm devoid of organic material) based on categorical values of soil texture using the bolus method (Northcote and Glenside 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 = sand to clayey sand) and (7) counted the dung of all herbivores. Litter volume was calculated as the product of litter cover by litter depth. 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). It was then classified into three categories: (1) ungrazed (no dung), (2) low grazing (dung dry mass < 15 kg ha^{-1}), (3) moderate grazing (dung dry mass > 15 kg ha^{-1}). At each site, we measured the canopy diameter of at least 20 trees, 20 shrubs and the basal diameter of 50 perennial grasses and calculated the average canopy area or basal area as the measure of canopy size (m^2) for each patch type.

Laboratory 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, and samples bulked at the site level for each patch type. About 5 g of soil was frozen below −20 °C for soil enzyme analyses, and other soils were air or oven dried (< 35 °C) to assess soil infiltrability, electrical conductivity (EC), pH and labile carbon. We used a laboratory-derived index of infiltrability as our measure of soil infiltration based on the syringe method (Mills et al. 2006). Put simply, soil placed within a plastic syringe was saturated to ensure that soils of different water repellency were brought to the same level of field capacity, and the time taken for a given volume of soil-

water filtrate to drain completely through the soil column was used as our index of infiltrability. We calculated soil EC and pH on a 1:5 soil water extract with the SMARTCHEM-Lab multi-parameter laboratory analyser (TPS Pty Ltd, Brendale, Australia). Soil labile carbon was determined following the methods of Weil et al. (2003) and measured by spectrophotometry 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 decomposing cellulose; N-acetyl- β-glucosaminidase (NAG) for nitrogen cycling, and phosphatase (PHOS) for phosphate cycling (Bell et al. 2013). Enzyme activity (nmol activity g^{-1} dry soil^{-1} h^{-1}) was measured, as described in Bell et al. (2013) at 365 nm excitation wavelength and 450 nm of emission wavelength in the microplate reader (CLARIOstar, BMG Labtech, Germany).

Statistical analysis

We calculated the relative interaction index (RII; Armas et al. 2004) to assess the magnitude of the fertile island effect, defined as the relative difference between different attributes beneath a given patch and the open (unvegetated) interspace. RII was calculated as:

$$RII = (X_V - X_O)/(X_V + X_O) \qquad (1)$$

where X is the biotic (i.e. plant cover, plant richness, litter volume, biocrust cover) or abiotic (i.e. infiltrability, labile carbon, enzymes) attributes. X_V and X_O represent the value under the vegetation canopy and in the open interspace, respectively. RII ranges from −1 to 1 with positive value indicating greater levels of attributes under vegetation canopies. RII was calculated for the averaged vegetation (i.e. X_V is the average value across perennial plant patches) and for tree, shrub and grass patches, respectively. We calculated the mean and 95% confidence interval (CI) of RII for each attribute to explore evident of biotic and abiotic fertile island effects based on whether the 95% CI cross the zero line. We then fitted linear regressions between RII and aridity, and compared coefficients among tree, shrub and grass patches using Tukey's HSD test to explore whether the effect significantly changes with increasing aridity and whether the magnitude differs among patch types. The 95% CI was calculated using 'Rmisc' package (Ryan 2013), figures created using 'ggplot2' packages

(Wickham 2016) and linear regressions fitted in R 3.4.1 version (R Core Team 2018).

We used Structural Equation Model (SEM; Grace 2006) to explore the major driving factors of biotic (plant cover, plant richness, litter volume, biocrust cover) and abiotic (infiltrability, labile carbon, enzymes that average BG, CB, NAG and PHOS) fertile island effects. Among the driving factors, categorical grazing intensity was coded as -1 (ungrazed), 0 (low grazing), 1 (moderate grazing) in the model. Structural equation modelling allowed us to test hypothesized relationships among predictors and the fertile island effect based on an *a priori* model (see Fig. S2 in Appendix S2) that constructs pathways among model terms based on *prior* knowledge (Table S1 in Appendix S2). Our *a priori* model predicted that aridity would affect soil properties and they both have direct and indirect effect on the fertile island effect by affecting plant canopy size or grazing intensity. We predicted that plant canopy size

would affect the fertile island effect either directly or indirectly *via* influencing grazing intensity. 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 its total effect. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

