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Key Points:

- Spatial patterns of 19 soil elements were quantified to characterize nutrient island formation following woody encroachment in a savanna
- Only a subset of soil nutrients (i.e., N, P, S, Ca, Cu, and Sr) were accumulated underneath woody canopies following woody encroachment
- Spatial distributions of other soil nutrients (e.g., K, Mg, Fe) were related to landscape-scale variation in soil pH, clay content, and slope

Supporting Information:

Supporting Information may be found in the online version of this article.

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Divergent Patterns and Spatial Heterogeneity of Soil Nutrients in a Complex and Dynamic Savanna Landscape

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Abstract Many grassy ecosystems around the world are experiencing woody encroachment. These woody encroachers often cause nutrient enrichment in the plant-soil environment, potentially facilitating their growth and reproduction. However, studies of encroachment effects on nutrient distributions have been confined to a few major elements (e.g., N, and P) and limited in spatial extent. We analyzed 19 elements in dominant plants and in georeferenced soils across a subtropical savanna landscape experiencing woody encroachment to quantify their spatial patterns and elucidate drivers responsible for these patterns. We found divergent patterns of spatial heterogeneity of these elements in surface soils across this complex landscape. Nutrient accumulation and redistribution underneath woody canopies occurred in a subset of elements (i.e., N, P, S, Ca, Cu, and Sr). Though some of these elements are not necessarily growth-limiting, they do occur in higher concentrations in woody compared to herbaceous plants. Distributions of the other elements were closely related to spatial variation in soil pH, clay content, and slope rather than to woody encroachment. Our nuanced spatial sampling approach and analysis reveal significant variation in nutrient distributions in response to woody encroachment, and illustrate the role of landscape patterns in mediating ecosystem processes. These changes in the concentrations and distributions of key essential nutrients broaden our understanding of the biogeochemical consequences of woody encroachment, and provide new insights regarding the significance of long-term vegetation dynamics in dryland ecosystems.

Plain Language Summary Encroachment of trees and shrubs into grass-dominated ecosystems, is geographically widespread and likely caused by land uses and global change phenomena. Previous studies suggest this dramatic vegetation change may alter the distribution and abundance of chemical elements in the soil that are critical for ecosystem structure and function. Therefore, understanding how woody encroachment affects soil nutrient stores and distribution patterns can provide key insights regarding the long-term vegetation dynamics of grass-dominated ecosystems. We examined spatial distributions of 19 elements in surface soils, many of which are essential plant nutrients, across a savanna landscape experiencing woody encroachment. Woody plants enriched only a subset of soil elements (i.e., N, P, S, Ca, Cu, and Sr) underneath their canopies following their establishment. However, spatial distributions of other soil elements were more related to variation in soil pH, clay content, and slope rather than to woody encroachment. Results demonstrate that the abundance and distribution of woody plants in savannas alters storage and distribution of some (but not all) plant essential nutrients. These increased stores of several potentially limiting elements may influence competitive interactions between plant species and influence the future trajectory of vegetation dynamics in regions where woody plants are encroaching.

1. Introduction

Tropical and subtropical grasslands, savannas, and other dryland ecosystems are geographically extensive and provide critical support for human livelihoods (Parr et al., 2014). In these ecosystems, woody plant cover and abundance have been increasing in response to changes in climate, fire frequency, herbivory, and atmospheric CO₂ concentration during the past century (Archer et al., 2017). This geographically widespread phenomenon has dramatic impacts on multiple ecosystem functions and services (Eldridge et al., 2011). For example, numerous studies conducted across a wide range of ecosystems have shown that soil nutrient

storage and availability is generally higher underneath the canopies of woody encroachers compared to surrounding grasslands (e.g., Blaser et al., 2014; Zhou et al., 2018), forming a potential positive feedback loop that facilitates the growth and reproduction of woody encroachers (Bond, 2008; O'Connor et al., 2014; Scholes & Archer, 1997; Zhou et al., 2018). Since nutrient availability has been hypothesized as one of the important factors determining the distribution of savannas by limiting the productivity of woody plants (Pellegrini, 2016), a better understanding of nutrient redistribution following woody encroachment is therefore critical to our ability to develop predictive models of ecosystem structure and function in this era of global environmental change.

The process of nutrient redistribution was first identified in desert systems, where shrubs accumulate nutrients beneath their canopies and promote the development of “islands of fertility” (Crawford & Gosz, 1982; D’Odorico et al., 2012; Ravi, Breshears, et al., 2010; Ravi, D’Odorico, et al., 2010; Schlesinger et al., 1990, 1996). Since then, similar phenomena have been documented during grassland-to-woodland transitions where woody encroachers also cause higher concentrations of soil nutrients (e.g., Blaser et al., 2014; D’Odorico et al., 2012; Hibbard et al., 2001; Zhou et al., 2018). Several physical and biological mechanisms have been proposed to explain nutrient redistribution and accumulation in soils following woody encroachment into grasslands. Physical mechanisms include the trapping and interception of windblown materials as woody encroachers generally having larger canopy areas compared to the herbaceous species they displace (Ridolfi et al., 2008; Schlesinger & Pilmanis, 1998). However, a recent study demonstrated that the mere physical structure of woody plants in grasslands is insufficient to account for nutrient enrichment in soils beneath their canopies (Li et al., 2017), indicating the predominant role of biotic mechanisms driving nutrient redistribution. Although the consensus view is that woody encroachers take up nutrients and deposit them underneath their canopies via litterfall and root turnover (Ridolfi et al., 2008; Schlesinger et al., 1996; Zhou et al., 2018), there is some uncertainty regarding where those nutrients originate. There are two hypotheses, though not mutually exclusive, one of which proposes that redistributed nutrients are derived primarily from soils in grassy or bare areas beyond the extent of the woody plant canopy (Schlesinger et al., 1996), and the other suggests that they are more likely obtained from deeper portions of the soil profile that lie beyond the reach of herbaceous plant roots (Zhou et al., 2018). However, despite these basic and potentially widespread effects of woody encroachment on nutrient redistribution, our understanding is limited largely to a few key macronutrients (e.g., nitrogen [N], and phosphorus [P]) (but see Schlesinger et al., 1996). In addition, we often fail to consider how landscape characteristics may affect variation in spatial patterns of soil nutrient stores.

Analyses of canopy effects on soil N and P suggest a general increasing trend following woody encroachment, though directions and magnitudes vary considerably according to site-specific characteristics, the duration of encroachment, and the identity (e.g., N_2 -fixer vs. non- N_2 -fixer) of encroachers (e.g., Blaser et al., 2014; Eldridge et al., 2011; Zhou et al., 2018). Cationic nutrients (e.g., potassium [K], calcium [Ca], sodium [Na], and magnesium [Mg]) have been studied in the context of shrub-grass or tree-grass systems (e.g., Hagos & Smit, 2005; Schlesinger et al., 1996; Ward et al., 2018), but no consensus exists among these studies regarding the processes that might drive redistribution of soil cations (Schlesinger et al., 1996). Since soil pH tends to decrease following encroachment (Eldridge et al., 2011), it is possible that the exchange capacity for these base cations could decline as a consequence (Ward et al., 2018). However, what we really lack is a more comprehensive examination of which elements display modified soil distribution patterns in response to woody encroachment in grasslands and savannas. Although studies in desert ecosystems have speculated that soil nutrient enrichment may develop most rapidly for the elements most essential and/or limiting to shrub growth (Schlesinger et al., 1996), the potential redistribution of other nonessential nutrients following woody encroachment remains poorly understood and merits attention.

The transition from grassland to woodland is recognized as a process driving soil heterogeneity (Throop & Archer, 2008; Zhou et al., 2018), but approaches to examine this heterogeneity vary depending on spatial scales. Though controversial, the distribution of soil nutrients in grasslands is generally assumed to be relatively homogenous prior to woody encroachment. With this assumption, the majority of studies have concentrated on comparing differences in soil resource levels between woody vs. herbaceous areas at the individual tree or woody patch-scale (e.g., Throop & Archer, 2008; Ward et al., 2018; Weltzin & Coughenour, 1990). However, this fine-scaled approach generally fails to detect larger scale patterns of spatial

heterogeneity in soil nutrients and overlooks the stochastic effect arising from sample size limitation. Although line-transect sampling of multiple trees or woody patches allows insights regarding the scale of soil heterogeneity (e.g., Liu et al., 2010; Wang et al., 2013), it is not able to characterize landscape position and patterns of physical and hydrological processes that have been shown to determine the influence of trees on nutrient distribution in grasslands and savannas (Schade & Hobbie, 2005). Therefore, a comprehensive understanding of nutrient distribution response to woody encroachment might be achieved by considering landscape context, which not only includes a sufficient sample size of trees or woody patches to accurately represent the biotic influence, but also captures subtle gradients in soil physical characteristics and topography across the landscape that may modulate the biotic influence.

