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

Laura Turnbull¹, John Wainwright², Roland Bol⁴ & Richard E Brazier³

¹Global Institute of Sustainability, Arizona State University, Tempe, Arizona ***

²Sheffield Centre for International Drylands Research, Department of Geography, University
of Sheffield, Winter Street, Sheffield, S10 2TN, UK

³Department of Geography, University of Exeter, Amory Building, Rennes Drive, Exeter,
EX4 4RJ, UK

⁴ Biogeochemistry of Soils and Water Group, North Wyke Research, Okehampton, EX20 2SB,
UK

Email address of the corresponding author

Laura.Turnbull@asu.edu

34 **Abstract**

35 In this study we investigate changes in ecosystem structure that occur over a gradient of land-
36 degradation in the southwestern USA, where shrubs are encroaching into native grassland. We
37 evaluate a conceptual model which posits that the development of biotic and abiotic structural
38 connectivity is due to ecogeomorphic feedbacks. Three hypotheses are evaluated: 1. over the
39 shrub-encroachment gradient, the difference in soil properties under each surface-cover type will
40 change non-linearly, becoming increasingly different; 2. there will be a reduction in vegetation
41 cover and an increase in vegetation-patch size that is concurrent with an increase in the spatial
42 heterogeneity of soil properties across the shrub-encroachment gradient; and 3. over the shrub-
43 encroachment gradient, the range at which soil properties are autocorrelated will progressively
44 exceed the range at which vegetation is autocorrelated. Field-based monitoring of vegetation and
45 soil properties was carried out over a shrub-encroachment gradient at the Sevilleta National
46 Wildlife Refuge in New Mexico, USA. Results of this study showed that vegetation cover
47 decreases over the shrub-encroachment gradient, but vegetation-patch size increases, with a
48 concurrent increase in the spatial heterogeneity of soil properties. Typically, there were
49 significant differences in soil properties between non-vegetated and vegetated surfaces, but for
50 grass and shrub patches, there were only significant differences for the biotic soil properties.
51 Results suggest that it is the development of larger, well-connected, non-vegetated patches that is
52 most important in driving the overall behaviour of shrub-dominated sites. Overall, results of this
53 study support the hypothesis that feedbacks of functional connectivity reinforce the development
54 of structural connectivity, which increase the resilience of the shrub-dominated state, and thus
55 make it harder for grasses to re-establish and reverse the vegetation change.
56

57 **1 Introduction**

58 Land degradation is a widespread problem in semi-arid regions. One form of land
59 degradation in the southwestern USA is the invasion of native grasslands by woody shrubs
60 (Buffington and Herbel, 1965; Schlesinger et al, 1990). It is well established that vegetation
61 in semi-arid and arid areas has the potential to transition rapidly from one vegetation state
62 to another; a transition that is not easily reversible on human timescales (Westoby et al.
63 1989; Laycock, 1991; Lockwood and Lockwood, 1993; Scheffer and Carpenter, 2003a).
64 Turnbull et al. (2008a) hypothesized that the timing and strength of change in the structure
65 of the ecosystem (in particular the connectivity of soil properties) during the process of
66 shrub invasion is a key determinant of whether or not a catastrophic vegetation shift will
67 occur, since the amount, spatial distribution and heterogeneity of soil properties are key
68 controlling variables over the (re)establishment and growth of vegetation, and the
69 functional connectivity of runoff and erosion. We use the term *structural connectivity* to
70 describe the extent to which landscape elements (such as vegetation or soil structural
71 properties) are contiguous or physically linked to one another (With et al, 1997;
72 Tischendorf and Fahrig, 2000; Turnbull et al, 2008), and the term *functional connectivity* to
73 refer to the connectivity of processes across a landscape elements, such as the connectivity
74 of ecologic, hydrologic and geomorphic processes over a landscape (Turnbull et al, 2008).
75 We propose that structural changes which enhance the functional connectivity of processes
76 such as runoff and erosion, and thus the amount and extent of the redistribution of
77 resources, are more important in controlling vegetation change than random structural
78 changes that do not affect the functional connectivity of processes.

