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Multi-scale influences on the fertile island effect: Landscape-scale and patch-level processes drive patterns of soil fertility in the Chihuahuan Desert

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Research Article

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Abstract

Islands of fertility, patches of locally enhanced soil conditions, play a key role in increasing productivity in dryland regions. The fertile island effect (FIE) influences a range of variables including nutrient availability, soil moisture and microbial activity. While most examinations of the FIE focus on islands created by perennial plants at local scales, the effect may vary across spatial scales and under cover types including shrubs, grasses and biological soil crusts (biocrusts). This study explored differences in the FIE between soil depths across landforms and patch types for biogeochemical factors (nutrient availability) and biotic properties (microbial community structure, extracellular enzymatic activity). The FIE differed across landforms and soil depths, suggesting that soil geomorphology may play a major role in predicting soil fertility. Additionally, the FIE of enzymatic activity and available nutrients varied by patch type consistently across landforms, suggesting patch-scale processes influencing nutrient availability and acquisition are independent of landscape-scale differences. We show that biocrusts can have an FIE similar to that of shrubs and grasses, an underexplored control of variability and productivity in drylands. These findings necessitate further work to improve our understanding of how ecosystem processes vary across scales to influence patterns of productivity and soil fertility.

Impact statement

Drylands cover about 40% of the Earth's land surface. Despite scarce water and nutrients, these regions are responsible for about 40% of global net primary productivity. Primary productivity in drylands is enhanced by islands of fertility, which are defined as patches of increased resources (e.g. water and nutrients) and improved soil conditions beneath plant canopies. Islands of fertility are often defined as trees, shrubs or perennial grasses which, largely due to their size, drive the processes that form these islands such as the accumulation of nutrient-rich dust and plant litter as well as water. However, in addition to plants, the microbial community is also a key driver of soil fertility and can dominate land-cover in drylands. This study explores the factors influencing soil fertility across a range of spatial scales. Understanding the variables that affect soil fertility across spatial scales can reveal novel insights into the role of islands of fertility in productivity and land-cover change in dryland ecosystems. These findings highlight the need for additional research to develop our understanding of how ecosystem processes vary across different scales to impact patterns of soil fertility and productivity.

Introduction

Islands of fertility are an inextricable characteristic of drylands and a key driver of productivity in arid and semi-arid ecosystems (Noy-Meir, 1973; Schlesinger et al., 1990; Sala and Aguiar, 1996; Aguiar and Sala, 1999). Fertile islands form through the concentration of resources (e.g. nutrients and water) below plant canopies, as a result of biotic and abiotic processes that occur beneath plants, including the accumulation of nutrient-rich dust and plant litter, the modification of soil water holding capacity, and biological nitrogen fixation by symbiotic microbes associated with shrubs (Schlesinger et al., 1990; Sala and Aguiar, 1996; Ridolfi et al., 2008). The concentration of resources creates a biological feedback where improved soil conditions promote growth in vegetated patches, further improving soil fertility compared to bare areas between plants (Charley and West, 1975; Schlesinger et al., 1990). The formation of fertile islands and the biological feedbacks they create are well understood (e.g. Garner and Steinberger, 1989; Sala and Aguiar, 1996; Okin et al., 2015; Li et al., 2017; Eldridge et al., 2024);

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however, past work has mainly focused on fertile islands at the local plant scale despite evidence that soil fertility, and by extension the fertile island effect (FIE), may vary across multiple scales (Ding and Eldridge, 2021; Duniway et al., 2022; Osborne et al., 2022).

The development of fertile islands and thus the magnitude of the FIE are mainly influenced at three spatial scales: (1) landscape level (e.g. climatic, topographic and edaphic properties), or at the local scales of (2) patch level (e.g. dominant cover type within a patch), and (3) micro-site level (e.g. soil depth, areas with different microbial community compositions) (Ochoa-Hueso et al., 2018; Ding and Eldridge, 2021). At the landscape scale, physical and chemical soil properties (e.g. texture, calcite abundance) and other landscape factors (e.g., slope, elevation, runoff rates, dust or sediment accumulation) vary across landforms (Monger and Bestelmeyer, 2006), which can considerably influence ecosystem properties that contribute to the FIE such as nutrient availability, soil moisture content and vegetation cover and distribution (Lajtha and Schlesinger, 1988; McAuliffe, 1994; Parker, 1995; Buxbaum and Vanderbilt, 2007; Rachal et al., 2012). At the local scale, patch-level (patch type) and microsite-level (soil depth) differences can also affect properties that influence the FIE including heterogeneity of soil nutrients, plant cover and soil microbial community structure. Although past studies have examined the relationship between the FIE and variables including elevation (Thompson et al., 2005), aridity and patch type (Ding and Eldridge, 2021), soil depth (Ma et al., 2024), and patch size (Fitzpatrick et al., 2024), it remains unclear how geomorphic context may influence the FIE and whether these large-scale changes in soil characteristics could influence the FIE at the patch scale.

Additionally, the FIE is often considered only in the context of plants, as fertile islands are typically defined as islands formed by perennial plants (i.e. shrubs and grasses, see Ding and Eldridge, 2021; Ma et al., 2024). However, biocrusts – soil surface aggregates containing communities of cyanobacteria, algae, lichens, mosses and fungi (Pietrasiak et al., 2013; Weber et al., 2022) – can also enhance soil fertility between plant patches (Bowker et al., 2018; Sepehr et al., 2022; Maestre et al., 2024). Despite their importance to a range of ecosystem processes (e.g. Belnap et al., 2016), studies exploring the FIE often only consider biocrusts in relation to plants and not in isolation. Because they play a key role in many ecological processes (e.g. nutrient and moisture content), biocrusts may act as fertile islands (or "mantles," as in Garcia-Pichel et al., 2003; Reed et al., 2019) regardless of plant presence to enhance dryland productivity. In biocrusts, the FIE may change at different scale than for plants, as microbial biomass is typically concentrated in the top few centimeters of soil, and the community composition of biocrusts can vary at the scale of centimeters and even millimeters (Garcia-Pichel et al., 2003; Steven et al., 2013).