We examined nutrient distribution patterns of 19 elements, including the majority of plant essential macro- and micronutrients, in a subtropical savanna landscape in Texas, U.S.A. Historical aerial photos, tree rings, and coupled stable and radiocarbon isotope measurements confirm that woody encroachment into upland C₄ grasslands occurred over the past 100 years (Archer, 1995; Boutton et al., 1998). Spatially specific soil samples and plant tissue samples were used to quantify distribution patterns of these elements across a complex landscape consisting of woody patches within a matrix of remnant grasslands. Specifically, we aimed to: (a) compare differences in elemental concentrations in the plant-soil environment between herbaceous and woody associations; (b) quantify and characterize patterns of spatial heterogeneity of these elements in surface soil; and (c) elucidate biotic factors (e.g., fine root biomass) and abiotic factors (e.g., soil clay content) responsible for spatial distributions of these elements.

2. Methods & Materials

2.1. Study Site

Research was conducted at the Texas A&M AgriLife La Copita Research Area (27°40 N, 98°12 W) in southern Texas, USA. This area has a subtropical climate, with mean annual precipitation of 680 mm, mean annual temperature of 22.4°C, and mean daily relative humidity of 69%. Elevation ranges from 75 to 90 m above sea level. Landscapes consist of gentle slopes (<3%) grading from well-drained uplands into lower-lying drainage woodlands. This study was confined to upland portions of the landscape where soils classify as Typic and Pachic Argiustolls. Before its designation as a research area in the early 1980s, this area was grazed moderately by livestock since the late 1800s.

At this site, woody encroachment is typically initiated by the establishment of *Prosopis glandulosa* (an N₂-fixing tree legume) in the grassland, which appears to serve as a nurse plant facilitating the recruitment of other subordinate trees and shrubs (Archer et al., 1988). Therefore, current upland vegetation has a two-phase pattern consisting of woody clusters (<100 m²) and groves (>100 m²) interspersed within a remnant grassland matrix (Whittaker et al., 1979) (Figure 1). Woody clusters and groves share the same species composition and the remnant grassland matrix consists of C₃ forbs and C₄ grasses. Dominant grasses, forbs, and woody plant species are listed in Table S1 of Supporting Information S1.

2.2. Field Sampling

On an upland portion of this site, a 160 × 100 m landscape subdivided into 10 × 10 m grid cells (i.e., 160 grid cells in total) was established in 2002. The corner coordinates of each grid cell were determined using a global positioning system based on the UTM coordinate system. In July 2014, two sampling points were randomly selected within each grid cell, yielding a total of 320 points (Figure 1). Vegetation cover at each sampling point was classified as grassland ($n = 200$), cluster ($n = 41$), or grove ($n = 79$). Distances from each sampling point to two georeferenced cell corners were recorded to calculate the exact location of each point. A color-infrared aerial photograph (0.5 m in resolution) of this landscape taken in 2014 was acquired from Texas Natural Resource Information System (<https://tnris.org/>) (Figure 1). This aerial photograph includes all three upland landscape elements: (a) grasslands, (b) clusters, and (c) groves. Additionally, based on this aerial photograph and georeferenced sampling points, the distance from each sampling point to the nearest woody patch edge was calculated.

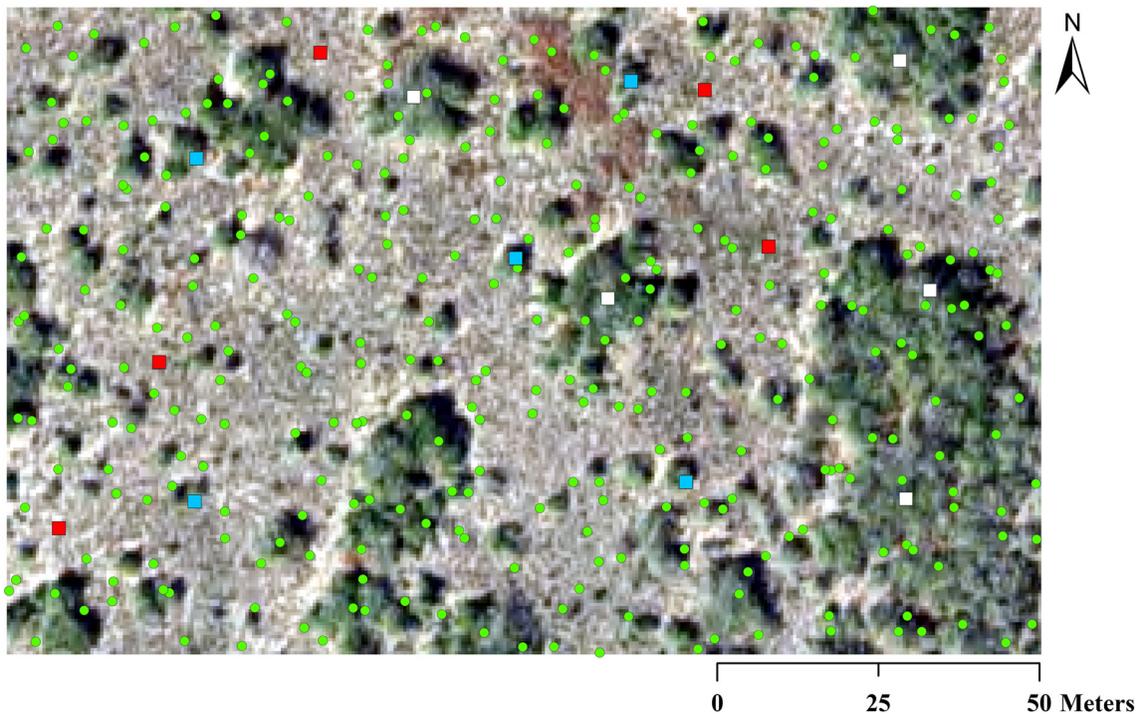


Figure 1. Aerial view of the 160 × 100 m subtropical savanna landscape. Green areas represent woody vegetation, while gray areas represent grasslands. Green dots indicate 320 soil sampling locations, while squares indicate locations where leaf litter and bulk fine roots were collected for grasslands (red, $n = 5$), woody clusters (blue, $n = 5$), and woody groves (white, $n = 5$).

At each sampling point, two adjacent soil cores (2.8 cm in diameter and 5 cm in length) were collected. One soil core was used to estimate fine root (<2 mm) biomass by washing through sieves. The other core was air-dried and then passed through a 2 mm sieve to remove coarse organic matter prior to subsequent analyses. In addition, fine roots and fully expanded new leaves were collected from 16 dominant plant species (woody species = 5, grasses = 6, and forbs = 5) during the peak of the growing season (Table S1 in Supporting Information S1). Four replicates were obtained for each species. In addition, leaf litter and bulk fine roots were collected from grasslands and woody patches (Figure 1). Leaf litter was collected within a 25 × 25 cm frame. After removing leaf litter, soil cores (7 cm diameter × 5 cm length) were collected to obtain bulk fine roots. All plant samples were carefully washed with deionized water and then oven-dried at 65°C for subsequent analyses.

2.3. Lab Analyses

All plant and soil samples were analyzed for a suite of biologically essential macronutrients (N, P, K, Ca, Mg, and S), essential micronutrients (Fe, Mn, Cu, Zn, Ni), and nonessential micronutrients (Al, Ba, Co, Cr, Li, Sr, V, and Zr). It should be noted that most of the nonessential elements analyzed in this study (such as Al, Co, and V in particular) actually do play significant roles in the biochemistry of some plant and microbial species (Fortescue & Marten, 1973; Maret, 2016). All analyses were carried out in the Texas A&M Trace Element Research Laboratory.

Soil samples were pulverized by mortar and pestle while plant samples were pulverized using a Retsch MM400 mixer mill (Retsch GmbH, Haan, Germany) with a titanium grinding jar to avoid metal contamination. For each sample, 0.1 g sample, 0.5 mL nitric acid (16M), 0.5 mL hydrochloric acid (12M), and 4 mL deionized water were placed within a disposable borosilicate glass tube with a Teflon cap, and digested in a single reaction chamber microwave system (ultraWAVE, Milestone Inc., Milan, Italy) (USEPA, 2007). Digestions in the reaction chamber were conducted at 175°C in a 5 MPa N₂ atmosphere. Temperature ramp-up time was 10 min., digestion time at 175°C was 10 min., and cool down and depressurization occurred over 20 min. Digested solutions were diluted with deionized water to 50 mL, transferred to a screw-cap vial, and

then analyzed with an Avio 500 inductively coupled plasma optical emission spectrometer (PerkinElmer, Inc., Waltham, MA, USA). For quality control, each batch of samples (10 soil or plant samples) contained a method blank, a blank spike, a certified reference material, a duplicate sample, and a spiked sample. The reference material for soil samples is the Marine Sediment Reference Materials for Trace Metals and other Constituents (MESS-3) from NRC Canada. For plant samples, we used NIST SRM-1515 (apple leaves) from U.S. National Institute of Standards and Technology. Concentrations of all analyzed elements are reported as mg/kg. Elemental recovery rates for both reference materials are shown in Table S2 of Supporting Information S1, and are comparable to those reported for other NIST materials digested using similar methods (Mackey et al., 2010). Recovery rates of a few elements from soil samples (e.g., Al, K, Cr, V) were lower than 70% due to the fact that the acid digestion method may not fully solubilize the mineral lattices where some proportion of these elements may reside (Mackey et al., 2010).

