Biotic and abiotic changes in ecosystem structure over a shrub-encroachment gradient in the southwestern USA

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Abstract

In this study we investigate changes in ecosystem structure that occur over a gradient of land-degradation in the southwestern USA, where shrubs are encroaching into native grassland. We evaluate a conceptual model which posits that the development of biotic and abiotic structural connectivity is due to ecogeomorphic feedbacks. Three hypotheses are evaluated: 1. over the shrub-encroachment gradient, the difference in soil properties under each surface-cover type will change non-linearly, becoming increasingly different; 2. there will be a reduction in vegetation cover and an increase in vegetation-patch size that is concurrent with an increase in the spatial heterogeneity of soil properties across the shrub-encroachment gradient; and 3. over the shrub-encroachment gradient, the range at which soil properties are autocorrelated will progressively exceed the range at which vegetation is autocorrelated. Field-based monitoring of vegetation and soil properties was carried out over a shrub-encroachment gradient at the Sevilleta National Wildlife Refuge in New Mexico, USA. Results of this study showed that vegetation cover decreases over the shrub-encroachment gradient, but vegetation-patch size increases, with a concurrent increase in the spatial heterogeneity of soil properties. Typically, there were significant differences in soil properties between non-vegetated and vegetated surfaces, but for grass and shrub patches, there were only significant differences for the biotic soil properties. Results suggest that it is the development of larger, well-connected, non-vegetated patches that is most important in driving the overall behaviour of shrub-dominated sites. Overall, results of this study support the hypothesis that feedbacks of functional connectivity reinforce the development of structural connectivity, which increase the resilience of the shrub-dominated state, and thus make it harder for grasses to re-establish and reverse the vegetation change.

1 Introduction

Land degradation is a widespread problem in semi-arid regions. One form of land degradation in the southwestern USA is the invasion of native grasslands by woody shrubs (Buffington and Herbel, 1965; Schlesinger et al, 1990). It is well established that vegetation in semi-arid and arid areas has the potential to transition rapidly from one vegetation state to another; a transition that is not easily reversible on human timescales (Westoby et al. 1989; Laycock, 1991; Lockwood and Lockwood, 1993; Scheffer and Carpenter, 2003a). Turnbull et al. (2008a) hypothesized that the timing and strength of change in the structure of the ecosystem (in particular the connectivity of soil properties) during the process of shrub invasion is a key determinant of whether or not a catastrophic vegetation shift will occur, since the amount, spatial distribution and heterogeneity of soil properties are key controlling variables over the (re)establishment and growth of vegetation, and the functional connectivity of runoff and erosion. We use the term *structural connectivity* to describe the extent to which landscape elements (such as vegetation or soil structural properties) are contiguous or physically linked to one another (With et al, 1997; Tischendorf and Fahrig, 2000; Turnbull et al, 2008), and the term *functional connectivity* to refer to the connectivity of processes across a landscape elements, such as the connectivity of ecologic, hydrologic and geomorphic processes over a landscape (Turnbull et al, 2008). We propose that structural changes which enhance the functional connectivity of processes such as runoff and erosion, and thus the amount and extent of the redistribution of resources, are more important in controlling vegetation change than random structural changes that do not affect the functional connectivity of processes.

Current understanding of how ecosystem structure changes during the process of shrub encroachment into grassland is limited, yet integral to the future management and prevention of shrub invasion into grassland. Understanding concurrent changes in both the properties and spatial structure of soil resources over a shrub-encroachment gradient will not only improve our ability to identify ecosystems at risk of catastrophic vegetation shifts, but also help characterize what stage of land degradation the system is in, thus enabling land managers to employ targeted measures to mitigate such shifts.

Changes in ecosystem structure from grassland to shrubland are often explained using the ‘island of fertility’ model, whereby it is proposed that intershrub areas are progressively degraded while positive plant-soil feedbacks create shrub-occupied islands of fertility (Charley and West, 1975; Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). This model was tested by Schlesinger et al. (1996), who found that grasslands showed a fine-scale distribution of plant-limiting nutrients, while shrubland showed a coarse-grained distribution autocorrelated to the area of biogeochemical cycling under the shrub canopy. However, other processes such as runoff and erosion (by both wind and water) affect the spatial distribution of soil properties at spatial scales greater than those characterized by 'islands of fertility' (Turnbull et al., 2010a; Müller et al., 2008; Wainwright et al., 2000; Okin et al, 2009; Ravi et al, 2007). For example, Müller et al. (2008) sampled over broader spatial scales and found that the autocorrelation lengths are not simply a function of average shrub sizes, but may be related to a more complex pattern that is controlled by the spatial layout of rill and interrill areas and other localized transfers of soil resources through wind and water redistribution.

The structure and function of an ecosystem is determined by feedbacks and interactions between biotic and abiotic structure and function (Turnbull et al., 2008a). The spatial heterogeneity of vegetation and soil characteristics thus represent a link between pattern and process(es) – both biotic and abiotic (Gustafson, 1998). Turnbull et al. (2008a) hypothesized that the dynamics of land degradation, such as those characterized by transitions from grassland to shrubland, can conform to a cusp-catastrophe model (Thom, 1975) in which the two controlling variables are abiotic and biotic structural and functional connectivity. To test this hypothesis and to understand the mechanisms by which the structure of an ecosystem changes during a transition from grassland to shrubland, it is necessary to investigate processes that occur during transitions from grassland to shrubland. It is also imperative that research into the structure of ecosystem properties over a shrub-encroachment gradient be carried out at appropriate spatial scales.

The aim of this paper is therefore to determine how the spatial structure of key biotic and abiotic ecosystem variables changes over a shrub-encroachment gradient. The specific objectives of this research are:

1. To characterize plant-essential soil properties over an example of a shrub-encroachment gradient at the SNWR in New Mexico;
2. To characterize how the spatial distribution of soil properties changes over the same shrub-encroachment gradient, in comparison with vegetation distributions.