This study aimed to compare how the magnitude of the FIE at two soil depths varies across spatial scales (landform and patch type) for both biogeochemical factors (e.g. nutrient availability) and biotic processes (e.g. microbial community structure, extracellular enzymatic activity). We hypothesized that, while the size of the FIE would vary across patch types and soil depth, landform-driven differences would be the largest due to significant edaphic differences between landforms. We also hypothesized that the effect size of most variables would be positive for all patch types, though shrubs would have the largest effect sizes, as plant canopy size generally exhibits a positive relationship with soil resource availability (Fitzpatrick et al., 2024).

Methods

Study site

This study was conducted in the Jornada Experimental Range (JER) in southern New Mexico, USA, at the northern extent of the Chihuahuan Desert. Mean annual precipitation in the area is 23 cm, with about 52% of precipitation occurring during the summer monsoon (July 1–September 30) (Greenland and Anderson, 1997). Air temperatures range from a monthly average maximum of 36 °C in June to an average minimum of 13 °C in January (Greenland and Anderson, 1997). The JER was historically dominated by black grama (*Bouteloua eriopoda*) grassland but has been transitioning to shrubland in response to factors such as grazing and extreme drought in the last 50–150 years (Peters and Gibbens, 2006).The JER has 22 unique soil types, each having high inorganic carbon (calcium carbonate) content and little to no organic matter, distributed across 24 distinct geomorphic units (Gile et al., 1981; Monger, 2006).

Sites were selected on four distinct geomorphic units (landforms hereafter) along the basin's piedmont slope, based on the classification described in Monger (2006): (1) alluvial flat – the lowest topographic landform on the slope, characterized by alluvial sediments brought in by sheet floods from upslope; (2) erosional scarplet – a lower portion of piedmont slope with arcuate ridges of quartzose sand deposits derived from the basin floor. Our study focused on the sandy ridges; (3) fan piedmont – the dominant landform on the piedmont slope, largely comprising coalescent alluvial deposits and (4) alluvial fan remnant – the topographically highest landform on the piedmont slope, often containing petrocalcic horizons (see Table 1 for physical and chemical soil properties of each landform and Figure 1a for spatial distribution of sampling sites). Within each landform, three representative patches of four patch types were selected: (1) shrub – below a tarbush (*Flourensia cernua*) plant canopy; (2) grass – beneath an individual of the dominant grass at each site, tobosa grass (*Pleuraphis mutica*) or bush muhly (*Muhlenbergia porteri*); (3) biocrust – soil with a distinct biocrust layer in the plant interspace and (4) interspace – bare, uncrusted soil (Figure 1b).

Soil sampling

Samples were collected in June 2021 using sterile soil sampling techniques. At each patch within a site, we used a 6-cm-diameter corer to collect five soil cores to a depth of 2 cm within a 25 cm^2 area. These surface cores were combined into one composite sample representing each patch at each site. This sampling depth was chosen to reflect the typical thickness of topsoil including biological soil crusts in this system. Subsurface (2–30 cm) soil samples (representing a general Bw horizon) were collected from soil pits excavated at the same locations as surface samples at the edge of the plant canopy. Soil pits were 100 cm by 50 cm wide for shrubs and 50 cm × 50 cm for grasses. For biocrust and interspace patches, pits were 25 cm × 25 cm. Pits extended to a depth of 30 cm or the top of the caliche, whichever was shallower. Pits reached caliche at two interspace patches on the alluvial fan remnant. Subsurface soils were collected from the soil profile as a composite sample from a depth of 2–30 cm, focusing consistent sampling within a 25-cm-wide area. Soil samples were transported in a cooler to a 4 °C cool room for storage until processing.

Laboratory analyses

Physical and chemical soil analysis

The fine earth fraction (<2 mm) was obtained by removing litter and gravel and passing soil aggregates through a 2-mm sieve. After

Table 1. Mean values of physical and chemical soil qualities at each sampling scale

Landform	Patch type	Soil depth (cm)	Gravel (%)	Sand (%)	Silt (%)	Clay (%)	Percent saturation	Soil pH	EC (dS/m)	% Calcite
Alluvial flat	Shrub	0–2	0.09	42	55	3	51	7.23	2.81	2.16
		2–30	0	21	70	9	29	7.47	0.87	1.97
	Grass	0–2	0.01	46	51	3	49	7.20	1.20	1.79
		2–30	0	20	71	8	29	7.37	0.64	1.65
	Biocrust	0–2	0	20	71	9	32	7.33	0.73	1.6
		2–30	0	20	72	8	28	7.43	0.51	2.05
	Interspace	0–2	0	20	74	6	34	7.40	0.67	1.97
		2–30	0	19	72	8	30	7.30	1.42	1.94
Erosional scarplet	Shrub	0–2	0.60	54	44	2	24	7.47	0.97	0.64
		2–30	1.29	29	64	8	22	7.47	0.84	1.84
	Grass	0–2	0.05	59	39	1	33	7.20	0.93	1.23
		2–30	0.36	34	58	8	22	7.34	0.62	1.63
	Biocrust	0–2	0.34	29	65	6	22	7.40	0.67	1.42
		2–30	4.32	18	72	9	25	7.40	0.43	2.94
	Interspace	0–2	0.01	87	13	0	17	7.60	0.47	0.35
		2–30	0.41	30	62	9	20	7.50	0.45	1.54
Fan piedmont	Shrub	0–2	3.27	57	41	2	24	7.47	0.86	1.77
		2–30	11.96	28	66	6	29	7.47	0.65	3.32
	Grass	0–2	0.03	64	35	1	35	7.20	1.27	1.40
		2–30	11.27	45	52	3	28	7.33	0.99	2.09
	Biocrust	0–2	1.03	42	55	3	26	7.43	0.68	2.13
		2–30	20.49	37	58	5	27	7.50	0.82	3.20
	Interspace	0–2	19.44	40	54	5	21	7.57	0.46	1.83
		2–30	6	29	65	6	29	7.53	0.50	4.03
Alluvial fan remnant	Shrub	0–2	7.16	51	46	2	23	7.70	0.75	4.21
		2–30	15.34	38	57	5	26	7.73	0.74	5.21
	Grass	0–2	2.55	64	34	1	27	7.43	1.05	2.72
		2–30	4.78	52	44	3	26	7.70	0.47	3.44
	Biocrust	0–2	11.70	55	43	1	25	7.40	0.63	2.13
		2–30	66.64	49	48	3	23	7.57	0.54	4.19
	Interspace	0–2	37.98	45	49	6	18	7.60	0.48	3.25
		2–30	19.37	34	60	6	25	7.67	0.37	4.12