79
80 Current understanding of how ecosystem structure changes during the process of shrub
81 encroachment into grassland is limited, yet integral to the future management and
82 prevention of shrub invasion into grassland. Understanding concurrent changes in both the
83 properties and spatial structure of soil resources over a shrub-encroachment gradient will
84 not only improve our ability to identify ecosystems at risk of catastrophic vegetation shifts,
85 but also help characterize what stage of land degradation the system is in, thus enabling
86 land managers to employ targeted measures to mitigate such shifts.

87
88 Changes in ecosystem structure from grassland to shrubland are often explained using the
89 'island of fertility' model, whereby it is proposed that intershrub areas are progressively

90 degraded while positive plant-soil feedbacks create shrub-occupied islands of fertility
91 (Charley and West, 1975; Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). This
92 model was tested by Schlesinger et al. (1996), who found that grasslands showed a fine-
93 scale distribution of plant-limiting nutrients, while shrubland showed a coarse-grained
94 distribution autocorrelated to the area of biogeochemical cycling under the shrub canopy.
95 However, other processes such as runoff and erosion (by both wind and water) affect the
96 spatial distribution of soil properties at spatial scales greater than those characterized by
97 'islands of fertility' (Turnbull et al., 2010a; Müller et al., 2008; Wainwright et al., 2000; Okin
98 et al, 2009; Ravi et al, 2007). For example, Müller et al. (2008) sampled over broader spatial
99 scales and found that the autocorrelation lengths are not simply a function of average shrub
100 sizes, but may be related to a more complex pattern that is controlled by the spatial layout
101 of rill and interrill areas and other localized transfers of soil resources through wind and
102 water redistribution.

103

104 The structure and function of an ecosystem is determined by feedbacks and interactions
105 between biotic and abiotic structure and function (Turnbull et al., 2008a). The spatial
106 heterogeneity of vegetation and soil characteristics thus represent a link between pattern
107 and process(es) – both biotic and abiotic (Gustafson, 1998). Turnbull et al. (2008a)
108 hypothesized that the dynamics of land degradation, such as those characterized by
109 transitions from grassland to shrubland, can conform to a cusp-catastrophe model (Thom,
110 1975) in which the two controlling variables are abiotic and biotic structural and functional
111 connectivity. To test this hypothesis and to understand the mechanisms by which the
112 structure of an ecosystem changes during a transition from grassland to shrubland, it is
113 necessary to investigate processes that occur during transitions from grassland to
114 shrubland. It is also imperative that research into the structure of ecosystem properties
115 over a shrub-encroachment gradient be carried out at appropriate spatial scales.

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

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

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

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

136

137 **2 Methods**

138 **2.1 Site description**

139 The sites chosen for this study are located in the Sevilleta National Wildlife Refuge (SNWR)
140 in central New Mexico, USA (34°19' N, 106°42' W) which is situated at the northern margin
141 of the Chihuahuan desert, and is a transition zone between four major biomes: the Great
142 Plains grassland, the Great Basin cool shrub-steppe, the Mogollon coniferous woodland and
143 the Chihuahuan warm-temperate semi-desert (Figure 1). Since the SNWR is a biome-
144 transition zone, many of the plant species found there are at the edge of their physiological
145 tolerance, and therefore minor changes in soils (resulting from feedbacks between biotic
146 and abiotic processes), topography or other environmental/anthropic disturbance can
147 result in the crossing of thresholds by vegetation due to changing conditions and ecosystem
148 feedbacks (Hochstrasser et al., 2002). Of particular interest in this study is the transition
149 zone between the desert grassland and desert shrubland. To the east of the Rio Grande in
150 the SNWR, an ecotone marks the transition from desert grassland, dominated by black
151 grama (*Bouteloua eriopoda*; a C₄ bunchgrass) to desert shrubland dominated by
152 creosotebush (*Larrea tridentate*; a C₃ shrub).