Turnbull et al. (2008a) hypothesized that it was not simply structural change but changes in structural *connectivity* that are important during shrub encroachment. The change in structural connectivity and thus the amount and extent of the redistribution of resources is the key determinant of the connectivity of ecological and geomorphic processes (and thus functional connectivity). Therefore, we hypothesize here that:

1. Over the shrub-encroachment gradient, the difference in soil properties under each surface-cover type will change non-linearly, becoming increasingly different;
2. There will be a reduction in vegetation cover and an increase in vegetation-patch size that is concurrent with an increase in the spatial heterogeneity of soil properties across the shrub-encroachment gradient; and
3. Over the shrub-encroachment gradient, the range at which soil properties are autocorrelated will progressively exceed the range at which vegetation is autocorrelated.

2 Methods

2.1 Site description

The sites chosen for this study are located in the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA (34°19' N, 106°42' W) which is situated at the northern margin of the Chihuahuan desert, and is a transition zone between four major biomes: the Great Plains grassland, the Great Basin cool shrub-steppe, the Mogollon coniferous woodland and the Chihuahuan warm-temperate semi-desert (Figure 1). Since the SNWR is a biome-transition zone, many of the plant species found there are at the edge of their physiological tolerance, and therefore minor changes in soils (resulting from feedbacks between biotic and abiotic processes), topography or other environmental/anthropic disturbance can result in the crossing of thresholds by vegetation due to changing conditions and ecosystem feedbacks (Hochstrasser et al., 2002). Of particular interest in this study is the transition zone between the desert grassland and desert shrubland. To the east of the Rio Grande in the SNWR, an ecotone marks the transition from desert grassland, dominated by black grama (*Bouteloua eriopoda*; a C_4 bunchgrass) to desert shrubland dominated by creosotebush (*Larrea tridentate*; a C_3 shrub).

The SNWR was established as a wildlife refuge in 1973, prior to which it was grazed by cattle for 37 years. In areas of the SNWR, the vegetation has changed from perennial bunchgrass to woody shrubs, a change which has been observed across New Mexico (e.g. Buffington and Herbel, 1965). This vegetation change has been accompanied by a shift in ecosystem structure at the landscape level (Cross and Schlesinger, 1999). Aerial photographs in the region of the grassland to shrubland transition over the period 1935–1984 indicate that the number of creosotebush clumps have increased and extended their range into the grassland (Gosz, 1992), thus indicating that the grass-shrub ecotone is actively changing. $\delta^{13}C$ analysis of soil organic matter from soil cores at each of the study sites indicates that all of the sites were occupied by grass in the recent past (Turnbull et al. 2008b).

The SNWR has a semi-arid climate. The mean annual precipitation is 242 mm, of which an average of 140 mm falls during the summer monsoon period from July to September. The SNWR experiences hot summers, with a mean July temperature of 33.6 °C and cold winters with a mean January minimum temperature of -7.1 °C (http://sev.lternet.edu; Dahm and Moore, 1994). The Sevilleta is predominantly underlain by Tertiary and Quaternary sedimentary rocks of the Santa Fe Group (Rawling, 2004).

An ergodic approach was employed to monitor changes in ecosystem structure over an example of a single spatial gradient of shrub encroachment into grassland, which is analogous to changes in ecosystem structure over time. Measurement of key biotic and abiotic components of ecosystem structure (vegetation and soil-surface characteristics) was carried out at four sites over the shrub-encroachment gradient, from a grassland end-member (site 1) through to a shrubland end-member (site 4) (Figure 2). The nature of the geostatistical analyses undertaken (autocorrelation of vegetation and soil characteristics at their relative scales) lessens the need for replication, since this approach deals explicitly with associations over a landscape (Hargrove and Pickering, 1992; Oksanen, 2001). It is acknowledged however, that without replication of this study over multiple transitions from grassland to shrubland, interpretations and extrapolations to the wider region are more limited than they would be with a fully replicated study. Nevertheless, they do provide the first measurements at an appropriate scale of what these landscape-scale patterns are likely to be and aid in identifying processes and defining characteristics that can be extrapolated to other semi-arid and arid systems.

The soils at sites 1 and 2 are a Turney loam (Rawling, 2004). Sites 3 and 4 are located on the boundary between the Turney loam and Turney loamy sand. We propose that these differences in soil type are in fact the effect of vegetation-soil feedbacks resulting from creosotebush invasion into the native black grama grassland. Soils within the vicinity of the study sites are underlain by a well-developed calcium carbonate layer which occurs between 25 and 45 cm below the soil surface. To varying extents, stone pavements cover the study sites (most well-developed over sites 3 and 4), which are a primary factor controlling infiltration rates (Abrahams et al., 1989; Parsons et al., 1996). The sites are gently sloping with gradients of 2.7°, 2.1°, 3.8° and 1.8° from sites 1 to 4, respectively.

2.2 Field Methods

To characterize changes in the key determinants of structural connectivity, a series of vegetation and soil properties were measured over four stages of the shrub-encroachment gradient, targeting factors likely to control the structure and function of these ecosystems. The properties investigated were:

1. *the spatial properties and patterns of vegetation,* which are a key component of ecosystem structure;
2. *soil bulk density (BD),* which exerts a control over hydrological and ecological processes;
3. *stone pavement cover and soil particle-size distribution (PSD),* which exert a control over the infiltration characteristics and can affect the nutrient content of the soil;
4. *soil organic matter (SOM) content,* which is a key source of plant-essential nutrients;
5. *the total nitrogen (TN) content of the soil,* which reflects the total amount of nitrogen stored within the soil and the *nitrate content of the soil* since this is the immediately bioavailable store of nitrogen in the soil (in addition to ammonium, although it was not possible to measure the ammonium content of the soil in this study) (Fisher et al 1988; Belsky et al 1989; Hooper and Johnson, 1999).
6. *$\delta^{15}N$ of soil nitrogen pools:* which are used as a gross tracer of net soil-nitrogen cycling effects since they ultimately represent the balance of biological N transformations (Amundson and Baisden, 2000; Bol et al. 2008; Senbayram et al. 2008). Variations in the stable nitrogen-isotope ratio δ^{15}N reflect the gross overall N-cycling processes within ecosystems (Hogberg, 1997; Robinson, 2001), such as differences in type and rates of N transformations by processes including

ammonification, nitrification and denitrification (Hibbard et al., 2001, McCulley et al., 2004; Bol et al. 2008).