Note: A multiway ANOVA was used to detect significant differences in each variable across landforms, patch types, and soil depths. See Supplementary Table S1 for significant effects.

sieving, gravel was weighed and compared against total sample weight to determine gravel content. The fine earth fraction was homogenized and split using sterile techniques in a laminar flow hood for soil microbial, chemical, physical and nutrient analyses.

We determined soil pH and electric conductivity (EC) using the saturated paste method using 150–200 g of soil depending on texture via an Oakton Cole-Palmer pH/CON 510 Benchtop Meter (Vernon Hills, IL, USA) (US Salinity Laboratory Staff, 1954). Soil texture was assessed using a Malvern Mastersizer 2000 laser diffractometer (Malvern Instruments Ltd., Worcestershire, UK). Soil particle size distribution was calculated as the percentage of three sizes: sand (2.0–0.063 mm), silt (0.063–0.002 mm), and clay (< 0.002 mm), with gravel >2 mm. Total soil carbon was determined using a LECO SC632 Sulfur/Carbon Determinator (LECO Corporation, MI, USA). Soil inorganic carbon content was determined using a pressure calcimeter (Sherrod et al., 2002; Sparks, 2009) – soil was acidified in a sealed bottle, and the resultant CO_2 was quantified based on the pressure change. Organic carbon content was determined as the difference between total and inorganic soil carbon.

Microbial community analysis

A 20-g subsample was sent to Ward Laboratories, Inc. (Kearney, NE, USA) for microbial biomass and composition determination by the phospholipid fatty acid method as described in Quideau et al. (2016)

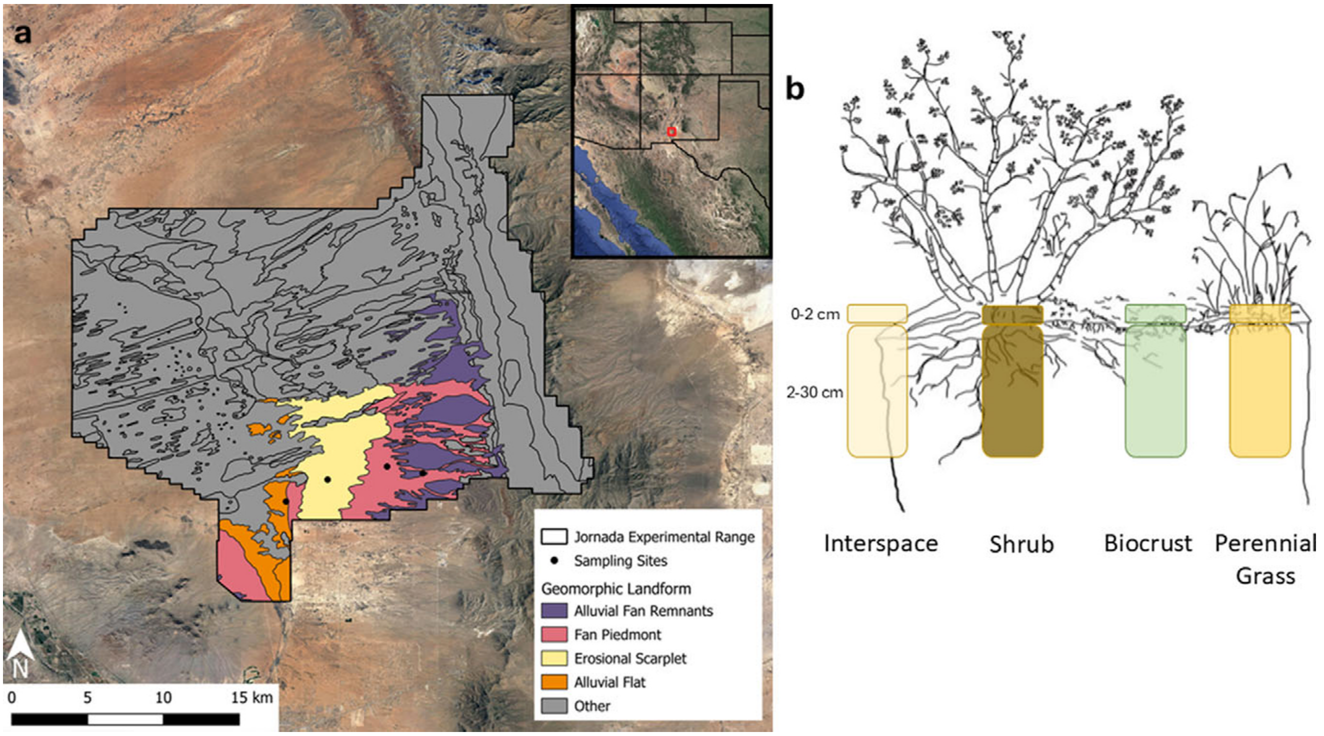

Figure 1. (a) Map of the study's sampling sites (shown as black points) along the piedmont slope with the four sampled landforms colored. (b) On each landform, three replicates of each of the four patch types were selected, and soil samples were collected at two depths (0–2 and 2–30 cm). *Source*: Created by Megan S. Stovall (b).

within 2 weeks of sample collection (Findlay, 2004). The Shannon Diversity Index, an index of functional group diversity of the microbial community, was calculated using the "vegan" package in RStudio Version 12.1.402 (Oksanen et al., 2022).