Results

Fertile island effect varies with patch type and aridity

Averaged over all plant patch types, the fertile island effect was evident for all biotic and abiotic attributes, except the enzymes cellobiosidase and phosphatase (Fig. 2a). The fertile island effect was strongly positive for litter volume
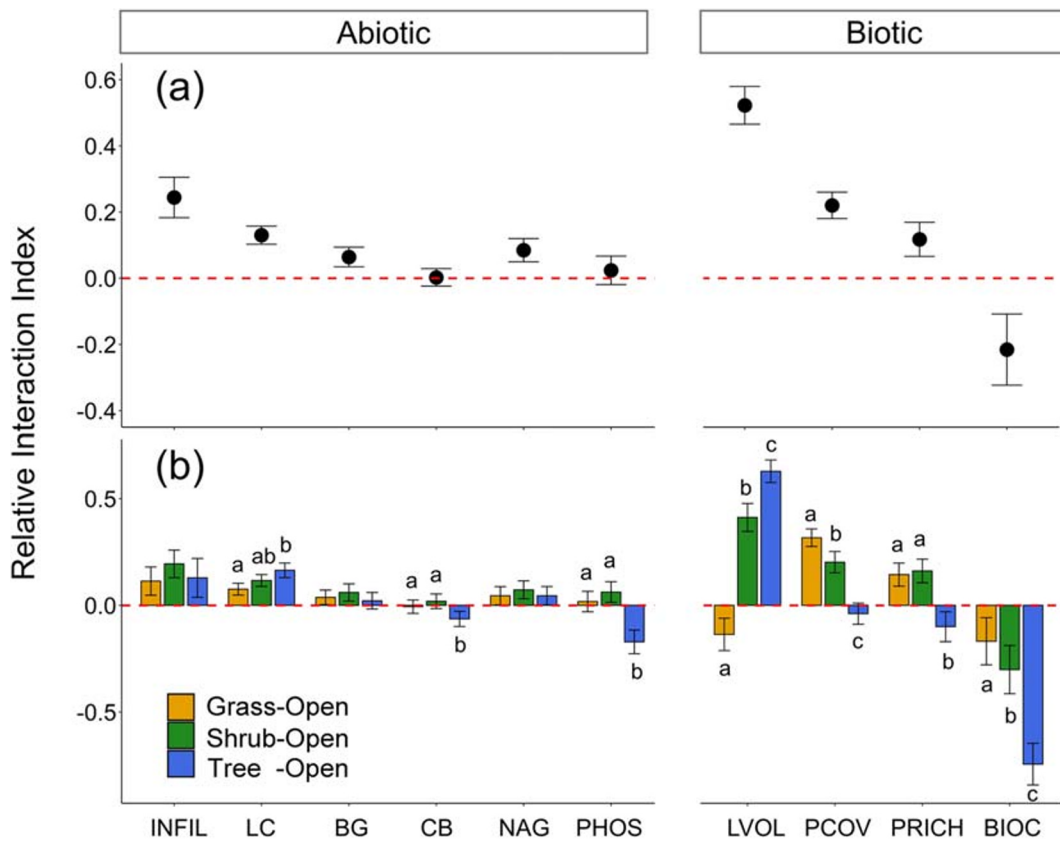
Fig. 2 (**a**) Relative interaction index (RII) of biotic and abiotic attributes beneath vegetation patches compared with the interspaces, and (**b**) RII of biotic and abiotic attributes beneath trees, shrubs and grasses. INFIL = soil infiltrability; LC = labile carbon; enzymes (BG, CB, NAG, PHOS); LVOL = litter volume; PCOV = plant cover; PRICH = plant richness; BIOC = biocrust cover. Within an attribute, different letters indicate significant differences among patches

and strongly negative for biocrust cover (Fig. 2a). The fertile island effect differed among patch types, with trees, and to a lesser extent shrubs, significantly different to grasses for labile carbon, cellobiosidase, phosphatase, and the four biotic attributes (Fig. 2b).

The strength of the fertile island effect on soils (i.e. soil infiltrability, soil labile carbon) and plants (i.e. plant richness, litter volume) increased with increasing aridity (Figs. 3, S3 in Appendix S3), but the magnitude of this effect differed among patch types. For example, litter volume, soil infiltrability, and soil labile carbon increased more strongly with increasing aridity under woody plants (tree or shrubs) than under grasses (Figs. 3, S4 in Appendix S3).