In addition, N concentrations for soil and plant samples were analyzed using an EA 4010 Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) at the Texas A&M Stable Isotopes for Biosphere Science Laboratory. Soil pH was determined on a 1: 2 (10 g soil: 20 ml, 0.01 mol/L CaCl₂) mixture using a glass electrode. Soil texture was analyzed using the hydrometer method (Sheldrick & Wang, 1993) as described in Zhou et al. (2017).

2.4. Data Analyses

Cohen's *d*, a standardized effect size estimation, was applied to determine responses of macronutrients (i.e., N, P, K, Ca, Mg, and S), micronutrients (i.e., Fe, Mn, Zn, Cu, and Ni), and other elements (i.e., Al, Ba, Co, Cr, Li, Sr, V, and Zr) in plant leaf, fine root, leaf litter, bulk fine root, and soil to woody encroachment. Cohen's *d* was calculated by taking the difference between two means (e.g., woody species vs. herbaceous species, or woody patches vs. grasslands) and dividing it by the pooled standard deviation of the two groups. Generally, if Cohen's *d* is greater than 0.8, it is considered that there is a larger difference between two groups (Cohen, 1988). However, this minimum level of statistical power (i.e., 0.8) is based on a significance criterion of 0.05 and the ratio of a type II error to a Type I error of 0.20/0.05 (Lakens, 2013). A small sampling size increases the probability of committing a type II error (Lakens, 2013; Thompson, 2007). Therefore, we used a larger Cohen's *d* (i.e., 0.95) (Lakens, 2013) for comparing plant samples where we had small sample sizes, while a standard value (i.e., 0.8) was used for soil samples where sample sizes were large.

Ordinary kriging was used for spatial interpolation based on parameters obtained from the variogram analysis with outliers removed (Table S3 in Supporting Information S1) and a predicted map (0.5 m in resolution) of each element in the surface soil (0–5 cm) was generated accordingly. The kriged map was subsequently used to calculate the lacunarity index, a scale-dependent measurement of spatial heterogeneity of a landscape structure (Plotnick et al., 1996). Briefly, a moving window of different box sizes ($r = 0.5, 1, 2, 4, 8, 16, 32, \text{ and } 64 \text{ m}$) was first placed at one corner of the kriged map, and the “box mass” $S(r)$, the sum of pixel values within the box, was calculated. The moving box was then systematically moved through the map one pixel at a time and the box was recorded at each location. The lacunarity value $\Lambda(r)$ was calculated according to $\Lambda(r) = \text{Var}(S(r))/\text{Mean}(S(r))^2 + 1$, where $\text{Mean}(S(r))$ is the mean and $\text{Var}(S(r))$ is the variance of the box mass $S(r)$ for a given box size r . The lacunarity curve, natural log transformation of lacunarity values $\Lambda(r)$ vs. box size (r), was plotted to quantify the spatial heterogeneity of each element at different scales, with a higher value of lacunarity indicating a more heterogeneous distribution pattern across the landscape. Significant differences in lacunarity values between different soil elements were detected based on a linear mixed-effects model with the box size as a nested random effect following a Tukey post hoc comparison.

A redundancy analysis (RDA) was applied to test if variation in a set of soil elements was related to biotic and abiotic factors (Legendre & Anderson, 1999), using the “rda” function in the “vegan” package (Oksanen et al., 2019). Here, all soil elements were considered as response variables, while explanatory variables included both biotic (normalized difference vegetation index (NDVI) and fine root biomass) and abiotic factors (soil clay content, soil pH, and slope) (Figure S1 in Supporting Information S1). The color-infrared aerial photograph was used to calculate the NDVI, which is equal to the difference in the intensities of reflected light in the red and infrared range divided by the sum of these intensities. The slope of this landscape was derived from a digital elevation model product (Ritter, 1987) acquired from Texas Natural Resource Information System (Figure S1f in Supporting Information S1). Prior to performing RDA, all variables were

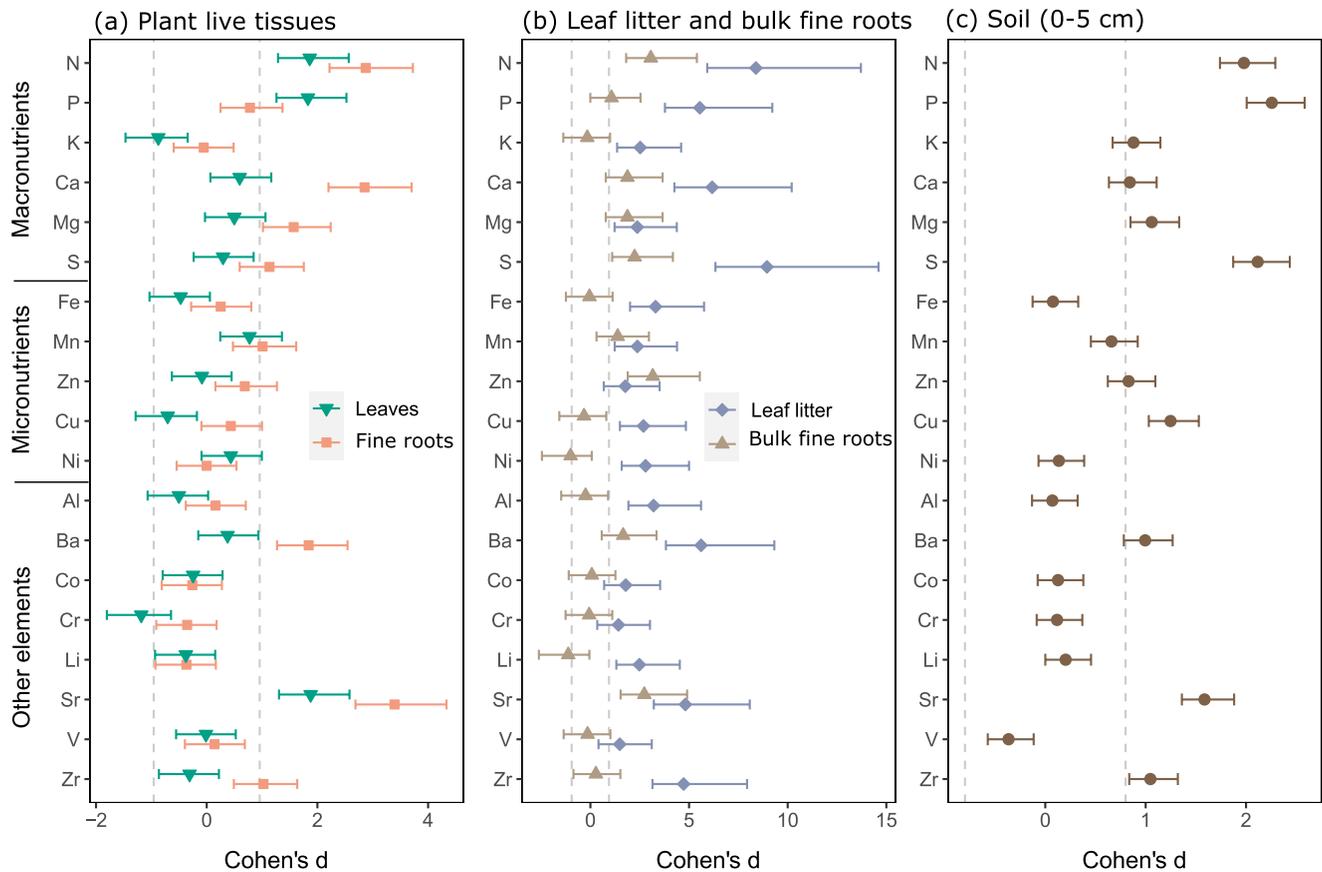


Figure 2. Responses of macronutrients, micronutrients, and other elements to woody encroachment in plant live tissue (a), plant litter and bulk fine roots (b), and soil (0–5 cm) (c). Symbols indicate the effect size (Cohen's *d*) of woody species (or patches) compared to herbaceous species (or grassland). In panel (a) fine root tissues are average values for individual plant species, while in panel (b) bulk fine roots are those extracted from soil cores and comprised a mixture of multiple species. The error bars show the 95% confidence interval. Dashed lines in panel (a) and (b) indicate the locations where the values of Cohen's *d* are -0.95 and 0.95 , but in panel (c) indicate the locations where the values of Cohen's *d* are -0.8 and 0.8 .

centered at their mean because they were measured using different units. Statistical significance of explanatory variables was determined by permutation tests with 999 randomizations. All statistical analyses were performed using R 3.6.1 software (R Core Team, 2019).

3. Results

Based on the Cohen's *d* effect size analysis, concentrations of N, P, and Sr in leaves of woody species were larger than those of herbaceous species, and concentrations of N, Ca, Mg, Ba, and Sr in fine roots of woody species were larger than those of herbaceous species (Cohen's *d* > 0.95) (Figure 2a) (Table S4 in Supporting Information S1). Concentrations of all measured elements (except Zn, Co, Cr, and V) were higher in leaf litter derived from woody patches than in litter from grasslands, and concentrations of N, S, Zn, and Sr in bulk fine roots of woody patches were higher than those of grasslands (Cohen's *d* > 0.95) (Figure 2b) (Table S5 in Supporting Information S1). In addition, concentrations of N, P, Mg, S, Cu, Sr, and Zr in surface soil (0–5 cm) underneath woody patches were higher than those underneath the remnant grasslands (Cohen's *d* > 0.8) (Figure 2c, Table S6 in Supporting Information S1).