Extracellular enzymatic potential activity

Potential activity of 10 extracellular enzymes (Table 2) was measured using methods modified from Saiya-Cork et al. (2002) and McLaren et al. (2017). One gram of soil was blended with modified universal buffer ($pH = 7.75$), and slurries pipetted onto 96-well microplates along with fluorescing, 4-methylumbelliferone-tagged substrates. Assays were incubated at 20 °C for 3.5 h with half-hourly measurements, ensuring activity was measured in the linear range of the reaction. Sample fluorescence (i.e. cleaved substrate) was read at 360 nm excitation, 460 nm emission (BioTEK Synergy HT microplate reader; BioTek Instruments Inc., Winooski, VT, USA).

Soil nutrient analysis

Available nitrate (NO_3^-) and ammonium (NH_4^+) were determined by extracting 5 g of soil with 25 mL of 0.5 M potassium sulfate and shaking for 2 hours before filtering through glass filter paper. Extracts were analyzed using colorimetric microplate assays with a vanadium (III) chloride assay for nitrate (Doane and Horwáth, 2003) and a Berthelot reaction assay for ammonium (Rhine et al., 1998). Available phosphate (PO_4^{3-}) was extracted using 30 mL of 0.5 M sodium bicarbonate ($pH = 8.5$) added to 5 g of soil and shaken for 16 hours before filtering (Olsen, 1954). Biologically based phosphorus pools were measured using the method outlined by DeLuca et al. (2015). Briefly, this method uses four extractants to emulate strategies used by plants or microbes to access P: 0.01 M

Table 2. Aggregated variables and abbreviations

Group	Variables included	Abbreviation
Carbon-acquiring enzymes	A–1,4-glucosidase β–1,4-glucosidase β–1,4-xylosidase β-D–1,4-cellobiosidase	C-acq
Nitrogen-acquiring enzymes	β–1,4-N-acetyl-glucosaminidase Leucine amino peptidase	N-acq
Phosphorus-acquiring enzymes	Phosphodiesterase Acid phosphatase	P-acq
Oxidative enzymes	Phenol oxidase Peroxidase	Oxi
Microbial biomass	Total microbial biomass	Total MB
Microbial diversity	Microbial Shannon diversity index	Shannon Div
Readily available nutrients	Olsen-P K_2SO_4 Extractable NO_3^-, NH_4^+, and PO_4^{3-}	Avail. nutrients
Nutrients accessible with biological effort	Citric acid extractable phosphate Enzyme extractable phosphate	Biol. Effort
Occluded P	HCl extractable PO_4^{3-}	Occl. P
Organic matter	Organic carbon	Org. C

When possible, variables were aggregated based on most closely related biogeochemical or biological processes. Microbial biomass, microbial diversity, occluded P, and organic matter were not closely related to any other variables and were thus separated into distinct categories.

calcium chloride – P available in soil pore water; 0.01 M citric acid – P sorbed to clay or weakly bound to the soil matrix made accessible through organic acids released by plant roots and microbes; 1 M hydrochloric acid – P strongly bound to mineral surfaces and locked in mineral lattice (e.g. pedogenic carbonate) which is less biologically accessible; and 0.2 EU/mL phosphatase – labile organic P available through enzyme hydrolysis. Extractions were conducted in parallel by shaking 0.5 g of each sample in 10 mL of each extractant for 3 hours before centrifuging at 2500 rpm for 2 minutes and filtering. Phosphate in extracts was analyzed using colorimetric microplate assays (BioTEK Synergy HT microplate reader; BioTek Instruments Inc., Winooski, VT, USA) with a malachite green assay (D'Angelo et al., 2001).

Numerical and statistical analyses

The FIE size was calculated using the relative interaction index (RII) (Equation 1; Armas et al., 2004) to represent the magnitude of the difference between a fertile island patch and bare interspace soil between plants as described in Ding and Eldridge (2021) and Ochoa-Hueso et al. (2018):

$$\mathrm{RII} = \left(\mathrm{X_p} - \mathrm{X_i}\right) / \left(\mathrm{X_p} + \mathrm{X_i}\right), \qquad (1)$$

where $\mathrm{X_p}$ is the value of the biotic (e.g. microbial biomass) or abiotic (e.g. available nutrients) variables for the patch type of interest, and $\mathrm{X_i}$ is the value of the same attribute in the interspace soils from the same site and soil depth. RII ranged from −1 to 1, where positive values showed increased soil fertility compared to interspace soils, and negative values reflected a decrease in the variable relative to the interspace. We calculated the RII for each cover type and soil depth combination, considering the RII to be significantly positive or negative when the mean ± one standard error (SE) did not intersect zero.

We aggregated closely related variables based on the biogeochemical processes to which each variable was most closely related (Table 2) and calculated the mean RII of the selected variables for each sample. The FIE of each aggregated group was analyzed using a multi-factor analysis of variance (ANOVA) with the main factors such as landform, patch type and soil depth. In the presence of multi-factor interactions, aggregated variables were separated by factor and analyzed using a one-way ANOVA followed by a Tukey's HSD post-hoc test. Plots were made using the "ggplot2" package in R Version 12.1.402 (Posit team, 2024; Wickham, 2016). Assumptions of normality were tested using the Shapiro–Wilk test. When needed, variables were transformed to meet the assumptions; figures present untransformed data.