7. *Soil C:N ratios:* which are used as an indicator of soil quality (Gallardo and Schlesinger, 1992).

At each site the vegetation characteristics were determined by taking close-range aerial photographs over an area of 300 m^2. This extent was chosen to characterize changes in vegetation structure at a resolution larger than plant-interspace. A Canon Powershot 6-megapixel digital camera was suspended from a cable above the ground and 75 photographs were taken of the ground surface. Ground-control points were marked on the ground, so that each of the photographs had six ground-control points. The ground-control points were surveyed, enabling the photographs to be geo-corrected and then mosaiced together using Erdas Imagine™ image processing software. The mosaiced images were processed in ENVI 4.0™ for surface-cover classification which was carried out by manually mapping individual grass and shrub patches. These high-resolution aerial photographs were also used to manually map the percentage stone pavement cover over each site.

Determining the extent to which soil characteristics are spatially structured depends upon the spatial scale at which soil characteristics are measured (Thomas and Kunin, 1999). According to Western and Blöschl (1999), large-scale measurements will only characterize large-scale variability and vise versa for small-scale measurements. Therefore, to quantify short and medium range variations in soil-surface characteristics a nested sampling strategy was employed (Müller, 2008). In order to reveal whether surface characteristics were spatially structured and to what extent, soil characterization areas were set up at each site. At each of the four sites across the shrub-encroachment gradient, 90 sampling points were established, across two spatial scales: broad scale (36 sampling points randomly distributed across the 300-m^2 site) and fine scale (nine sampling points randomly distributed within six 3 × 3 m nested sampling areas which were located randomly within the 300-m^2 site) (Figure 3).

For SOM, BD and PSD, soil samples (5 cm diameter cores) were taken from the top 5 cm (which characterizes the active layer of sediment entrainment [Wainwright et al, 2008] and thus characterizes structural connectivity that affects and will be affected by runoff and erosion dynamics) at each sampling point and were air-dried. Soil samples were sub-sampled using a riffle sample divider to provide approximately 10 g of soil for the analysis of SOM and particle size.

2.3 Laboratory analysis

Intact soil cores were collected to measure BD by driving a cylindrical tin (5 cm depth, 7.5 cm diameter) into the soil. The soil was then excavated from around the tin and a trowel was used to slice the tin out of the soil so that the soil surface was flush with the tin. Soil samples were oven dried at 100°C for 24 hours. BD was calculated as:

$$BD = \frac{s}{v} \tag{1}$$

where BD is in g cm^{-3}, s is the mass of soil (g) and v is the volume of the intact soil core (cm^3). Particle-size analysis was carried out by dry sieving soil samples through 12 mm, 4 mm, 2 mm, 1 mm and 0.5 mm meshes, after removing coarse organic matter fragments by hand. A sub-sample of the <0.5-mm fraction was treated in H_2O_2 to remove fine organic matter and was then analyzed on a Horiba LA 910 laser particle-size analyzer for fine particle-size fractions. Particle-size analysis for the <2 mm fraction was carried out for 18 samples from each site (from the broad-scale sampling points – see Figure 3). The SOM content of the <2-mm soil fraction was determined by loss on ignition by heating samples at 425 °C for 16 hours.

Total N and δ^{15}N values of the samples were analyzed using an automated continuous flow ANCA 20/20SL system (Europa, Crewe, UK). The analytical precision of the δ^{15}N measurements was <0.2‰. Nitrate was extracted from the <2-mm soil fraction using 2 M KCl, and was shaken for 1 hour. Extracts were filtered through pre-leached Whatman 42 (2.5 μm) filter paper. The supernatant, was then analyzed on a Bran and Luebbe autoanalyser.

2.4 Statistical analysis

The Kolmogorov-Smirnov test was used to test the extent to which the patch-size distributions were significantly different between sites. To determine statistically significant differences in soil characteristics between different surface-cover types at each site, analysis of variance was carried out combined with Tamhane's t test. To upscale pointbased measurements of soil properties to the ecosystem scale accounting for differences in vegetation cover between sites, area-weighted averages of measurements of soil properties for the different vegetation types were calculated. Pearson's correlation coefficient (r) was used to test the strength of correlations between variables at each site. Significant correlations are reported at the $p < 0.05$ level. The coefficient of variation (CoV) associated with the mean concentration of each soil variable under each surface-cover type at each site is used as an index of the overall variation in soil properties (after Schlesinger et al., 1996).

To investigate changes in the spatial structure of soil characteristics, geostatistical analysis was employed. Geostatistical analysis has been used to quantify spatial structure by determining the extent to which a variable is spatially autocorrelated (Olea, 1999), which has been used previously to characterize the spatial variability of soil-surface properties associated with degradation (e.g. Müller et al., 2008; Zhao et al., 2007, Schlesinger et al., 1996). Geostatistical analysis is sensitive to the spatial scale at which surface properties are measured. For example, Schlesinger et al. (1996) did not find larger scale spatial dependence because they sampled uniformly over a 10 × 10 m grid. However, in this study, quantification of predominant spatial patterns that exist at fine or broad spatial scales is possible because of the nested, multi-scale sampling approach employed (Müller et al. 2008). The scale of spatial dependence in surface characteristics was determined by calculation of the semi-variogram (e.g. Rossi et al., 1992), which is estimated as half the average of squared differences, the semivariance $\gamma(h)$, between data separated by the lag distance vector h, where n is the number of pairs of sample points of the values of attribute z at location separated by distance h:

$$\gamma(h) = \frac{1}{2n}\sum_{i=1}^{n}\left[z(x_i) - z(x_i + h)\right]^2 \qquad (2)$$

Prior to implementing the geostatistical analysis, exploratory data analysis was carried out, to determine the underlying structure of the data sets. If outliers were detected in the data sets (which can greatly affect the shape of the semi-variogram), they were only removed if there was not a plausible explanation for their presence. If the data displayed a strongly non-normal distribution, the data were transformed to approximate a normal distribution using a log transformation prior to variogram analysis. All datasets were standardized, using a normal-score transformation, to enable comparisons of semi-variograms to be made between datasets with disparate measurement units and levels of spatial variability (Bekele and Hudnall, 2006; Rossi et al., 1992).