Kriged maps of soil elements in the surface soil (0–5 cm) displayed divergent patterns of spatial heterogeneity across this subtropical savanna landscape (Figure 3). Visual comparisons revealed that spatial patterns of soil N, P, S, Ca, Cu, and Sr displayed strong resemblance to patterns of vegetation cover. Concentrations of these elements were generally highest at the centers of woody patches, decreased toward edges of woody canopy, and reached lowest values within the remnant grassland matrix. Therefore, negative relationships

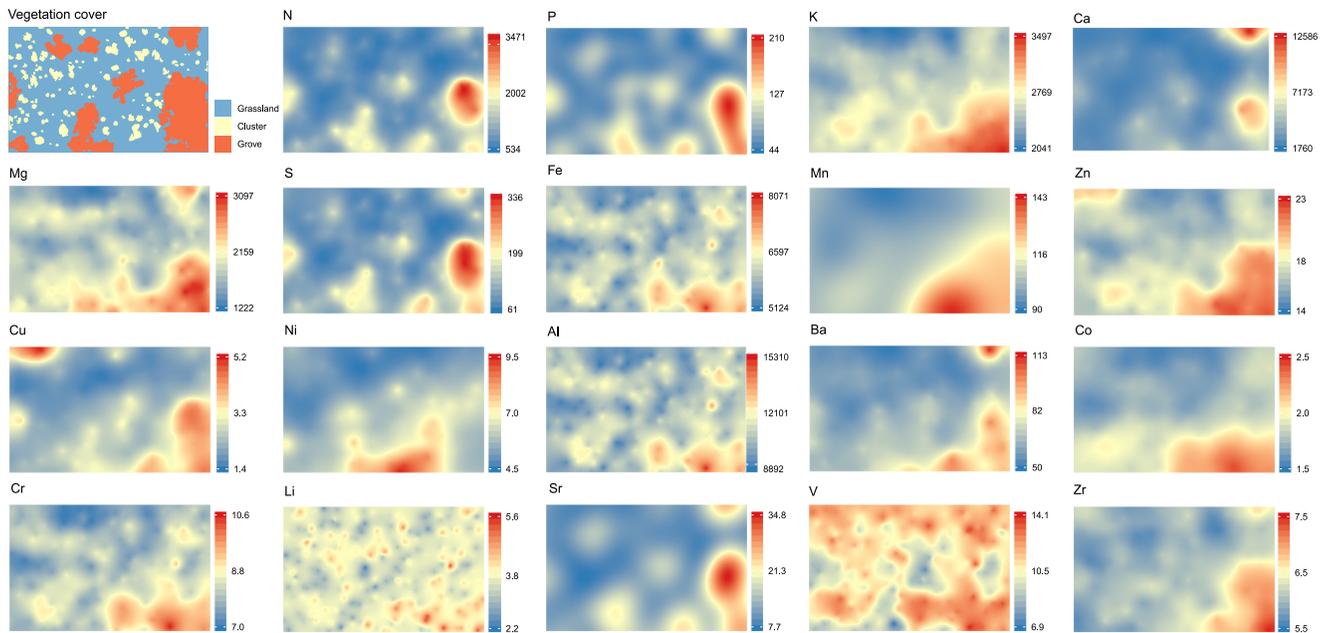


Figure 3. Classified map of vegetation cover derived from the aerial photo, and kriged maps of all soil elements (mg/kg) for this 160 × 100 m subtropical savanna landscape.

were observed between soil elemental concentrations and distances to canopy edges within woody patches, while no trends were detected within grasslands (Figure 4). Lacunarity analysis also indicated that spatial distributions of these elements were more heterogeneous than those of other elements (Figure 5).

The RDA model, including NDVI, fine root biomass, soil clay content, soil pH, and slope as explanatory variables, explained 37.1% of the variation in the soil element composition (Figure 6). The variation in a subset of soil elements, including N, P, S, Sr, Ca, Cu, Ba, Zr, was strongly related to biotic factors, as spatial distributions of these soil elements were more or less similar to spatial patterns of fine root biomass and

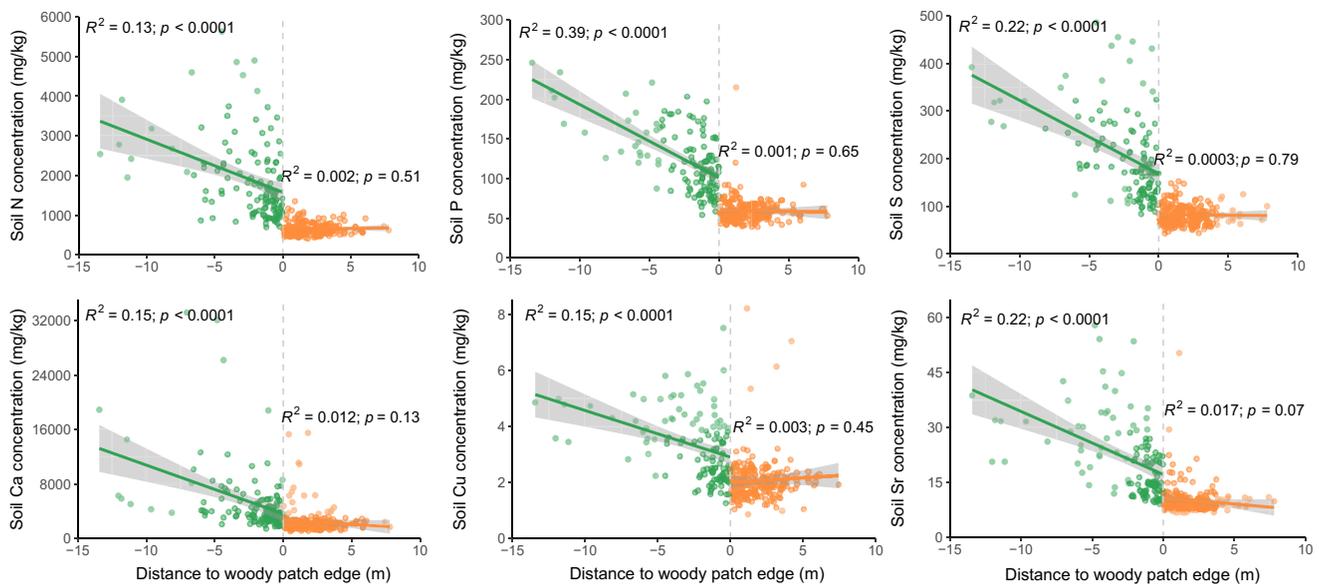


Figure 4. Change in concentrations of soil N, P, S, Ca, Cu, and Sr as a function of distance to woody patch edge. Dashed lines at zero on the x axis represent woody patch edge. Negative distances (green dots) indicate that sampling points were within woody patches while positive distances (orange dots) indicate that sampling points were within the remnant grasslands. Gray shading areas around the regression lines indicate the 95% confidence intervals.

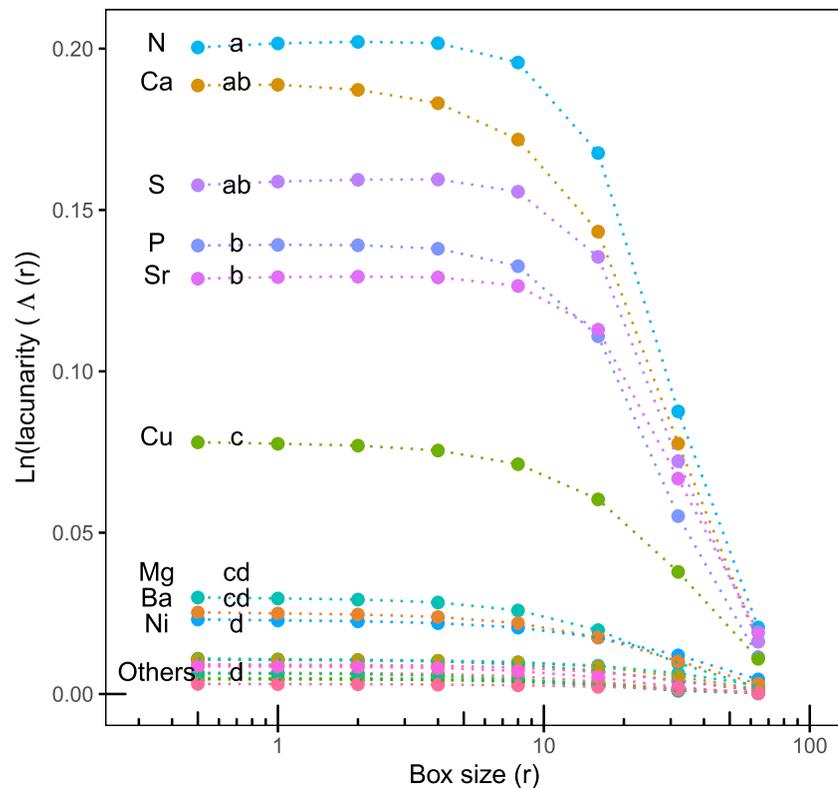


Figure 5. Lacunarity curves for all soil elements which were calculated based on their spatial patterns. Significant differences ($p < 0.05$) between different elements were detected based on linear mixed-effects model with the box size as nested random effect following a Tukey *post hoc* comparison and were indicated as different letters. Clustered points labeled as others are in the order of K, Co, Mn, Zn, V, Al, Li, Cr, Fe, and Zr.