Results

Physical and chemical soil characteristics

Soil particle size varied across all spatial scales (landform, patch type and soil depth; Table 1). For most variables related to particle size, there was a significant interaction between all three spatial scales (Supplementary Table S1). Generally, gravel and sand content were lowest and silt and clay highest at the basin floor (alluvial flat); these increased or decreased respectively up the piedmont slope. Gravel content was marginally higher in the unvegetated soils, while soils beneath grasses and shrubs had higher sand content and lower silt and clay content than the other patch types for three out of four landforms. Surface soils had higher gravel, silt, and clay but lower sand content than subsurface soils.

Differences in soil EC varied at all spatial scales, with the multi-way ANOVAs revealing a significant three-way interaction between landforms, patch types and soil depths (Table 1 and Supplementary Table S1). EC in surface soils was generally higher than in subsurface soils beneath shrubs and grasses but not in biocrust and interspace patches. In surface soils, EC was significantly higher below all cover types compared to interspaces. The magnitude of these differences largely depended on landform. In subsurface soils, EC below shrubs, grasses and biocrusts was higher than interspace soils in upland landforms, and this difference decreased downslope. In the alluvial flat, the EC in subsurface soils in all vegetated patches was lower than in interspace soils. Soil pH ranged from 7.20 to 7.47. pH was elevated at the top of the piedmont slope (alluvial fan remnant) compared to the other landforms. pH was similar across patch types and soil depths.

Landscape-scale variations in the FIE

There was a significant landform effect or an interaction between landform and another factor for the FIE of all aggregated variables except organic carbon (Figures 2 and 3; Supplementary Tables S2 and S3). Landform effects interacted with soil depth for microbial diversity, N-acquiring enzymes, oxidative enzymes, available nutrients, unavailable nutrients and nutrients requiring biological effort.

The FIE of total microbial biomass was smaller at the bottom of the piedmont slope (alluvial flat and erosional scarplet) than the upper slope (fan piedmont and alluvial fan remnant). Similarly, the FIE of microbial diversity in surface soils was around zero in lower landforms and significantly higher at the top of the slope. In subsurface soils, microbial diversity had a negative or zero FIE across all landforms.

The FIE of both C- and P-acquiring enzymes was smallest at the bottom of the piedmont slope (alluvial flat), with no difference between the other three landforms. The FIE of N-acquiring enzymes followed the same trend but only in subsurface soils. In surface soils, the FIE of N-acquiring enzymes was elevated in the middle of the piedmont slope (erosional scarplet and fan piedmont) compared to the top and bottom of the slope (alluvial flat and alluvial fan remnant). The FIE of oxidative enzymes in surface soils was positive in the erosional scarplet, negative in the fan piedmont, and absent at the top and bottom of the slope. In subsurface soils, oxidative enzymes showed little to no FIE across all landforms. In surface soils, available nutrients and biologically acquired nutrients exhibited a positive FIE in all landforms except at the top of the slope, where biologically acquired nutrients had a negative FIE. The FIE of HCl-extracted P was positive in the erosional scarplet and negative in all other landforms. In subsurface soils, all forms of nutrients followed a similar trend – the FIE was about 0 in the alluvial flat and fan piedmont, less than or around 0 in the erosional scarplet, and positive at the top of the slope (alluvial fan remnant).

Patch-level variations in the FIE

Patch-level effects were present only for C-, N-, and P-acquiring enzymes and available nutrients (Figures 2 and 3 – significant effects). Although the FIE of C- and P-acquiring enzymes showed an effect of patch type, post-hoc analysis did not show significant differences between patch types. The FIE of N-acquiring enzymes was suppressed beneath biocrusts compared to shrubs and grasses.

The patch-level effect on the FIE of available nutrients interacted with soil depth (Figure 3 – significant effects). The effect of patch type was only evident in surface soils, where the FIE of available