Omnidirectional experimental variograms were calculated using GSTAT within Idrisi32. Because of the nested structure of the sampling points employed in this study, experimental variograms were calculated using irregular lag distances, with shorter lag distances at fine scales, to present more clearly the spatial autocorrelation at these finer scales (Jackson and Caldwell, 1993). The lag distances used to calculate the experimental semi-variograms were 0.7, 1, 1.4, 1.9, 2.5, 3.5, 5, 7, 10, 14, 18.5 and 25 m. The minimum number of data points that was allowed within a lag width was 30, since this number was considered to be statistically viable. Therefore, the shortest lag distance used to calculate the experimental semi-variograms was 0.7 m, since at this distance, the aforementioned criteria were met over all sites. For vegetation cover, binary coding was used to distinguish between vegetated and non-vegetated areas and geostatistical analysis was performed on this binary dataset.

3 Results

3.1 Vegetation characteristics

Over the shrub-encroachment gradient there is an overall decrease in vegetation cover, from 45.5 % cover at site 1 (grass end-member) to 23.3 % cover at site 4 (shrub end-member) (Table 1) and a concurrent decrease in the area covered by grass with an increase in non-vegetated areas. Associated with this change in vegetation cover is a change in vegetation structure (Figure 4). At site 1, grass cover is made up of patches ranging in size from small (0.5 m^2) to large (> 3 m^2). At site 2, along with a small decrease in grass cover, there is a change in the structure of grass patches, with grass patches decreasing in size. At site 3 remaining grass patches are very small with 90 % of grass patches being smaller than 0.5 m^2. The $\delta^{15}N$ of creosotebush leaves is 6.1 ‰ (S.D. is 0.5 ‰) and the C:N ratio is 24.1 (S.D. is 0.78). The $\delta^{15}N$ of black grama is -1.0 ‰ (S.D. is 0.4 ‰) and the C:N ratio is 38.0 (S.D. is 2.9).

3.2 Soil characteristics

Stone pavements are present at each site, with percent covers of 14.4, 11.5, 49.0 and 51.3 at site 1 to 4 respectively. At each site soil BD is lower under vegetation compared to non-vegetated surfaces (Figure 5). The weighted mean BD measurements for sites 1, 2, 3 and 4 are 1.22, 1.23, 1.44 and 1.31 g cm^3 respectively.

At all sites, there is a significant difference in the soil PSD of non-vegetated and vegetated surfaces, in particular for the coarser fractions ($p<0.05$) which predominate in the non-vegetated surface soil (Table 2). The non-vegetated soil has more coarse particles, while the soil underneath grass patches has more fine particles, in particular fine sand. For the most part there are no significant differences in the silt and clay fractions between surface cover types.

The area-weighted mean SOM content at sites 1, 2, 3 and 4 is 20.19, 22.69, 19.2 and 22.87 mg cm^3 respectively. At site 1 there are no significant differences in the SOM content between different surface cover types ($p = 0.19$). At site 2 the SOM content under shrubs is significantly greater than the SOM for non-vegetated and grass-covered surfaces ($p \leq 0.0005$). At site 3 there are significant differences in the SOM content between all surface-cover types ($p = 0.001$ for non-vegetated versus grass, $p \leq 0.0005$ for non-vegetated versus shrub and $p = 0.001$ for grass versus shrub) with higher SOM content under grass and shrub-covered surfaces and higher SOM content under shrubs than grass. At site 4, the SOM content is significantly greater under shrubs than non-vegetated surfaces soil ($p \leq 0.0005$). The TN content of the soil is significantly lower for non-vegetated surfaces at each site ($p<0.05$). Highest soil TN content was measured under shrub-covered surfaces. The area-weighted mean soil TN content at sites 1, 2 3 and 4 is 0.34, 0.43, 0.32 and 0.36 mg cm^3 respectively. Over all sites the nitrate content of the soil is higher under vegetation, in particular under shrubs. The area-weighted mean nitrate content of the soil at sites 1, 2, 3 and 4 is 0.005, 0.006, 0.005 and 0.005 mg cm^3 respectively. At all sites, soil $\delta^{15}N$ is significantly lower under grass than non-vegetated and shrub-covered surfaces. There is an overall reduction in the soil $\delta^{15}N$ of non-vegetated surfaces over sites 1 to 4. The C:N ratio of surface soil is greater in soil under vegetation than non-vegetated surfaces and is typically higher in soil under shrubs than soil under grasses ($p = 0.03$ at site 2 and $p = 0.05$ at site 3).

Generally, the CoV for abiotic soil variables (BD and percent of soil less than 2 mm) is lower than biotic soil variables (SOM, TN, Nitrate, $\delta^{15}N$, C:N ratio). The highest CoV is for TN, nitrate and δ^{15}N across all sites. Generally, the CoV for δ^{15}N is less for soil under shrubs and grasses than non-vegetated surfaces.

3.4 Correlations between soil characteristics

For the most part, the percentage of soil less than 2 mm, SOM, TN and the soil C:N ratio are negatively correlated with BD over each site (Table 3). Soil δ^{15}N is the only biotic variable that is positively correlated with bulk density across all sites. TN is significantly positively correlated with the percent of soil less than 2 mm and the soil C:N ratio across all sites. Nitrate is significantly positively correlated with SOM across all sites. Soil δ^{15}N is significantly negatively correlated with C:N over all sites (Table 3). Soil δ^{15}N is negatively correlated with TN over all sites (although this correlation is only significant at site 1). Over the grass-dominated sites (1 and 2) BD is positively correlated with SOM and nitrate, while at the shrub-dominated sites (3 and 4) there is a negative correlation between these variables. All variables (apart from δ^{15}N) are positively correlated with the percentage of soil less than 2 mm.