NDVI (Figure 3 and Figure S1 in Supporting Information S1). In contrast, the variation in all of the other soil elements was more closely related to abiotic factors (Figure 6). For example, spatial distributions of soil Mg and K were influenced by soil pH (Figure 5, Figures S1e and S2 in Supporting Information S1), while soil Fe, Mn, Zn, Al, Co, Cr, and Li were more influenced by soil clay content (Figure 6, Figures S1d and S3 in Supporting Information S1).

4. Discussion

Our spatially extensive sampling approach, which provided a sufficient sample size of woody patches and captured subtle gradients in environmental conditions, allowed us to characterize spatial distributions of soil nutrient elements in this subtropical savanna landscape. Results revealed divergent patterns of spatial heterogeneity of soil elements across this complex landscape and indicated that a subset of soil elements (i.e., N, P, S, Ca, Cu, and Sr) was responsive to woody encroachment at the landscape scale. Most of the macro- and micronutrients examined in this study play key roles in plant and microbial processes, such as protein and enzyme structure and function, synthesis of structural and functional biochemicals, transformation reactions in many biogeochemical cycles, and growth and productivity (Naeem et al., 2017). Therefore, we suggest that the changes in elemental concentrations documented in this study are not just a consequence of woody encroachment, but may now be part of a complex of factors that is enabling the persistence and continuing spread of tree/shrub patches across this landscape.

Changes in the concentrations of many of the elements examined in this study may be contributing to observed changes in the rates of multiple ecosystem processes known to have occurred following woody encroachment, including above- and belowground plant biomass and primary productivity (Archer et al., 2001; Boutton et al., 1998; Zhou et al., 2019), soil respiration (McCulley et al., 2004), structural and

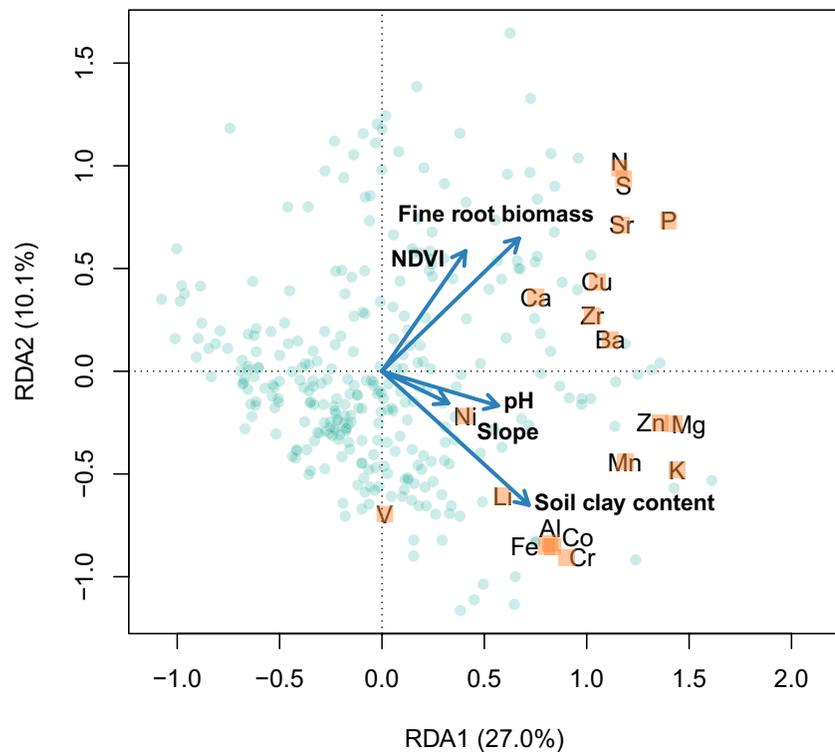


Figure 6. Distance-based redundancy analysis in which soil elements were considered as response variables while explanatory variables included fine root biomass ($p < 0.001$), normalized difference vegetation index (i.e., NDVI) ($p < 0.001$), soil clay content (%) ($p < 0.001$), soil pH ($p < 0.001$), and slope ($^{\circ}$) ($p = 0.075$). Soil sampling points were ordinated as light green dots while levels of soil elements were plotted as light orange square.

functional attributes of the soil biota (Biederman & Boutton, 2010; Creamer et al., 2016; Liao & Boutton, 2008), and nitrogen transformations (Hibbard et al., 2001; McCulley et al., 2004; Soper et al., 2015). In North American grasslands, woody plants generally maintain biomass and primary productivity several times higher than herbaceous plants in areas where woody encroachment has occurred (Archer et al., 2001; Barger et al., 2011; Hughes et al., 2006; Jackson et al., 2002). In our study area, net primary productivity in upland woody patches ($900 \text{ g m}^{-2} \text{ yr}^{-1}$) is ~ 2.6 times higher than in the surrounding grassland matrix ($350 \text{ g m}^{-2} \text{ yr}^{-1}$) (Knapp et al., 2008), indicating an increasing demand for essential plant nutrient elements during grassland-to-woodland transition, assuming that demand scales with biomass production. These additional nutrients are initially incorporated into woody plant tissues and ultimately delivered to soils through aboveground litterfall and root turnover, but why do only a subset of nutrient elements (i.e., N, P, S, Ca, Cu, and Sr) have patterns of spatial heterogeneity significantly amplified by woody encroachment? Early studies in desert ecosystems speculated that plant-limiting nutrients are more efficiently recycled and are more likely to be accumulated underneath shrubs (Schlesinger et al., 1996). However, previous studies at our site have shown that the growth of woody encroachers is not limited, at least, by N and S. This is because the dominant encroacher (i.e., *P. glandulosa*) has the capability to biologically fix N from the atmosphere (Soper et al., 2015; Zitzer et al., 1996), and the atmospheric S deposition in this region (*ca.* $0.4 \text{ g S/m}^2/\text{yr}$) is sufficient to satisfy S demand for woody plant growth (Hinckley et al., 2020; Zhou et al., 2021). In addition, Sr is not an essential plant nutrient (Epstein & Bloom, 2005), and is presumably not functioning as a limiting nutrient for plant growth. Alternatively, our empirical evidence suggests that if nutrient elements have concentrations that are higher in woody plants than in herbaceous plants (Figures 2a and 2b), and if these same elemental concentrations are multiple times larger in woody plants than in soils (Figure S4 in Supporting Information S1), then their spatial distributions in soils should be responsive to woody encroachment (Figure 3). The question then remains where did these redistributed nutrients in surface soils come from?

It is conceivable that the larger canopy volumes and larger leaf areas characteristic of woody encroachers may intercept more windblown soil and atmospheric deposition than the short-statured herbaceous species in the remnant grasslands, but Li et al. (2017) showed that these purely physical plant attributes are insufficient to drive the development of fertile islands in drylands. This in turn suggests that there may be biotic mechanisms of nutrient redistribution, which is also supported by our results showing that fine root biomass and NDVI (as a proxy of aboveground biomass) explained the most variation in redistributed nutrients in response to woody encroachment (Figure 6). As a result, it is reasonable to infer that the nutrient elements accumulated in surface soils underneath woody encroachers must be translocated from surrounding grassland areas and/or from deep soils by root acquisition and subsequent litterfall and root turnover (Green et al., 2008; Schlesinger & Pilmanis, 1998; Schlesinger et al., 1996; Zhou et al., 2018). Although there is no direct evidence to examine the relative importance of each pathway, we speculate that the redistributed nutrients are primarily from deeper portions of the soil profile at this site. We calculated the distance to the nearest edge of woody canopy for each sampling point within grasslands and did not find any evidence for lower soil nutrient concentrations (i.e., N, P, S, Ca, Cu, and Sr) in grasslands immediately adjacent to woody patches compared to grasslands >5 m away from any woody vegetation (Figure 4). In addition, our previous study showed that root density decreased exponentially with increasing distance from woody patch perimeters and that few woody roots actually extended more than 1 m beyond those perimeters (Zhou et al., 2019). Furthermore, the dominant woody encroacher (i.e., *P. glandulosa*) has a tap root that can reach to more than 10 m below the surface in this subtropical savanna (as per field observation) and also in other ecosystems (Canadell et al., 1996; Phillips, 1963; Virginia et al., 1986), whereas root biomass in the grassland matrix is largely confined to the upper 1.5 m of the profile (Boutton et al., 1999). Collectively, this information strongly suggests that woody encroachers at this site are much better able to forage for soil nutrients in deeper portions of the soil profiles underneath their canopies rather than in the soils beneath the remnant grasslands that surround them (Walter, 1939; Ward et al., 2013). However, we also recognize that trees in some African savannas have lateral roots that do extend significant distances away from their trunks and out into the grassland matrix (e.g., O'Donnell et al., 2015; Schleicher et al., 2011; Zhou et al., 2020), potentially indicating that the source of redistributed nutrients might be site-specific, warranting further investigations in other ecosystems.