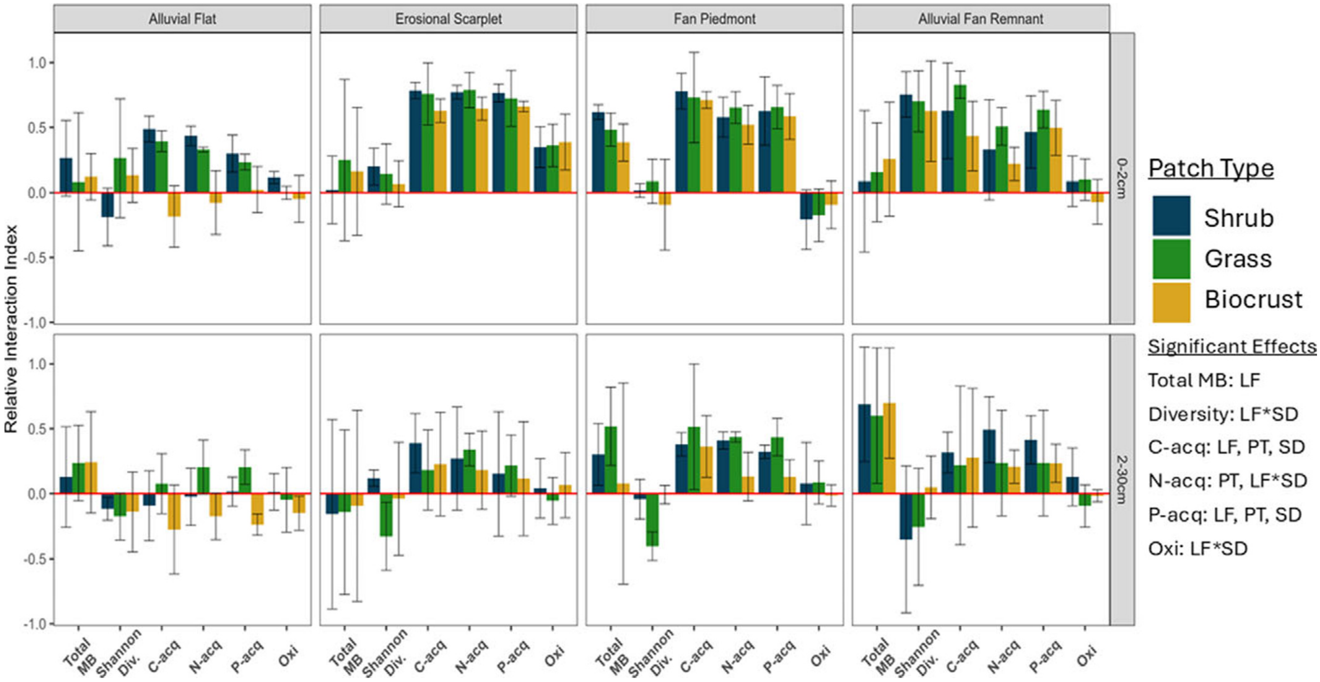

Figure 2. Differences in the fertile island effect for variables related to microbial community activity across geomorphic LFs, PTs, and SDs. *Note*: The fertile island effect is displayed as the relative interaction index (RII), described in Equation 1. Bar height represents the mean of replicates (n = 3) within a sampling site, and error bars show one standard error. RII is considered either positive or negative if the mean ± SE does not intersect 0. Significant ANOVA effects ($p < 0.05$) are displayed. Interactive effects are displayed as two factors joined with an asterisk. LF, landform; PT, patch type; SD, soil depth.

nutrients below biocrusts was smaller than that of shrubs and grasses.

Microsite-level variations in the FIE

Soil depth only significantly affected C- and P-acquiring enzymes and organic C (Figures 2 and 3 – significant effects) independent of other spatial scales. The FIE of organic C was larger in surface soils than subsurface soils. C- and P-acquiring enzymes had a similar trend, where the FIE was on average higher in surface soils than subsurface soils.

Discussion

We examined the magnitude of the FIE on a range of biogeochemical and microbial variables at two soil depths (0–2 and 2–30 cm) across multiple patch types (shrub, perennial grass and biocrust) in four landforms which varied in age and geomorphology. Our results reinforce the prevalence of the FIE in dryland ecosystems – metrics of soil fertility were generally higher below shrubs, grasses and biocrusts compared to bare interspace soils. However, the size of the FIE varied considerably across spatial scales, revealing distinct trends at each scale. These trends varied between response variables, suggesting that the magnitude and importance of the FIE may ultimately depend on a variety of biogeochemical and biological processes acting at vastly different spatial scales.

We found that the presence or size of the FIE is mainly influenced by variability in physical soil properties like texture at the landscape and microsite scales. Meanwhile, multiple patch types had a significant impact on nutrient availability and access, and differences in the FIE between patch types were consistent across the landscape (Figures 2 and 3). Although landform-level effects had a substantial impact on soil fertility as hypothesized, soil depth was similarly important, illustrating the highly variable nature of dryland soils, which can vary both across the landscape and within 2 cm in a soil profile. Surprisingly, the FIE was similar between biotic patch types for many response variables, with soils from biocrusts and grasses sometimes exhibiting an effect equal to or larger than shrubs, and these patch-specific effects influenced the FIE independently from the effects of landforms and soil depths.

The Fertile Island Effect is widespread across spatial scales

While patterns in the FIE varied across the spatial scales considered here, measured variables generally exhibited a positive FIE across all landforms in all or most patch types (Figures 2 and 3). Our results reinforce and expand our current understanding of the FIE (Garner and Steinberger, 1989; Ochoa-Hueso et al., 2018; Eldridge et al., 2024). First, all biotic patch types (including biocrusts) typically had enriched soil (e.g. elevated soil nutrients), elevated soil microbial activity (enzymatic activity, microbial biomass), more available soil moisture and increased organic matter across all landforms compared to bare interspace soils. Additionally, the coarser soils below grasses and shrubs compared to unvegetated patches shows that vegetation stabilizes the soil and captures aeolian sediments, especially larger particles like sand. Finally, the FIE was more apparent in surface soils (0–2 cm), though it was also observed in subsurface soils (2–30 cm) depending on landform and patch type. The elevated FIE in surface soils reflects the concentration of microbial activity and plant roots close to the soil surface; unsurprisingly, biological activity was generally higher where soil fertility was higher (Gibbens and Lenz, 2001; Taylor et al., 2002; Kirschner et al., 2021).

Occluded P presents a notable exception to the trend of a positive FIE. Occluded P exhibited a positive FIE in both surface and subsurface soils in only one landform (erosional scarplet for