3.5 Geostatistical analysis

The range at which vegetation cover is autocorrelated increases from sites 1 to 4, although site 3 has the highest range at 1.1 m (Table 4). At sites 1, 3 and 4 the range of autocorrelation of soil properties varied greatly. At sites 1 and 4, the range of autocorrelation of bulk density is much greater than the range at which vegetation is autocorrelated, while at site 3 the range of autocorrelation was similar to that of vegetation. The strength of spatial dependence was moderate across these sites. At site 2, no spatial dependence in bulk density is observable at the minimum lag distance of 0.7 m. No spatial structure in the proportion of soil greater than 2 mm is observable at the minimum lag distance of 0.7 m at site 1. At site 2 the percent of soil less than 2 mm is autocorrelated at a range more than double that of vegetation, and a strong degree of spatial dependence is indicated by a nugget variance of 0.2. The percent of soil less than 2 mm is autocorrelated at a range approximately double that of vegetation at sites 3 and 4, with a moderate strength of spatial dependence. The distribution of SOM at site 1 shows no spatial autocorrelation. At site 2, SOM is autocorrelated at a range similar to that of vegetation. SOM at site 3 is autocorrelated at a range much greater than that of vegetation, while at site 4 the range of autocorrelation is similar to that of vegetation. At site 1, TN is autocorrelated at the same range as vegetation while at site 2 it is autocorrelated at a range more than double that of vegetation. The nitrate content of the soil at sites 1 and 2 is autocorrelated at a range similar to that of vegetation. Nitrate is autocorrelated at 1.8 m at site 3, while no autocorrelation is observable at site 4, even though significant differences are observable in the soil-nitrate content of non-vegetated and shrub-covered soil ($p \leq 0.0005$). The soil C:N ratio is autocorrelated at the same range as vegetation at site 1, but at ranges much greater than vegetation at the other sites. Similarly, soil δ^{15}N is autocorrelated at the same range as vegetation at site 1, but at ranges much greater than vegetation at sites 2, 3 and 4. At sites 1 and 2, the nitrate content of the soil is autocorrelated at a range slightly greater than that range at which vegetation was autocorrelated. The strength of spatial dependence of soil-nitrate content is greater over site 2 than site 1.

4 Discussion

Overall, the ranges at which soil characteristics are autocorrelated change over the gradient of shrub encroachment and are typically greater than the increase in the range at which vegetation is autocorrelated. Thus, differences in the spatial distribution of vegetation and soil-surface characteristics at each site suggest that it is a combination of processes operating at multiple spatial scales (such as plant-soil feedbacks at the plant-patch scale and broader-scale hydrological and geomorphological controls over the redistribution of materials across the landscape at broader spatial scales) that result in the observed spatial distributions and explain why they differ across the transition.

Hypothesis 1. At each stage over the shrub-encroachment gradient, soil properties for each surface-cover type (i.e. non-vegetated, grass or shrub) will be significantly different

The soil under shrubs has a greater store of SOM, and therefore has a greater store of mineralizable nutrients leading to increased potential nutrient. Since microbial biomass is greatest in soil underneath shrub canopies and lower in the intershrub areas (Ewing et al., 2007), the increase in SOM underneath shrubs increases the potential for enhanced nutrient availability, compared to grasses (Ewing et al., 2007; Gallardo and Schlesinger, 1992). The nitrate content of the soil at sites 2 and 3 is greater under creosotebush than black grama, which is indicative of the onset of resource-island development from the earliest stages of shrub encroachment. The higher nitrate content of the soil under the shrubs is likely to give shrubs a competitive advantage over the grasses in times when nutrient availability is reduced. Although creosotebush vegetation has a lower C:N ratio than black grama grass, the soil C:N ratio under creosotebush is higher than the soil C:N ratio under black grama. Typically, the soil C:N ratio has an influence on N mineralization rates (Booth et al., 2005) with higher C:N ratios (such as those under creosotebush) exerting a negative influence on N mineralization rates (Hart et al., 1994; Mack and D'Antonio, 2003). However, in spite of the potential negative influence of higher C:N ratios under creosotebush, the nitrate content of soil is higher which suggests that microbial populations in soil under creosotebush are more readily able to mineralize nitrogen, or that the nitrogen in soil under shrubs is in a more bioavailable form that can be mineralized more readily. The $\delta^{15}N$ of soil under grasses was also lower than non-vegetated surface soil and soil under shrubs, which may be due to the lower $\delta^{15}N$ in black grama compared with creosotebush or the overall change in gross soil N dynamics and losses under these two distinct vegetation systems (Amundson and Baisden, 2000; Robinson, 2001; Bol et al. 2005 and 2008; Senbayram et al. 2008).

The overall increase in soil bulk density over the shrub-encroachment gradient is due to an increase in the both the area of non-vegetated surfaces that have a higher bulk density due to an increase in the amount of rock fragments in the soil and increased compaction of non-vegetated surfaces since these soils are more exposed to raindrop impact (Parsons et al, 1992; Wainwright et al, 2000). The higher percentage of stone pavement cover at sites 3 and 4 increases runoff generation and the connectivity of runoff over these surfaces (Turnbull et al, 2010a), leading to further changes in soil structure due to soil erosion.

From a biotic perspective, the greater proportion of pebbles (and thus a decrease in fine soil) that make up the soil matrix in non-vegetated areas in combination with the increase in non-vegetated area over the shrub-encroachment gradient has great implications for biogeochemical cycling, since fine soil has a greater surface area and therefore has a higher cation exchange capacity than coarse soil (Lister, 2007). This effect is reinforced by the (typically) higher water availability beneath shrubs because of higher infiltration rates associated with reduced stone pavement cover under vegetation (Turnbull et al, 2010a). Gallardo and Schlesinger (1992) found that soils with higher clay content may have a direct effect on microbial communities since soils with higher clay content have the capacity to preserve or protect the microbial biomass. Therefore, it is possible that the observed difference in the particle-size distribution between non-vegetated and vegetated areas over each site can further affect the release of nutrients into plant-available forms by microbial activity, due to a feedback between soil particle size and the resilience of microbial populations. Therefore, the reduced SOM content and reduced proportion of fine sediment in non-vegetated, intershrub soil greatly reduces the potential for the release of plant-available forms of nitrogen.