153

154 The SNWR was established as a wildlife refuge in 1973, prior to which it was grazed by
155 cattle for 37 years. In areas of the SNWR, the vegetation has changed from perennial

156 bunchgrass to woody shrubs, a change which has been observed across New Mexico (e.g.
157 Buffington and Herbel, 1965). This vegetation change has been accompanied by a shift in
158 ecosystem structure at the landscape level (Cross and Schlesinger, 1999). Aerial
159 photographs in the region of the grassland to shrubland transition over the period 1935–
160 1984 indicate that the number of creosotebush clumps have increased and extended their
161 range into the grassland (Gosz, 1992), thus indicating that the grass-shrub ecotone is
162 actively changing. $\delta^{13}\text{C}$ analysis of soil organic matter from soil cores at each of the study
163 sites indicates that all of the sites were occupied by grass in the recent past (Turnbull et al.
164 2008b).

165

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

172

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

188

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

198

199 **2.2 Field Methods**

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

203 The properties investigated were:

- 204 1. *the spatial properties and patterns of vegetation*, which are a key component of
205 ecosystem structure;
- 206 2. *soil bulk density (BD)*, which exerts a control over hydrological and ecological
207 processes;
- 208 3. *stone pavement cover and soil particle-size distribution (PSD)*, which exert a control
209 over the infiltration characteristics and can affect the nutrient content of the soil;
- 210 4. *soil organic matter (SOM) content*, which is a key source of plant-essential nutrients;
- 211 5. *the total nitrogen (TN) content of the soil*, which reflects the total amount of nitrogen
212 stored within the soil and the *nitrate content of the soil* since this is the immediately
213 bioavailable store of nitrogen in the soil (in addition to ammonium, although it was
214 not possible to measure the ammonium content of the soil in this study) (Fisher et al
215 1988; Belsky et al 1989; Hooper and Johnson, 1999).
- 216 6. *$\delta^{15}\text{N}$ of soil nitrogen pools*: which are used as a gross tracer of net soil-nitrogen
217 cycling effects since they ultimately represent the balance of biological N
218 transformations (Amundson and Baisden, 2000; Bol et al. 2008; Senbayram et al.
219 2008). Variations in the stable nitrogen-isotope ratio $\delta^{15}\text{N}$ reflect the gross overall
220 N-cycling processes within ecosystems (Hogberg, 1997; Robinson, 2001), such as
221 differences in type and rates of N transformations by processes including

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

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

226

227 At each site the vegetation characteristics were determined by taking close-range aerial
228 photographs over an area of 300 m². This extent was chosen to characterize changes in
229 vegetation structure at a resolution larger than plant-interspace. A Canon Powershot 6-
230 megapixel digital camera was suspended from a cable above the ground and 75
231 photographs were taken of the ground surface. Ground-control points were marked on the
232 ground, so that each of the photographs had six ground-control points. The ground-control
233 points were surveyed, enabling the photographs to be geo-corrected and then mosaiced
234 together using Erdas Imagine™ image processing software. The mosaiced images were
235 processed in ENVI 4.0™ for surface-cover classification which was carried out by manually
236 mapping individual grass and shrub patches. These high-resolution aerial photographs
237 were also used to manually map the percentage stone pavement cover over each site.

238

239 Determining the extent to which soil characteristics are spatially structured depends upon
240 the spatial scale at which soil characteristics are measured (Thomas and Kunin, 1999).
241 According to Western and Blöschl (1999), large-scale measurements will only characterize
242 large-scale variability and vice versa for small-scale measurements. Therefore, to quantify
243 short and medium range variations in soil-surface characteristics a nested sampling
244 strategy was employed (Müller, 2008). In order to reveal whether surface characteristics
245 were spatially structured and to what extent, soil characterization areas were set up at each
246 site. At each of the four sites across the shrub-encroachment gradient, 90 sampling points
247 were established, across two spatial scales: broad scale (36 sampling points randomly
248 distributed across the 300-m² site) and fine scale (nine sampling points randomly
249 distributed within six 3 × 3 m nested sampling areas which were located randomly within
250 the 300-m² site) (Figure 3).