Our results also suggest that subtle gradients in soil pH and clay content are correlated with spatial distributions of soil cations and other metal elements across this landscape (Figures 3, 5, and Figure S1 in Supporting Information S1). Soil pH is influenced by the quantity of base cations, and also strongly affects the cation exchange capacity (Robertson et al., 1999). Cation nutrients (e.g., Mg and K) are better retained with increasing soil pH (Figure S2 in Supporting Information S1) (De Villiers & Jackson, 1967; Ward et al., 2018). In addition, it is well recognized that clay particles with large surface areas have higher tendency for adsorbing cations and heavy metals (e.g., Fe, Mn, Zn, Al, Co, Cr, and Li) than coarse-grained soils (Bradl, 2004; Dragović et al., 2008). Across this landscape, clay is relatively concentrated at the southeastern corner where the upland is transitioning into an adjacent lower-lying drainage woodland (Figure S1d in Supporting Information S1) (Wu & Archer, 2005). It is entirely possible that fine-clay particles along with their adsorbed metal elements are transported locally by surface runoff, creating patterns of spatial heterogeneity of these metal elements resembling the pattern of clay content in the surface soil across this landscape (Figure 3 and Figure S1d in Supporting Information S1).

5. Conclusion

In conclusion, our study is unique with respect to the chemical elements we have examined in an ecological context, and with respect to the quantitative spatial analyses that we used to quantify their patterns at the landscape scale. Results provide strong empirical support that nutrient redistribution by woody encroachers at the landscape scale occurred in six of the 19 elements examined (i.e., N, P, S, Ca, Cu, and Sr). These nutrient elements with amplified patterns of spatial heterogeneity in response to woody encroachment have concentrations in woody plants that are significantly higher than those in both herbaceous plants and soils. However, not all of these redistributed nutrients are growth-limiting ones. Despite this, these results support the argument that woody encroachers are better able to acquire essential and nonessential nutrients via their deeper root systems, which are then redistributed to upper portions of the soil profile via subsequent

litter deposition and root turnover, creating a nutrient-enriched environment able to facilitate their growth and reproduction (Blaser et al., 2014; Eldridge et al., 2011; Zhou et al., 2018). If woody encroachment continues in response to current disturbance regimes as predicted by dynamic models (Archer, 1995), landscape-scale spatial variability in these nutrient elements (i.e., N, P, S, Ca, Cu, and Sr) may ultimately become more homogenous as vegetation structure progresses toward a closed-canopy configuration. These results also demonstrate that within savannas, the abundance and distribution of woody species is key to soil biogeochemical cycles and other ecosystem functions. Although these results are derived from a single site, they do highlight the fact that concentrations of many elements that are rarely examined in ecosystem studies are significantly altered by woody encroachment into an area that was once open grassland. Additional studies in other dryland ecosystems across the globe that are being affected by woody encroachment are needed to assess the generality of these results. Such studies should also be extended to include the interactions between nutrient and water cycles, as water availability is another key factor driven dryland ecosystem functioning and services. Overall, insights on whether or not woody encroachment affects the redistribution of macro- and micronutrients would advance our understanding of the potential future consequences of plant-soil feedbacks in arid and semiarid ecosystems, which remains a continuing challenge to the field of global change ecology.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data set is available in the Dryad Digital Repository: <https://doi:10.5061/dryad.mgqnk990w>.

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Supporting information for

Divergent patterns and spatial heterogeneity of soil nutrients in a complex and dynamic savanna landscape.

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Table S1 A list of dominant plant species sampled across this landscape

Species name	Functional type
<i>Lesquerella gordonii</i>	Forb
<i>Gaillardia pulchella</i>	Forb
<i>Wedelia texana</i>	Forb
<i>Parthenium hysterophorus</i>	Forb
<i>Aphanostephus riddellii</i>	Forb
<i>Chloris cucullata</i>	Grass
<i>Bothriochloa ischaemum</i>	Grass
<i>Aristida purpurea</i>	Grass
<i>Heteropogon contortus</i>	Grass
<i>Bouteloua rigidiseta</i>	Grass
<i>Paspalum setaceum</i>	Grass
<i>Condalia hookeri</i>	Woody plant
<i>Prosopis glandulosa</i>	Woody plant
<i>Diospyros texana</i>	Woody plant
<i>Zanthoxylum fagara</i>	Woody plant
<i>Acacia rigidula</i>	Woody plant

Table S2 Overview of ICP-MS analytic results for the Marine Sediment Reference Materials for Trace Metals and other Constituents from National Research Council of Canada (*i.e.*, NRCC MESS-3) and the Standard Reference Materials 1515 Apple Leaves from National Institute of Standards and Technology (*i.e.*, NIST SRM 1515).

Element (mg/kg)	NRCC MESS-3					NIST SRM 1515				
	Certified value	Measured mean	SD	RSD	Recovery rate (%)	Certified value	Measured mean	SD	RSD	Recovery rate (%)
Al	85900.00	41816.00	3863.97	9.24	48.68	286.00	271.54	5.01	1.84	94.95
Ba	NA	NA	NA	NA	NA	49.00	44.33	0.92	2.07	90.46
Ca	14700.00	13871.96	474.35	3.42	94.37	15260.00	14680.52	210.89	1.44	96.20
Co	14.40	12.54	0.68	5.42	87.06	NA	NA	NA	NA	NA
Cr	105.00	58.32	4.07	6.99	55.54	0.30	0.43	0.08	19.07	141.90
Cu	33.90	23.81	1.29	5.44	70.23	5.64	6.29	0.09	1.37	111.59
Fe	43400.00	37183.71	1284.26	3.45	85.68	83.00	65.22	0.96	1.47	78.58
K	26000.00	11351.63	981.83	8.65	43.66	16100.00	14974.56	358.90	2.40	93.01
Li	73.60	55.88	3.08	5.52	75.93	NA	NA	NA	NA	NA
Mg	16000.00	14888.18	563.75	3.79	93.05	2710.00	2629.49	59.85	2.28	97.03
Mn	324.00	294.87	10.79	3.66	91.01	54.00	49.57	0.89	1.80	91.80
Ni	46.90	41.68	1.32	3.17	88.86	0.91	0.75	0.05	6.51	82.22
P	1200.00	1107.45	49.69	4.49	92.29	1590.00	1643.69	16.79	1.02	103.38
S	1900.00	1788.27	79.62	4.45	94.12	1800	1901.54	108.93	5.73	105.64
Sr	129.00	82.29	3.03	3.68	63.79	25.00	24.27	0.54	2.22	97.06
V	243.00	138.94	10.90	7.84	57.18	NA	NA	NA	NA	NA
Zn	159.00	155.21	5.87	3.78	97.61	12.50	12.89	0.25	1.93	103.16

SD, standard deviation, n = 17 for MESS-3; n = 8 for SRM 1515.

RSD, relative standard deviation.

Table S3 Parameters for best fitted semi-variogram for each soil element in the 0-5 cm depth increment based on 320 soil samples across this subtropical savanna landscape.

	Model	Nugget	Partial sill	Sill	Range (m)	R ²	RMSD	(Sill-Nugget)/Sill (%)
Macronutrients								
N	Spherical	133335.21	173474.21	306809.42	39.57	0.35	704.31	56.54
P	Gaussian	367.44	580.95	948.39	16.91	0.56	27.88	61.26
K	Exponential	35619.79	95819.53	131439.32	53.90	0.58	229.09	72.90
Ca	Spherical	1896797.39	1149169.00	3045966.39	57.64	0.20	3310.15	37.73
Mg	Exponential	37745.75	111948.14	149693.89	19.43	0.58	282.01	74.78
S	Spherical	1449.06	2183.63	3632.69	40.69	0.38	66.30	60.11
Micronutrients								
Fe	Exponential	172841.57	288027.37	460868.94	9.36	0.31	594.09	62.50
Mn	Gaussian	129.20	80.49	209.69	34.31	0.42	13.03	38.39
Zn	Exponential	2.25	4.09	6.34	50.07	0.44	1.86	64.49
Cu	Exponential	0.31	1.73	2.04	154.11	0.40	0.88	85.05
Ni	Spherical	2.27	14.12	16.40	953.46	0.04	2.80	86.13
Other elements								
Al	Exponential	592121.95	1317981.05	1910103.00	9.35	0.33	1187.70	69.00
Ba	Exponential	68.36	193.36	261.72	92.20	0.31	14.99	73.88
Co	Spherical	0.07	0.07	0.13	138.77	0.33	0.27	50.63
Cr	Exponential	0.36	0.45	0.81	13.61	0.35	0.77	55.43
Li	Exponential	0.07	0.32	0.39	3.65	0.14	0.61	82.11
Sr	Gaussian	17.21	13.40	30.61	21.41	0.37	7.10	43.79
V	Exponential	0.61	2.04	2.66	10.44	0.32	1.33	76.98
Zr	Exponential	0.35	0.23	0.58	42.14	0.19	0.69	40.04

Table S4 Concentrations of macronutrients, micronutrients, and other elements in live leaf and root tissues from woody and herbaceous species across this subtropical savanna landscape. Values are mean \pm SE (n = 5 for woody species and n = 11 for herbaceous species).