Hypothesis 2. There will be a reduction in vegetation cover and an increase in vegetation-patch size that is concurrent with an increase in the spatial heterogeneity of soil properties across the shrub-encroachment gradient.

Results show an overall decrease in vegetation cover over the shrub-encroachment gradient, since the increase in shrub cover does not compensate for the decrease in grass cover. These results contrast with a previous study at Walnut Gulch, Arizona, where an overall increase in the percent vegetation cover between grassland to shrubland vegetation was observed, but are comparable with those from the Jornada LTER site, New Mexico (Wainwright et al., 2000). Concurrent with a change in dominance from grass to shrub over the shrub-encroachment gradient, is a change in the structure of grass patches over the transition with the patch-size frequency distribution varying significantly between sites ($p \leq 0.05$), which is indicative of a reduction in the structural connectivity of grass patches over the shrub-encroachment gradient. The observed changes in the percent cover and spatial distribution of grass patches over the shrub-encroachment gradient are likely to disrupt intra-patch processes and the integrity of the remaining grass patches, by producing a net imbalance between resource inputs and outputs (Wiens et al., 1985). The effect of such destabilization in one patch may spread into adjacent areas (Wiens et al., 1985), the extent of which will be determined by the strength of interactions and connectivity between biotic and abiotic and structural and functional components of the ecosystem. For example, in a comparable ecosystem at the Jornada Experimental Range, Li et al. (2007) found that sparsely distributed shrubs with the same fractional cover as grasses provided much less protection from wind erosion than grasses of the same fractional cover value, because of a change in the distribution of vegetation and the reduced effect of shrubs on decreasing the momentum of wind-eroded, saltating soil particles. Similarly, at Walnut Gulch higher shrub cover than grass cover promotes more water erosion because of the development of more concentrated flow pathways (and thus functional connectivity) and because of feedbacks leading to the development of enhanced microtopography (and thus higher structural connectivity) in the intershrub areas (Parsons et al 1996). Therefore, the observed changes in the type and distribution of vegetation over the shrub-encroachment gradient may cause changes in the dynamics of wind and water erosion, which is likely to reinforce the changing structure and consequently the function of the ecosystem and the distribution of soil nutrients, since it is the fine, nutrient-rich soil particles that are preferably eroded by wind (Okin et al., 2004; Okin, 2005) and water (Wainwright et al., 2000; Turnbull et al., 2010a; Lister, 2007). The observed hydrologic function of site 2 does not differ significantly from site 1 (Turnbull et al, 2010a), which suggests that irreversible changes in ecosystem structure only occur beyond a threshold level of grass loss. At present, it is only possible to suggest that this threshold occurs somewhere between the conditions observed on site 2 and those observed on site 3.

Concurrent with changes in the vegetation characteristics over the shrub-encroachment gradient, there are changes in the structural and resource characteristics of the soil. The greater store of SOM under shrubs is an important factor in soil fertility as a store of potentially mineralizable nutrients in the soil. Differences in the microbial communities beneath grasses and shrubs may also accentuate differences in nutrient processing between these different vegetation types (Booth et al, 2005; Herman et al, 1993; Whitford et al, 2002). The release of nutrients from SOM is strongly linked to the quality of litter inputs and to the nature and abundance of the microbial decomposer community (Sjögersten and Wookey, 2005). The higher TN content of soil underneath shrubs compared to soil underneath grasses indicates stronger vegetation-soil feedbacks associated with shrubs, which may be exacerbated further by faunal feedbacks such as higher termite colonization beneath the shrubs which have been noted to be a significant cause of the mechanical breakdown of litter (Whitford et al, 1988), as a precursor to full decomposition. The observed overall decrease in the δ^{15}N signature of non-vegetated surface soil over the shrub-encroachment gradient corroborates this interpretation. In whole soil, the δ^{15}N signature is positively correlated to the degree of humification (Nadelhoffer and Fry, 1988). Therefore, the reduction in non-vegetated soil-δ^{15}N signatures over the shrub-encroachment gradient indicates a reduction in humification in non-vegetated surface soil, from the grass-dominated state to the shrub-dominated state, which is likely to be due to a reduction in the clay fraction of soil which reduces the capacity of the soil to sustain microbial biomass (Gallardo and Schlesinger, 1992).

While there are no clear trends in the overall TN content of the surface soil over the shrub-encroachment gradient, the much higher TN content of the soils under shrubs is indicative of the significance of plant-soil feedbacks and the extent to which the spatial distribution of soil nitrogen changes with increasing shrub cover. The overall increase in the bulk density of the soil over the shrub-encroachment gradient and concurrent coarsening of the soil is indicative of progressive soil degradation (Abrahams et al., 1995; Parsons et al., 1992).

Hypothesis 3. Over the shrub-encroachment gradient, the range at which soil properties are autocorrelated will progressively exceed the range at which vegetation is autocorrelated.