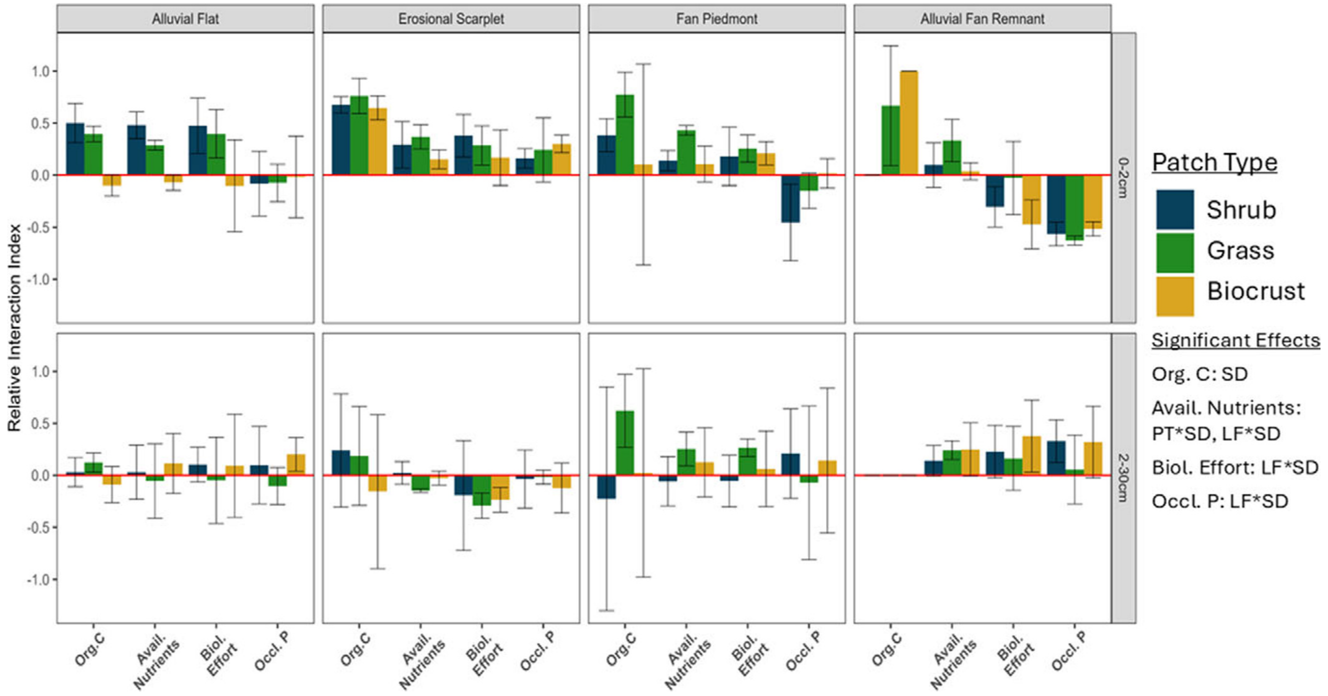

Figure 3. Differences in the fertile island effect for variables related to nutrient availability and soil organic matter across geomorphic LFs, PTs, and SDs. *Note*: The fertile island effect is displayed as the relative interaction index (RII), described in Equation 1. Bar height represents the mean of replicates (n = 3) within a sampling site, and error bars show one standard error. RII is considered either positive or negative if the mean ± SE does not intersect 0. Significant ANOVA effects ($p < 0.05$) are displayed. Interactive effects are displayed as two factors joined with an asterisk. LF, landform; PT, patch type; SD, soil depth.

surface and alluvial fan remnant for subsurface), and the FIE of occluded P was either absent or negative in all other landforms. The negative FIE in surface soils under all cover types compared to the interspace reflects the variety of effects that plants and biocrusts can have on nutrient cycling (Hobbie, 1992; Delgado-Baquerizo et al., 2014; Maestre et al., 2024). P is made unavailable through leaching to deeper soils or sorption to pedogenic carbonate in the soil; these processes may be increased in interspace soils where plants and microbes are not actively cycling the available P (Guppy et al., 2005; Belnap, 2011). As a result, this “stagnant” P may be more vulnerable to occlusion and leaching, thus decreasing P availability. The lack of a significant FIE on occluded P in subsurface soils in these landforms may show a comparably small influence of plant and microbial activity on P cycling compared to surface soils. As droughts and heat waves increase in frequency and severity, the increased occlusion of available P due to decreased biological demand could degrade dryland soil fertility, causing significant negative feedbacks in P cycling in arid regions.

The soil-geomorphic template influences the magnitude of the Fertile Island Effect

Geomorphology is the primary long-term control in structuring dryland landscapes and developing into units of similar soil properties and ecological conditions designated as the soil-geomorphic template, a conceptual framework predicting vegetation, animal and microbial community composition and structure (Monger, 2006; Monger and Bestelmeyer, 2006). Under the soil-geomorphic template, biotic processes are influenced by variation in soil properties (e.g. texture, salinity), topography (e.g. elevation, aspect), microclimate and parent material. Accordingly, the soil-geomorphic template considers many factors directly relevant to soil fertility including water, nutrients, root development and plant anchorage, and may help predict patterns of soil fertility in dryland systems as suggested in our study.

Due to their proximity (<10 km between sites), our study sites had similar climate, parent material and dominant vegetation types; consequently, differences in topography and soil properties (e.g. particle size, soil moisture) likely explain much of the variation between sampling sites. Lower elevation landforms typically had a gentle slope and fine-textured soils while higher elevations had a steeper slope and gravelly, coarser-textured soils. Although soil texture class did not change dramatically across the landscape (soils ranged from silty loam at the base of the slope to sandy loam at the top), sand and gravel contents did increase substantially with elevation, indicating the role of geomorphology in determining soil texture (Table 1). However, biotic processes can also alter texture, evidenced by coarser soils beneath shrubs and grasses compared to unvegetated patches (Table 1). This effect is the strongest at the bottom of the slope with finer soil texture, possibly because wind would be strongest at low elevations, thus increasing the trapping of coarse sediments by plants and biocrusts, while the weak effect at the top of the slope indicates that coarse sediments accumulate regardless of vegetation or biocrust presence.