Drivers of the fertile island effect

Canopy size, aridity and soil pH were the strongest drivers of the fertile island effect, but their effects varied among different attributes (Figs. 4 and 5, Fig. S5 in Appendix S4). Canopy size was positively associated with soil labile carbon and litter volume, but negatively associated with biotic attributes such as plant richness, plant cover and biocrust cover (Fig. 4). Aridity was directly positively associated with soil labile carbon

(Fig. 5b) and enzymes (Fig. S5a). Aridity also had indirect effects by suppressing the negative effect of canopy size on soil enzymes (Fig. S5a), plant cover (Fig. S5b), plant richness (Fig. 5c) and biocrust cover (Fig. S5c), or by enhancing the positive effect of soil pH on attributes such as soil infiltrability (Fig. 5a) and plant richness (Fig. 5c).

Soil sand content and pH were positively associated with abiotic fertile island effects (e.g. soil infiltrability, soil labile carbon, Fig. 5a-b), but had contrasting effects on plant richness (Fig. 5c), while soil EC indirectly affected the fertile island effect through its positive relationship with canopy size. By contrast, grazing intensity did not influence the fertile island effect for any attribute.

Discussion

Our results show clear evidence of the fertile island effect beneath perennial plants across the entire gradient, with enhanced soil resources (e.g. infiltrability, labile carbon) beneath woody plants, and greater plant performance (e.g. cover, richness) beneath perennial grasses. Importantly, we provide strong empirical evidence that the fertile island effect strengthens with increasing

Fig. 3 Coefficient of linear regressions between relative interaction index (RII) and aridity for vegetation patches (overall) and for tree, shrub and grass patches, respectively, on abiotic and biotic attributes (Tables S2, S3 in Appendix S5). Size of points represents the absolute value of the coefficient. * indicates significant aridity effect at *P* < 0.05. Different lowercase letters represent differences among patch types. INFIL = soil infiltrability; LC = labile carbon; enzymes (BG, CB, NAG, PHOS); LVOL = litter volume; PCOV = plant cover; PRICH = plant richness; BIOC = biocrust cover
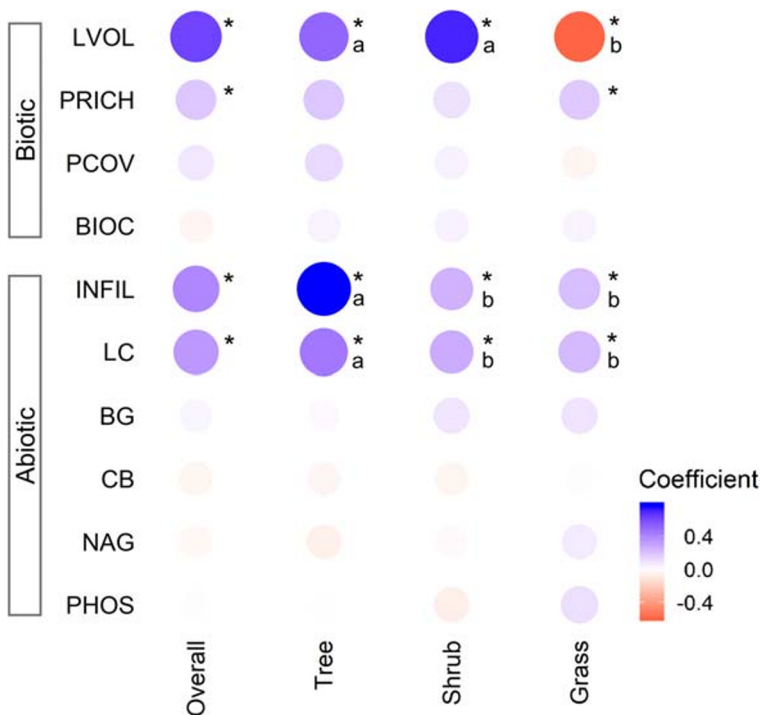
Fig. 4 Heatmap illustrating the standardized total effects (sum of direct plus indirect effects) of driving factors derived from the structural equation modelling for biotic and abiotic fertile island effects. INFIL = soil infiltrability; LC = labile carbon; PCOV = plant cover; PRICH = plant richness; LVOL = litter volume; BIOC = biocrust cover; SAND = soil sand content
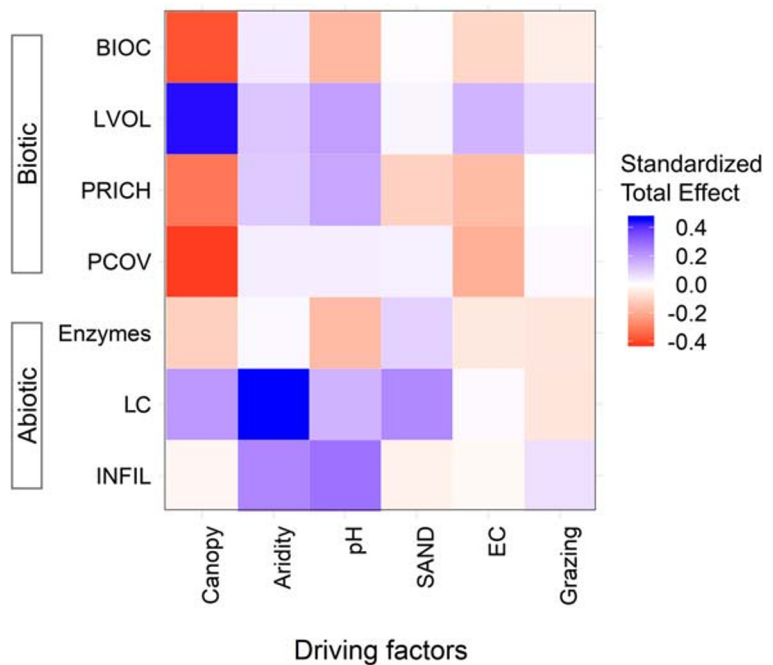