At sites 2 and 3 the observed range of spatial autocorrelation of SOM is greater than the range at which vegetation is autocorrelated, which indicates that at these transitionary sites, SOM is being redistributed over the landscape by other processes, such as the action of water and wind. The redistribution of resources such as SOM over the landscape is in part affected by other structural characteristics of the soil, such as bulk density and particle-size characteristics, which exert important controls over hydrology and erosion. The greater range at which coarse sediment (> 2 mm) is autocorrelated at site 2 compared to site 1 indicates that soil-structural changes occur at the onset of initial shrub encroachment. The spatial autocorrelation in the distribution of rock fragments with shrub encroachment is likely to increase the connectivity of flow in runoff-generating areas due to decreased transmission losses (Parsons et al., 1999; Wainwright et al, 2002). The range at which soil bulk density is spatially autocorrelated at site 1 is much greater than the range at which vegetation is spatially autocorrelated, which is thus indicative of broader-scale geomorphic controls (such as runoff and erosion) on soil bulk density over grassland. Although site 2 has only a slightly reduced percentage vegetation cover relative to site 1, the bulk density of the soil on site 2 is not spatially autocorrelated at the scale at which measurements were made. These findings indicate that even in the earliest stages of shrub encroachment, there appear to be functional changes that lead to changes in spatial structure of soil bulk density as noted above. Changes in the spatial structure of soil properties over the shrub-encroachment gradient, such as an increase in soil bulk density, result in observed increases in runoff (Turnbull et al., 2010a) that may, in turn, increase the preferential erosion of fine particles and modify further the spatial distribution of soil bulk density and soil particle-size characteristics.

The results showing no spatial structure in soil-nitrate content are consistent with the findings of Müller et al. (2008) in creosotebush shrubland at the Jornada Basin LTER site in New Mexico. The spatial characteristics of SOM and soil TN are different at each site, which indicates that factors other than SOM content regulate soil-nitrogen content, possibly factors such as nitrogen uptake by plants, abundance of microbial populations and spatiotemporal variations in soil-moisture content (Turnbull et al., 2010a). At site 1, soil C:N ratios and soil δ^{15}N are autocorrelated at the same range as vegetation (0.7 m). However, at sites 2, 3 and 4 soil C:N ratios and soil δ^{15}N are autocorrelated at ranges much greater than the range at which vegetation is autocorrelated. These results suggest that processes operating at scales larger than the range at which vegetation is autocorrelated are exerting a primary control over soil C:N ratios and soil δ^{15}N, such as the redistribution of water and materials across the landscape during runoff events, which becomes more pronounced over the transition from grassland to shrubland (Turnbull et al., 2010a, b). This interpretation is supported by an increase in the strength of the observed spatial autocorrelation of soil C:N ratios and soil δ^{15}N over the transition.

5 Conclusions

This study has considered three hypotheses to evaluate the conceptual model of Turnbull et al. (2008a) that the development of structural connectivity due to biotic-abiotic structural-functional feedbacks is critical in explaining shrub encroachment into semi-arid grasslands. It was found that there are significant differences in soil properties between non-vegetated and vegetated surfaces, but for grass and shrub patches, there are only significant differences for biotic soil properties. Vegetation cover was found to decrease as shrub encroachment continued, but vegetation-patch size increased, as did the spatial heterogeneity of soil properties. The disparity between the range at which soil properties and vegetation are spatially autocorrelated suggests that other processes are in operation that modify soil characteristics at spatial scales which differ from the scale of the individual plant, superimposing a broader spatial structure of soil properties across the landscape. This result suggests that although some feedbacks are driven by the vegetation change, it is the development of larger, more connected bare patches that is most important in driving the overall behaviour of shrub-dominated sites. It appears that changes in the spatial autocorrelation of biotic and abiotic soil properties over the shrub-encroachment gradient do not follow a linear trajectory which indicates that processes other than changes in vegetation cover and distribution have a significant effect on changes in ecosystem structure. Results of this study support the hypothesis that feedbacks of functional connectivity reinforce the development of structural connectivity, which increase the resilience of the shrub-dominated state, and thus make it harder for grasses to re-establish and reverse the vegetation change.

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Table 1. Descriptive statistics of ecosystem structure

Variable	Site 1		Site 2			Site 3			Site 4	
	NV (N = 44)	G (N = 46)	NV (N = 34)	G (N = 31)	S (N = 25)	NV (N = 32)	G (N = 35)	S (N = 23)	NV (N = 47)	S (N = 43)
% surface cover	54.5	45.4	57.0	38.6	4.4	73.8	14.3	11.9	76.7	23.3
Bulk density (g cm^{3})										
Mean ± S.E.	1.23 ± 0.01	1.20 ± 0.01	1.25 ± 0.01	1.19 ± 0.02	1.19 ± 0.02	1.37 ± 0.02	1.23 ± 0.02	1.21 ± 0.03	1.33 ± 0.01	1.27 ± 0.01
CoV (%)	8	8	6	8	8	9	9	12	4	5
Sig. dif. between cover types	a	a	a	b	b	a	b	b	a	b
% soil < 2 mm										
Mean ± S.E.	74.5 ± 2.5	78.4 ± 2.2	84.6 ± 2.1	82.6 ± 2.8	87.9 ± 2.5	50.9 ± 1.8	70.1 ± 2.1	75.0 ± 2.6	64.0 ± 1.1	88.5 ± 0.7
CoV (%)	22	19	14	19	14	19	15	19	11	5
Sig. dif. between cover types	a	a	a	a	a	a	b	b	a	b
Soil organic matter (mg cm^{3})										
Mean ± S.E.	19.41 ± 0.9	21.1 ± 0.9	20.3 ± 1.2	24.2 ± 1.3	40.0 ± 2.8	16.3 ± 1.0	22.9 ± 1.4	32.9 ± 2.1	20.4 ± 0.4	31.0 ± 2.5
CoV (%)	31	30	33	29	36	36	37	30	13	53
Sig. dif. between cover types	a	a	a	a	b	a	b	c	a	b
Total Nitrogen (mg cm^{3})										
Mean ± S.E.	0.29 ± 0.02	0.39 ± 0.02	0.37 ± 0.03	0.47 ± 0.03	0.81 ± 0.06	0.23 ± 0.01	0.48 ± 0.04	0.70 ± 0.07	0.27 ± 0.02	0.64 ± 0.04
CoV (%)	51	37	47	39	38	38	43	52	49	41
Sig. dif. between cover types	a	b	a	a	b	a	b	c	a	b
Nitrate (mg cm^{3})										
Mean ± S.E.	0.004 ± 0.000	0.006 ± 0.000	0.005 ± 0.000	0.007 ± 0.000	0.010 ± 0.001	0.004 ± 0.000	0.007 ± 0.001	0.008 ± 0.001	0.004 ± 0.000	0.007 ± 0.001
CoV (%)	32	24	36	24	36	36	69	40	21	48
Sig. dif. between cover types	a	b	a	b	c	a	b	b	a	b
δ^{15}N (‰)										
Mean ± S.E.	5.14 ± 0.16	3.37 ± 0.21	5.16 ± 0.20	4.05 ± 0.22	5.23 ± 0.19	4.50 ± 0.16	3.87 ± 0.19	4.29 ± 0.16	4.93 ± 0.14	4.26 ± 0.18
CoV (%)	20	43	23	30	18	19	25	21	20	28
Sig. dif. between cover types	a	b	a	b	a	a	b	ab	a	b
C:N ratio										
Mean ± S.E.	7.94 ± 0.13	8.37 ± 0.12	7.2 ± 0.14	7.67 ± 0.14	8.21 ± 0.14	7.34 ± 0.18	7.79 ± 0.22	8.50 ± 0.19	8.36 ± 0.14	8.97 ± 0.17
CoV (%)	11	10	12	10	8	14	15	12	12	12
Sig. dif. between cover types	a	b	a	b	b	a	a	b	a	b