251

252 For SOM, BD and PSD, soil samples (5 cm diameter cores) were taken from the top 5 cm
253 (which characterizes the active layer of sediment entrainment [Wainwright et al, 2008] and
254 thus characterizes structural connectivity that affects and will be affected by runoff and

255 erosion dynamics) at each sampling point and were air-dried. Soil samples were sub-
256 sampled using a riffle sample divider to provide approximately 10 g of soil for the analysis
257 of SOM and particle size.

258

259 **2.3 Laboratory analysis**

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

$$264 \quad BD = \frac{s}{v} \quad (1)$$

265 where BD is in g cm^{-3} , s is the mass of soil (g) and v is the volume of the intact soil core
266 (cm^3). Particle-size analysis was carried out by dry sieving soil samples through 12 mm, 4
267 mm, 2 mm, 1 mm and 0.5 mm meshes, after removing coarse organic matter fragments by
268 hand. A sub-sample of the <0.5-mm fraction was treated in H_2O_2 to remove fine organic
269 matter and was then analyzed on a Horiba LA 910 laser particle-size analyzer for fine
270 particle-size fractions. Particle-size analysis for the <2 mm fraction was carried out for 18
271 samples from each site (from the broad-scale sampling points – see Figure 3). The SOM
272 content of the <2-mm soil fraction was determined by loss on ignition by heating samples at
273 425 °C for 16 hours.

274

275 Total N and $\delta^{15}\text{N}$ values of the samples were analyzed using an automated continuous flow
276 ANCA 20/20SL system (Europa, Crewe, UK). The analytical precision of the $\delta^{15}\text{N}$
277 measurements was <0.2‰. Nitrate was extracted from the <2-mm soil fraction using 2 M
278 KCl, and was shaken for 1 hour. Extracts were filtered through pre-leached Whatman 42
279 (2.5 μm) filter paper. The supernatant, was then analyzed on a Bran and Luebbe
280 autoanalyser.

281

282 **2.4 Statistical analysis**

283 The Kolmogorov-Smirnov test was used to test the extent to which the patch-size
284 distributions were significantly different between sites. To determine statistically
285 significant differences in soil characteristics between different surface-cover types at each
286 site, analysis of variance was carried out combined with Tamhane's t test. To upscale point-

287 based measurements of soil properties to the ecosystem scale accounting for differences in
288 vegetation cover between sites, area-weighted averages of measurements of soil properties
289 for the different vegetation types were calculated. Pearson's correlation coefficient (r) was
290 used to test the strength of correlations between variables at each site. Significant
291 correlations are reported at the $p < 0.05$ level. The coefficient of variation (CoV) associated
292 with the mean concentration of each soil variable under each surface-cover type at each site
293 is used as an index of the overall variation in soil properties (after Schlesinger et al., 1996).

294

295 To investigate changes in the spatial structure of soil characteristics, geostatistical analysis
296 was employed. Geostatistical analysis has been used to quantify spatial structure by
297 determining the extent to which a variable is spatially autocorrelated (Olea, 1999), which
298 has been used previously to characterize the spatial variability of soil-surface properties
299 associated with degradation (e.g. Müller et al., 2008; Zhao et al., 2007, Schlesinger et al.,
300 1996). Geostatistical analysis is sensitive to the spatial scale at which surface properties are
301 measured. For example, Schlesinger et al. (1996) did not find larger scale spatial
302 dependence because they sampled uniformly over a 10×10 m grid. However, in this study,
303 quantification of predominant spatial patterns that exist at fine or broad spatial scales is
304 possible because of the nested, multi-scale sampling approach employed (Müller et al.
305 2008). The scale of spatial dependence in surface characteristics was determined by
306 calculation of the semi-variogram (e.g. Rossi et al., 1992), which is estimated as half the
307 average of squared differences, the semivariance $\gamma(h)$, between data separated by the lag
308 distance vector h , where n is the number of pairs of sample points of the values of attribute
309 z at location separated by distance h :