	Leaf tissue (mg/kg)		Fine root tissue (mg/kg)	
	Herbaceous species	Woody species	Herbaceous species	Woody species
Macronutrients				
N	16753 (1602)	29300 (4140)	6609 (760)	21290 (3912)
P	883 (60)	1450 (217)	307 (46)	418 (49)
K	20963 (2614)	14256 (1960)	6809 (1875)	6359 (819)
Ca	14429 (3617)	21579 (5728)	3329 (727)	17980 (3819)
Mg	2093 (428)	2808 (678)	587 (117)	1383 (321)
S	2315 (445)	2689 (291)	1299 (267)	2665 (802)
Micronutrients				
Fe	126.36 (31.27)	82.78 (19.51)	343.08 (68.99)	401.9 (64.68)
Mn	38.77 (3.79)	79.6 (43.43)	18.82 (3.01)	37.74 (12.5)
Zn	27.86 (4.99)	26.15 (11.87)	15.76 (3.42)	25.09 (6.41)
Cu	9.22 (1.76)	5.36 (0.52)	6.5 (0.75)	7.47 (0.42)
Ni	0.78 (0.1)	1.01 (0.28)	1.91 (0.32)	1.94 (0.44)
Other elements				
Al	195.85 (50.74)	118.35 (35.12)	708.91 (151.88)	790.75 (123.55)
Ba	60.59 (11.54)	75.16 (18.35)	30.4 (6.3)	72.66 (10.96)
Co	0.10 (0.01)	0.09 (0.00)	0.19 (0.08)	0.13 (0.03)
Cr	0.66 (0.05)	0.45 (0.05)	1.94 (0.41)	1.51 (0.12)
Li	1.48 (0.22)	1.24 (0.04)	1.44 (0.2)	1.19 (0)
Sr	35.83 (8.65)	122 (31.12)	12.19 (2.88)	134.25 (27.27)
V	0.40 (0.00)	0.40 (0.00)	0.97 (0.43)	1.18 (0.61)
Zr	0.33 (0.05)	0.28 (0.01)	0.57 (0.12)	0.95 (0.07)

Table S5 Concentrations of macronutrients, micronutrients, and other elements in leaf litter and bulk fine roots from grasslands, clusters, and groves across this subtropical savanna landscape. Values are mean \pm SE (n = 5).

	Leaf litter (mg/kg)			Bulk fine roots (mg/kg)		
	Grassland	Cluster	Grove	Grassland	Cluster	Grove
Macronutrients						
N	5480 (251)	24180 (999)	27500 (974)	15980 (1019)	24980 (978)	29840 (1753)
P	224 (10)	770 (37)	879 (62)	558 (21)	600 (28)	667 (34)
K	1222 (224)	2052 (75)	2146 (111)	3200 (388)	3134 (438)	3016 (101)
Ca	5718 (731)	40160 (3583)	39740 (2076)	16420 (2881)	25440 (1932)	28540 (2238)
Mg	572 (73)	3812 (810)	2946 (221)	1526 (157)	2100 (168)	2418 (149)
S	806 (47)	2888 (159)	3032 (57)	2162 (118)	2844 (131)	3452 (185)
Micronutrients						
Fe	243 (34)	1125 (151)	1536 (131)	2734 (309)	2108 (267)	3268 (405)
Mn	37.2 (5.7)	77.6 (5.1)	118.4 (10.3)	68.6 (7.2)	90.4 (9.5)	163.4 (14.7)
Zn	17.4 (1.0)	25.3 (1.2)	41.5 (3.5)	30.6 (2.1)	62.7 (5.5)	57.7 (3.6)
Cu	6.3 (0.4)	11.7 (1.0)	14.5 (1.3)	29.3 (3.3)	28.7 (3.5)	25.2 (2.0)
Ni	1.05 (0.11)	1.90 (0.20)	2.25 (0.10)	7.01 (0.85)	4.79 (0.45)	6.06 (0.54)
Other elements						
Al	468 (74)	2188 (316)	2928 (268)	6012 (733)	4458 (597)	6588 (894)
Ba	38 (4)	174 (16)	171 (7)	141 (22)	186 (11)	221 (8)
Co	0.10 (0.00)	0.32 (0.07)	0.57 (0.10)	1.99 (0.22)	1.75 (0.19)	2.31 (0.24)
Cr	1.93 (0.26)	2.53 (0.30)	3.21 (0.20)	4.83 (0.47)	3.75 (0.42)	5.71 (0.65)
Li	1.23 (0.01)	1.61 (0.11)	1.80 (0.07)	4.58 (0.70)	3.06 (0.32)	3.64 (0.23)
Sr	17.2 (2.6)	325 (42)	294 (15)	49.4 (7.4)	139 (20)	172 (16)
V	0.41 (0.00)	1.06 (0.39)	1.88 (0.24)	9.61 (0.93)	8.28 (1.06)	10.23 (0.94)
Zr	0.35 (0.03)	1.89 (0.16)	2.23 (0.18)	3.84 (0.42)	3.23 (0.42)	5.31 (0.69)

Table S6 Concentrations of macronutrients, micronutrients, and other elements in the surface soil (0-5 cm) underneath grasslands, clusters, and groves across this subtropical savanna landscape. Values are mean \pm SE. Number of replicates, grasslands = 200, clusters = 41, and groves = 79.

	Grassland	Cluster	Grove
Macronutrients (mg/kg)			
N	651.5 (10.7)	1572.9 (118.5)	2091.9 (121.5)
P	59.5 (1.1)	103.1 (4.8)	135.2 (4.7)
K	2489.1 (19.8)	2690.5 (50.2)	2830.1 (46.2)
Ca	2447.8 (130.2)	3999.5 (456.5)	6144.4 (650.2)
Mg	1789.8 (22.9)	2053.2 (59.23)	2291.4 (56.1)
S	81.6 (1.5)	174.6 (11.9)	224.0 (10.7)
Micronutrients (mg/kg)			
Fe	6072.3 (45.9)	6193.7 (131.9)	6118.2 (89.9)
Mn	103.3 (1.0)	109.4 (2.3)	117.1 (2.5)
Zn	16.9 (0.1)	17.8 (0.4)	19.4 (0.3)
Cu	2.1 (0.1)	2.8 (0.2)	3.6 (0.1)
Ni	5.8 (0.2)	6.2 (0.5)	6.3 (0.4)
Other elements (mg/kg)			
Al	10927.8 (94.9)	11103.4 (244.6)	11045.8 (186.9)
Ba	60.4 (0.7)	68.1 (1.9)	81.7 (3.0)
Co	1.8 (0.0)	1.8 (0.1)	1.9 (0.0)
Cr	8.2 (0.1)	8.3 (0.2)	8.3 (0.1)
Li	3.6 (0.0)	3.8 (0.1)	3.8 (0.1)
Sr	10.2 (0.3)	17.3 (1.3)	23.8 (1.2)
V	11.2 (0.1)	10.8 (0.3)	10.6 (0.2)
Zr	5.9 (0.0)	6.4 (0.1)	6.7 (0.1)

Figure S1 Classified vegetation cover (a), nominalized difference vegetation index (NDVI) (b), fine root biomass (kg/m^2) (c), soil clay content (%) (d), soil pH (e) at the 0-5 cm depth increment, and slope ($^\circ$) across this subtropical savanna landscape.