* Mean values of variables for each surface cover type (NV, G, S) followed by the same letter are not significantly different (t-test, $p < 0.05$).

Table 2. Detailed descriptive statistics of soil particle size Percentage of soil sample belonging to each size fraction at each site for non-vegetated (NV) and vegetated grass (G) and/or shrub (S).

Particle size	(mm)	Site 1		Site 2			Site 3			Site 4	
		NV	G	NV	G	S	NV	G	S	NV	S
Coarse pebbles	>12	17.5 a	4.8 b	11.5 a	2.3 a	3.0 a	36.4 a	16.3 ab	10.0 a	17.1 a	2.6 b
Fine pebbles	>2	22.0 a	9.1 b	18.8 a	5.8 b	6.3 b	19.7 a	16.4 a	12.7 a	22.6 a	12.6 b
Coarse sand	>0.5	4.4 a	7.0 b	5.2 a	9.0 b	10.3 b	5.6 a	8.4 ab	9.6 b	7.4 a	13.6 b
Medium sand	>0.25	1.5 a	3.6 b	1.8 a	4.1 b	4.2 ab	0.8 a	2.1 a	3.6 a	1.6 a	4.0 b
Fine sand	>0.0625	31.3 a	56. 4 b	37.4 a	58.7 b	57.2 b	20.4 a	34.1 a	41.6 a	28.9 a	45.7 b
Silt	>0.003906	19.9 a	17.5 a	21.4 a	18.9 a	17.5 a	15.6 a	21.0 b	21.4 b	20.0 a	20.1 a
Clay	<0.003906	3.4 a	1.6 b	3.9 a	1.4 a	1.5 a	1.5 a	1.6 a	1.1 a	2.5 a	1.4 b

* For each site, mean values followed by the different letters are statistically different (t-test, *p*<0.05).

Table 3 Pearson's correlation coefficient between variables. Correlations highlight in bold are significant (p < 0.05).

	Site	**BD (g cm^3)**	**% of soil < 2 mm**	**SOM (mg cm^3)**	**TN (mg cm^3)**	**Nitrate (mg cm^3)**	***δ*^{15}N (‰)**
% of soil < 2 mm	1	-0.17					
	2	**-0.26**					
	3	**-0.28**					
	4	**-0.36**					
SOM (mg cm^3)	1	0.17	0.10				
	2	0.07	0.12				
	3	**-0.35**	**0.66**				
	4	-0.20	**0.48**				
TN (mg cm^3)	1	-0.01	**0.59**	0.19			
	2	0.08	**0.36**	**0.58**			
	3	**-0.38**	**0.65**	**0.65**			
	4	**-0.24**	**0.65**	**0.62**			
Nitrate (mg cm^3)	1	0.09	**0.32**	**0.59**	**0.45**		
	2	0.11	0.11	**0.63**	**0.63**		
	3	**-0.30**	**0.56**	**0.72**	**0.58**		
	4	-0.16	**0.69**	**0.46**	**0.66**		
***δ*^{15}N (‰)**	1	0.13	-0.16	-0.09	**-0.51**	**-0.36**	
	2	0.02	0.06	**0.26**	-0.10	0.11	
	3	0.06	**-0.28**	-0.48	-0.15	0.02	
	4	0.05	-0.20	**0.37**	-0.11	-0.17	
C:N ratio	1	-0.08	0.20	-0.05	**0.49**	0.15	**-0.56**
	2	-0.10	0.11	**0.27**	**0.71**	**0.30**	**-0.29**
	3	**-0.30**	**0.22**	**0.49**	**0.58**	0.20	**-0.21**
	4	-0.09	0.20	-0.01	**0.38**	0.18	**-0.53**

Table 4 Geostatistical analysis for all soil variables. All variograms used a Gaussian model, unless no spatial autocorrelation was found at the scale of observation. *R* is the range of autocorrelation and *NV* is the nugget variance.

Variable	**Site 1**		**Site 2**		**Site 3**		**Site 4**	
	R (m)	**NV**	**R (m)**	**NV**	**R (m)**	**NV**	**R (m)**	**NV**
Vegetation	0.70	0.65	0.70	0.65	1.10	0.00	0.90	0.50
Bulk density	2.60	0.50	-	1.00	1.20	0.56	4.00	0.50
% soil < 2 mm	-	1.00	1.80	0.20	2.00	0.50	1.90	0.50
Soil organic matter	-	1.00	0.80	0.30	2.30	0.50	0.80	0.50
Total nitrogen	0.70	0.70	2.20	0.45	1.00	0.50	1.30	0.50
Nitrate	0.90	0.50	0.80	0.30	1.80	0.30	-	1.00
$\delta^{15}N$	0.70	0.45	2.70	0.45	2.00	0.30	3.20	0.25
C:N ratio	0.70	0.60	2.30	0.55	2.00	0.50	1.90	0.35