310
$$\gamma(h) = \frac{1}{2n} \sum_{i=1}^n [z(x_i) - z(x_i + h)]^2 \quad (2)$$

311 Prior to implementing the geostatistical analysis, exploratory data analysis was carried out,
312 to determine the underlying structure of the data sets. If outliers were detected in the data
313 sets (which can greatly affect the shape of the semi-variogram), they were only removed if
314 there was not a plausible explanation for their presence. If the data displayed a strongly
315 non-normal distribution, the data were transformed to approximate a normal distribution
316 using a log transformation prior to variogram analysis. All datasets were standardized,
317 using a normal-score transformation, to enable comparisons of semi-variograms to be made

318 between datasets with disparate measurement units and levels of spatial variability (Bekele
319 and Hudnall, 2006; Rossi et al., 1992).

320

321 Omnidirectional experimental variograms were calculated using GSTAT within Idrisi32.
322 Because of the nested structure of the sampling points employed in this study, experimental
323 variograms were calculated using irregular lag distances, with shorter lag distances at fine
324 scales, to present more clearly the spatial autocorrelation at these finer scales (Jackson and
325 Caldwell, 1993). The lag distances used to calculate the experimental semi-variograms were
326 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
327 was allowed within a lag width was 30, since this number was considered to be statistically
328 viable. Therefore, the shortest lag distance used to calculate the experimental semi-
329 variograms was 0.7 m, since at this distance, the aforementioned criteria were met over all
330 sites. For vegetation cover, binary coding was used to distinguish between vegetated and
331 non-vegetated areas and geostatistical analysis was performed on this binary dataset.

332

333 **3 Results**

334 **3.1 Vegetation characteristics**

335 Over the shrub-encroachment gradient there is an overall decrease in vegetation cover,
336 from 45.5 % cover at site 1 (grass end-member) to 23.3 % cover at site 4 (shrub end-
337 member) (Table 1) and a concurrent decrease in the area covered by grass with an increase
338 in non-vegetated areas. Associated with this change in vegetation cover is a change in
339 vegetation structure (Figure 4). At site 1, grass cover is made up of patches ranging in size
340 from small (0.5 m²) to large (> 3 m²). At site 2, along with a small decrease in grass cover,
341 there is a change in the structure of grass patches, with grass patches decreasing in size. At
342 site 3 remaining grass patches are very small with 90 % of grass patches being smaller than
343 0.5 m². The $\delta^{15}\text{N}$ of creosotebush leaves is 6.1 ‰ (S.D. is 0.5 ‰) and the C:N ratio is 24.1
344 (S.D. is 0.78). The $\delta^{15}\text{N}$ of black grama is -1.0 ‰ (S.D. is 0.4 ‰) and the C:N ratio is 38.0
345 (S.D. is 2.9).

346

347 **3.2 Soil characteristics**

348 Stone pavements are present at each site, with percent covers of 14.4, 11.5, 49.0 and 51.3 at
349 site 1 to 4 respectively. At each site soil BD is lower under vegetation compared to non-

350 vegetated surfaces (Figure 5). The weighted mean BD measurements for sites 1, 2, 3 and 4
351 are 1.22, 1.23, 1.44 and 1.31 g cm³ respectively.