aridity, with the greatest litter and soil resources accumulated beneath trees. Canopy size and aridity were the major environmental variables associated with the magnitude of the effect, exerting direct and indirect effects on different response variables. Furthermore, we identify tradeoffs between biotic (groundstorey plants) and abiotic (soils) resources beneath vegetation, driven by canopy size of perennial plants. Our results suggest that the strength of the fertile island effect is likely to intensify under drying climatic conditions, which are predicted for drylands globally, but that any effects will vary with the target attribute and patch type. This study extends our understanding of feedbacks between increasing dryness and plant-soil interactions, with implication for potential alterations in ecological processes and functioning of terrestrial ecosystems under forecasted drier climates.

Fertile island effect varies with response variable and patch type

Our extensive sub-continental survey revealed a defined fertile island effect beneath the canopies of all perennial vegetation; trees, shrubs and grasses, consistent with current understanding of the fertile island or fertile patch phenomenon globally (Ochoa-Hueso et al. 2018; Okin et al. 2015; Ravi et al. 2007). For example, compared with the interspaces, soil beneath perennial plants had more labile carbon, likely resulting from greater litter inputs and higher activity of enzymes associated with the breakdown of cellulose (cellobiosidase; Weintraub et al. 2013), and greater soil infiltration due to more porous structure (Daryanto et al. 2013). Perennial plant canopies are also known to ameliorate environmental conditions by buffering temperature extremes and reducing solar radiation (Belsky et al. 1989), creating preferred conditions for groundstorey protégé plants (Abella and Chiquoine 2019), but constraining the development of biocrusts (Soliveres and Eldridge 2020).