Soil texture directly influences an array of ecosystem processes including water and nutrient availability, microbial activity, plant survival and recruitment and C storage (Silver et al., 2000; Osborne et al., 2022; Veblen et al., 2022). However, we found that regardless of texture or topography, soil salinity (measured as electrical conductivity, Table 1), a proxy for water availability in such water-scarce environments, was higher in surface soils beneath plants than in unvegetated soils in all landforms. The consistency of this effect indicates plants’ ability to increase water availability and improve soil conditions beneath their canopies across a range of geomorphic conditions (Sala and Aguiar, 1996; Fitzpatrick et al., 2024). The increased salinity beneath plants may also stem from hydraulic lift, wherein plant roots bring potentially saline water from lower soil layers to the soil's surface (Caldwell et al., 1998; Armas et al., 2010). Additionally, the accumulation of litter and sediment beneath plants can increase decomposition, further explaining the elevated electrical conductivity in vegetated patches (Xu et al., 2016; Stavi et al., 2019; Anjum and Khan, 2021). While vegetation's effect on soil moisture persisted regardless of landform, the magnitude of the effect varied: the difference in salinity between vegetated and unvegetated patches was greatest at the valley floor where water availability is often highest, increasing accumulation around plants (Table 1). That the effect of vegetation can vary dramatically across landforms implies that landscape position plays a role in determining the strength of the FIE.

Variations in the FIE of both biogeochemical and microbial factors were observed across the landscape, which may be explained in part by processes comprising the soil-geomorphic template. The FIE of variables related to microbial activity (i.e. biomass, diversity, enzymatic activity) was generally highest at the top of the piedmont slope and lowest at the valley floor (Figure 2). However, nutrient availability generally exhibited the opposite trend, with a larger FIE in fine-textured soils at the bottom of the slope, though FIE was generally positive across all landforms (Figure 3). Additionally, the FIE of microbial activity and available nutrients was positive in both coarse and fine soils, indicating higher levels of each below fertile islands compared to interspace soils, but differences between fine and coarse soils were more pronounced for microbial activity than nutrient availability. The contrast between microbial activity and nutrient availability illustrates that fertile islands may differentially affect different biogeochemical processes depending on their geomorphic context. Naturally, factors not considered in this study such as heterogeneity of local precipitation, grazing intensity or time since patch formation likely contribute to the observed trends (Schlesinger et al., 1990; Ridolfi et al., 2008; Allington and Valone, 2014). The soil-geomorphic template provides a framework in which to consider and potentially predict how patterns of soil fertility may vary across a range of geomorphic conditions.

Patterns in the Fertile Island Effect across patch types are consistent across landforms

Islands of fertility are typically defined as vegetated patches, often shrubs or grasses, that improve soil conditions below their canopies (Schlesinger et al., 1990; Allington and Valone, 2014) while biocrusts in this context are typically only considered alongside vegetation (e.g. Ding and Eldridge, 2021). We provide evidence that unvegetated patches with pronounced biocrust cover can exhibit an FIE of similar strength to that of grasses and shrubs across key metrics of soil fertility. This finding necessitates further investigation into the ability of biocrusts to act as fertility islands (or "mantles," see Garcia-Pichel et al. (2003)) independently from vegetation. Proposed mechanisms explaining the origins of fertile islands often center on the initial establishment of the shrubs that in time become an island (see Sala and Aguiar, 1996; Ridolfi et al., 2008); our study contributes to a growing body of evidence that the formation of fertile island may be supported in part by facilitation from biocrust communities (e.g. Sepehr et al., 2022).

Despite the widespread landform effects on the FIE and the differences in physical soil characteristics between landforms, the effects of patch type on the FIE remained consistent across the landscape. Patch type effects on the FIE were limited to variables related to nutrient availability and acquisition (available nutrients and extracellular enzymatic activity), and these effects were largely unaffected by landform-level differences (Figures 2 and 3). The lack of an interactive effect between landforms and patch types on the FIE of available nutrients and enzymatic activity suggests that large, landscape-scale differences in soil properties do not affect the patch-level biological processes influencing nutrient availability and acquisition. Plants and biocrusts can act as ecosystem engineers to modify and improve soil conditions (van Breemen and Finzi, 1998; Xiao et al., 2022), and the microbial community may play a similar role through the use of extracellular enzymes. Consequently, plant and microbial activity may be more influential than landscape-scale processes in producing the patch-scale patterns described in this study.

However, patch-level effects on the FIE of available nutrients did differ across soil depths. The interactive effect between patch type and soil depth on available nutrients may be explained partly by the difference in soil depths that different organisms can access. Microbes are typically concentrated in the soil surface (topsoil) or around roots, while plant roots can extend deeper into the soil profile (Gibbens and Lenz, 2001; Garcia-Pichel et al., 2003; Kirschner et al., 2021). Thus, microbial uptake may be a dominant form of nutrient uptake in the top 2 cm of all patch types – but especially biocrusts – while uptake by plant roots and associated microbes may be dominant in deeper soils beneath grasses and shrubs. Our findings stress the importance of patch type, as each patch type can distinctly influence the FIE regardless of geomorphological context. The patch types considered in this study exhibited a positive FIE across many response variables and vastly different spatial scales, and the effect was often comparable between patch types, indicating that shrubs, grasses and biocrusts can all similarly affect soil fertility.

Conclusion

Our findings provide evidence that interactions between soil geomorphology and soil fertility vary across spatial scales while also demonstrating that biogeochemical processes are differentially affected by geomorphology depending on both biotic and abiotic processes. This new understanding of the relationship between geomorphology and soil fertility necessitates a more interdisciplinary approach to studying patterns of productivity in dryland ecosystems. Including the influences of processes acting on the FIE – and thus productivity – at a range of spatial scales will help improve models of dryland productivity and land-cover change. Additionally, our results show that biological soil crusts may also act as fertile islands; expanding our perception of fertile islands to include biocrusts in addition to perennial plants may reveal novel insights into the factors driving this key dryland phenomenon. These findings necessitate further work to improve our understanding of how ecosystem processes vary across scales to influence patterns of soil fertility and productivity.

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Author contribution. Dylan J. Stover: Writing – original draft preparation, review and editing, investigation, visualization, data curation. Lixin Jin: Writing – review and editing, methodology, investigation, funding acquisition, data curation. Nicole Pietrasiak: Writing – review and editing, methodology, investigation, data curation. Jennie R. McLaren: Writing – review and editing, methodology, data curation, supervision.

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