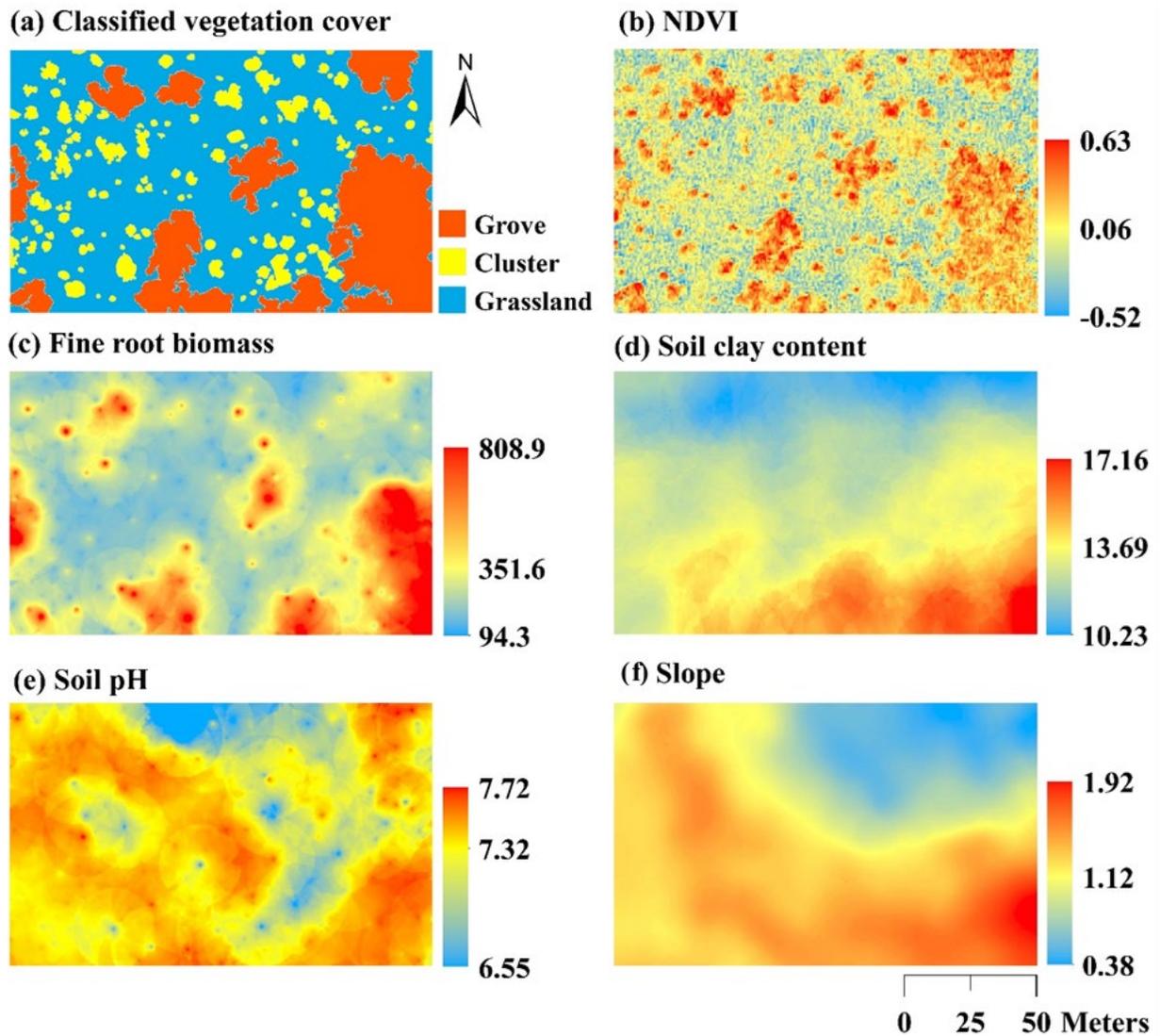


Figure S2 Correlations between soil pH and soil Mg and K concentrations across this landscape. Gray shading areas around the regression lines indicate the 95% confidence intervals.

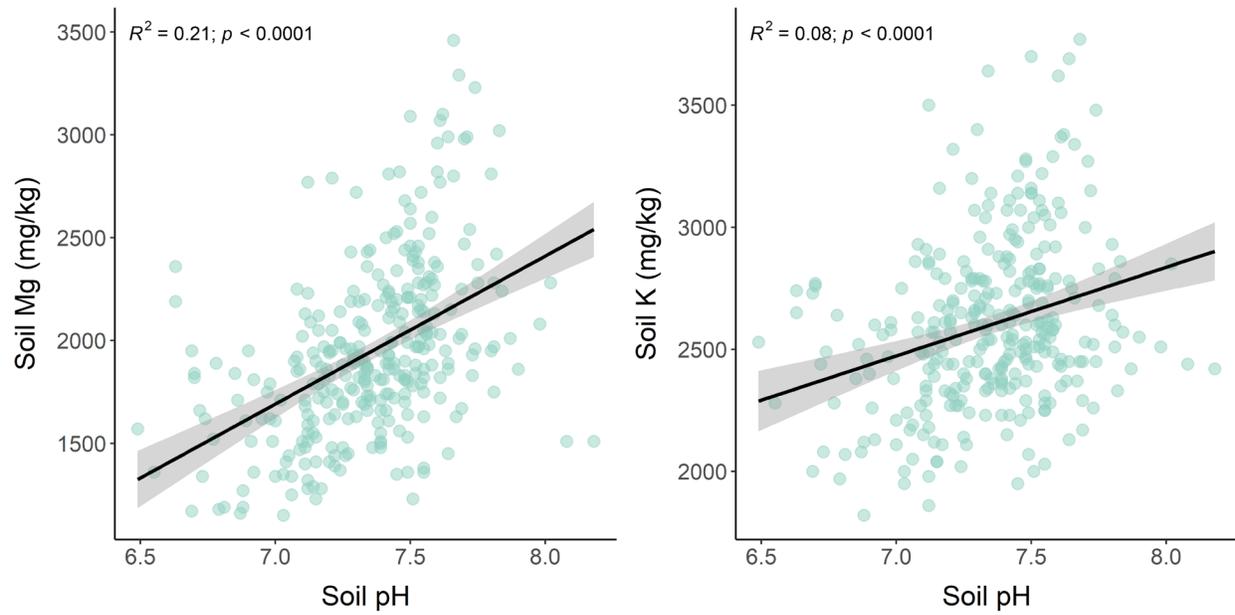


Figure S3 Correlations between soil clay content and soil Fe, Mn, Zn, Al, Co, Cr, and Li concentrations across this landscape. Gray shading areas around the regression lines indicate the 95% confidence intervals.

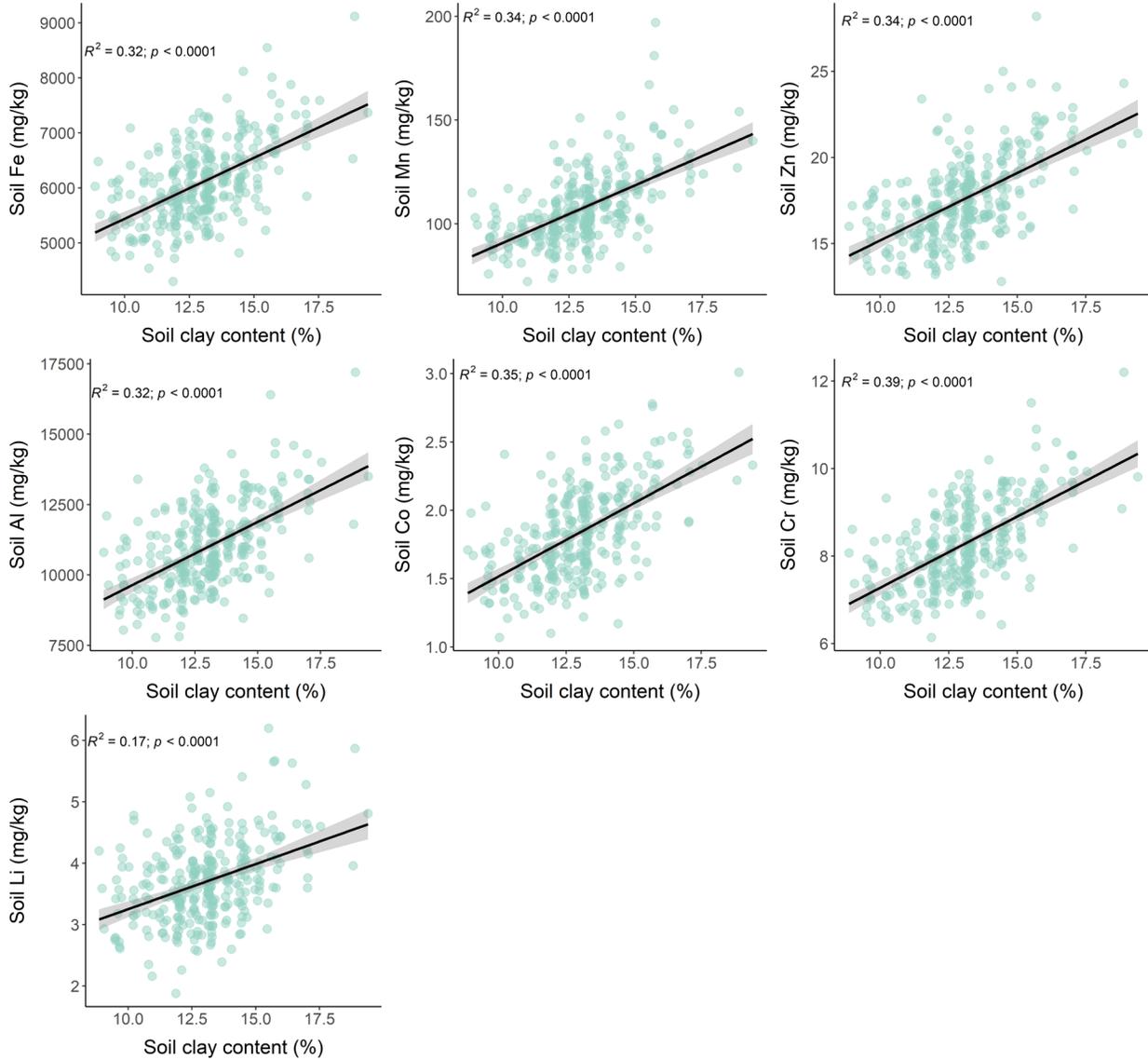


Figure S4 Ratios of element concentrations in woody plant compartments to those in soils underneath woody patches across this subtropical landscape. The dash line indicates the ratio equals to 1. For each element, the concentration in woody plant compartments was averaged over all of the plant measurements, including leaf and fine root tissues from individual woody plants, litter and bulk fine roots from woody patches; the concentration in soils was averaged over all of the soil measurements from woody patches (*i.e.*, $n = 41$ for clusters and $n = 79$ for groves) in the surface soil layer (0-5 cm).