Importantly, our results indicated the importance of plant canopy size in defining the magnitude of the fertile island effect. For example, woody plants characterized by large canopies were generally associated with greater soil resources (e.g. labile carbon and enzyme concentrations), but sparser plant and biocrust cover beneath them. Highly productive woody plants with well-developed root systems can enhance nutrient accumulation by increasing the input of organic matter (Ward et al. 2018) and scavenging resources from the interspaces and deeper in the soil profile (Li et al. 2017). A greater cover of woody plants likely supports an abundant microbial community with diverse effects on enzyme activities (Ochoa-Hueso et al. 2018; Van Der Heijden et al. 2008). In our study, soil beneath trees
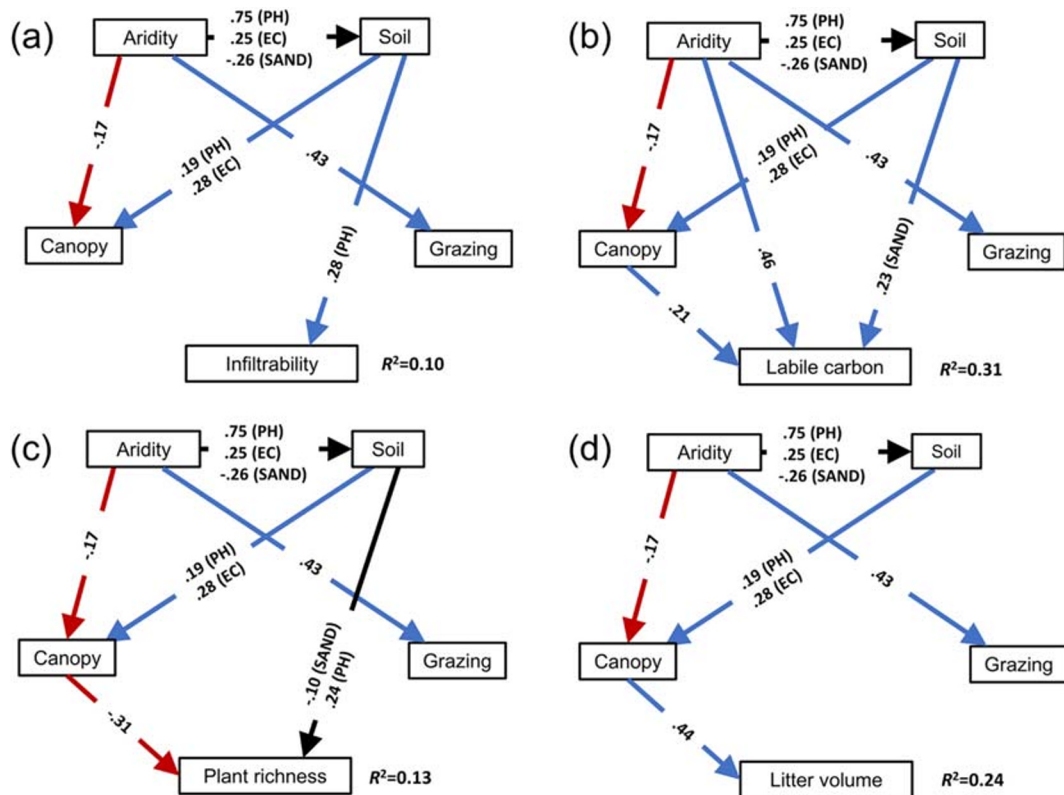
Fig. 5 Structural equation model assessing the direct and indirect effects of Aridity, Soil, Canopy size (canopy diameter of shrubs and trees, basal diameter of grasses), Grazing intensity on the fertile island effect of (a) infiltrability, (b) labile carbon, (c) plant richness and (d) litter volume. 'Soil' is represented by soil pH (PH), soil electrical conductivity (EC) and soil sand content (SAND); Pathways are significant negative (red unbroken line), significant positive (blue unbroken line) or mixed significant negative and significant positive (black unbroken lines), insignificant pathways were not shown in the models. Model fit: Infiltrability: $\chi^2 = 8.40$, df = 5, $P = 0.14$, $R^2 = 0.10$, RMSEA = 0.04. Labile carbon: $\chi^2 = 8.40$, df = 5, $P = 0.14$, $R^2 = 0.31$, RMSEA = 0.04. Plant richness: $\chi^2 = 8.40$, df = 5, $P = 0.14$, $R^2 = 0.13$, RMSEA = 0.04. Litter volume: $\chi^2 = 8.40$, df = 5, $P = 0.14$ $R^2 = 0.24$, RMSEA = 0.04

had a lower activity of the enzyme phosphatase, which is produced by plant roots and enzymes to mineralize organic phosphorus. This is likely due to the presence of greater levels of soil phosphorus beneath tree canopies, potentially resulting from mycorrhizal associations with the roots of *Eucalyptus* spp. (Burgess et al. 1993), the dominant tree genera along our gradient. Despite the potential facilitatory effects of large tree canopies (e.g. shading, fertile soils; Belsky et al. 1989; Eldridge and Wong 2005), their deep roots intensify below ground resource competition (e.g. water, nutrients) with groundstorey plants (Munzbergova and Ward 2002). Canopy closure and dense litter loads beneath trees, particularly in closed forests in higher rainfall areas, can also limit light penetration to the soil surface, restricting the establishment of vascular plants and

biocrusts (Abella and Chiquoine 2019; Ding and Eldridge 2020). These competitive effects apparent beneath tree canopies would diminish beneath perennial grasses that are characterized by sparse canopies and shallow roots.

We found that the impacts of canopy size on soils and groundstorey plants were exacerbated by increasing soil pH and EC. Increasing soil pH is known to enhance the activity of fungal phyla such as Ascomycetes but suppress the activity of bacteria (Angel et al. 2013; Tedersoo et al. 2014), likely increasing fungal breakdown of organic matter and thus nutrient accumulation (Sinsabaugh et al. 2008). However, high soil salinity (EC) would be expected to reduce groundstorey cover by suppressing plant metabolism (Bernstein 1975).

These contrasting effects of soil pH and EC intensified with canopy size, as plants with large canopies (e.g. woody plants) also accumulate soluble salts within sub-canopy 'salinity islands' (Yu and Wang 2018).

Fertile island effect strengthens with increasing aridity

Our results demonstrated that the fertile island effect on soils intensified with increasing aridity. This strengthening effect reflects weakening patch connectivity (Okin et al. 2015) and increasing separation between perennial plant canopies as dryness increases (Berdugo et al. 2020), thus greater differentiation in resources (e.g. litter, soil properties, microbe communities) between vegetated patches and their interspaces. Reductions in soil moisture with increasing aridity likely alter the tradeoffs between physical (e.g. aeolian processes, soil water leaching) and biological (e.g. by plants and micro- or macro-organisms; Garner and Steinberger 1989) transfers, with biological processes of resource accumulation supplanting abiotic processes of redistribution, thus leading to a greater fertile island effect around vegetations.

In addition, we found a stronger enhancement of the abiotic fertile island effect with increasing aridity beneath trees, many of which were eucalypts, up to 30 m tall, with deep tap roots that allow them to access groundwater (Eberbach 2003). Unlike grasses and shrubs that are susceptible to drought and disturbances (Koerner and Collins 2014), eucalypts are generally unpalatable to livestock and native herbivores (e.g. kangaroos; Oh et al. 1968), and resprout rapidly after fire through the production of epicormic buds (Burrows 2002). Furthermore, unlike grasses and shrubs, whose canopies contract under drying conditions, tree canopy size increased with increasing aridity (Fig. S6 in Appendix S6), enhancing their ability to sequester resources such as dust, nutrients, and rainfall (Belsky et al. 1989; Eldridge and Wong 2005; Ochoa-Hueso et al. 2018). However, we found that any enhancement of abiotic resources (e.g. soil carbon, enzymes) with increasing aridity was mitigated by a reduction in soil sand content along our gradient, potentially due to the trapping of finer aeolian material under perennial plants as environments become drier (Ravi et al. 2007).

Our results also suggest a strengthening of the fertile island effect on plant richness with increasing aridity,

resulting from alterations in species interactions. A refinement of the stress-gradient hypothesis (Maestre et al. 2009) suggests a greater frequency of facilitative interactions with intensifying stress, resulting from mechanisms such as hydraulic lift, heat buffering and fertile soils (Belsky et al. 1989; Caldwell et al. 1998), potentially overriding competitive effects between perennial plants and groundstorey vegetation (Dohn et al. 2013). We also found that aridity indirectly enhanced plant performance (i.e. greater cover and richness) by either mitigating the suppressive effects of canopy size (i.e. sparser canopies in drier areas) or by enhancing the positive effect of greater soil pH with increasing dryness (Berdugo et al. 2020).

Although increasing aridity was associated with a greater grazing intensity along our gradient, we did not detect any impacts of grazing on the fertile island effect for any resources. Though this might appear at odds with the general notion that the fertile island effect results from overgrazing (Allington and Valone 2014), the most parsimonious explanation is that low levels of grazing by native herbivores (kangaroos; *Macropus* spp.) are unlikely to drive major changes in resource redistribution compared with overgrazing by livestock (Bennett 1999), which may result in a collapse in the fertile island effect (Cai et al. 2020), an increasing land degradation.

Conclusions

Our study provides novel evidence that both biotic (groundstorey plants) and abiotic (soils) fertile islands are generally apparent beneath trees, shrubs and grasses, at all points along the aridity gradient (humid to arid), extending the fertile island effect from dryland ecosystems to a wider climatic envelope. Specially, we have shown that the fertile island effect depends on patch type, with biotic (plants) and abiotic (soils) attributes contrastingly regulated by canopy size, thus no single patch type optimizes both soil fertility and plant performance. Furthermore, our study suggests that predicted increases in aridity will likely strengthen the fertile island effect beneath trees, reinforcing the importance of trees in drier environments to support critical ecosystem functions and services (e.g. carbon fixation, habitat provision) particularly given their recruitment failure under drying conditions (Fensham et al. 2015). Finally, greater

biocrust cover in the interspaces will likely increase with intensifying dryness (Ding and Eldridge 2020; Mallen-Cooper et al. 2018), potentially compensating for reductions in soil stability and nutrient cycling as perennial plants getting sparse under forecasted aridification (Berdugo et al. 2020).

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

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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