352

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

359

360 The area-weighted mean SOM content at sites 1, 2, 3 and 4 is 20.19, 22.69, 19.2 and 22.87
361 mg cm³ respectively. At site 1 there are no significant differences in the SOM content
362 between different surface cover types ($p = 0.19$). At site 2 the SOM content under shrubs is
363 significantly greater than the SOM for non-vegetated and grass-covered surfaces ($p \leq$
364 0.0005). At site 3 there are significant differences in the SOM content between all surface-
365 cover types ($p = 0.001$ for non-vegetated versus grass, $p \leq 0.0005$ for non-vegetated versus
366 shrub and $p = 0.001$ for grass versus shrub) with higher SOM content under grass and
367 shrub-covered surfaces and higher SOM content under shrubs than grass. At site 4, the SOM
368 content is significantly greater under shrubs than non-vegetated surfaces soil ($p \leq 0.0005$).
369 The TN content of the soil is significantly lower for non-vegetated surfaces at each site
370 ($p < 0.05$). Highest soil TN content was measured under shrub-covered surfaces. The area-
371 weighted mean soil TN content at sites 1, 2 3 and 4 is 0.34, 0.43, 0.32 and 0.36 mg cm³
372 respectively. Over all sites the nitrate content of the soil is higher under vegetation, in
373 particular under shrubs. The area-weighted mean nitrate content of the soil at sites 1, 2, 3
374 and 4 is 0.005, 0.006, 0.005 and 0.005 mg cm³ respectively. At all sites, soil $\delta^{15}\text{N}$ is
375 significantly lower under grass than non-vegetated and shrub-covered surfaces. There is an
376 overall reduction in the soil $\delta^{15}\text{N}$ of non-vegetated surfaces over sites 1 to 4. The C:N ratio
377 of surface soil is greater in soil under vegetation than non-vegetated surfaces and is
378 typically higher in soil under shrubs than soil under grasses ($p = 0.03$ at site 2 and $p = 0.05$
379 at site 3).

380

381 Generally, the CoV for abiotic soil variables (BD and percent of soil less than 2 mm) is lower
382 than biotic soil variables (SOM, TN, Nitrate, $\delta^{15}\text{N}$, C:N ratio). The highest CoV is for TN,

383 nitrate and $\delta^{15}\text{N}$ across all sites. Generally, the CoV for $\delta^{15}\text{N}$ is less for soil under shrubs and
384 grasses than non-vegetated surfaces.

385

386 **3.4 Correlations between soil characteristics**

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

398

399 **3.5 Geostatistical analysis**

400 The range at which vegetation cover is autocorrelated increases from sites 1 to 4, although
401 site 3 has the highest range at 1.1 m (Table 4). At sites 1, 3 and 4 the range of
402 autocorrelation of soil properties varied greatly. At sites 1 and 4, the range of
403 autocorrelation of bulk density is much greater than the range at which vegetation is
404 autocorrelated, while at site 3 the range of autocorrelation was similar to that of vegetation.
405 The strength of spatial dependence was moderate across these sites. At site 2, no spatial
406 dependence in bulk density is observable at the minimum lag distance of 0.7 m. No spatial
407 structure in the proportion of soil greater than 2 mm is observable at the minimum lag
408 distance of 0.7 m at site 1. At site 2 the percent of soil less than 2 mm is autocorrelated at a
409 range more than double that of vegetation, and a strong degree of spatial dependence is
410 indicated by a nugget variance of 0.2. The percent of soil less than 2 mm is autocorrelated at
411 a range approximately double that of vegetation at sites 3 and 4, with a moderate strength
412 of spatial dependence. The distribution of SOM at site 1 shows no spatial autocorrelation. At
413 site 2, SOM is autocorrelated at a range similar to that of vegetation. SOM at site 3 is
414 autocorrelated at a range much greater than that of vegetation, while at site 4 the range of
415 autocorrelation is similar to that of vegetation. At site 1, TN is autocorrelated at the same

416 range as vegetation while at site 2 it is autocorrelated at a range more than double that of
417 vegetation. The nitrate content of the soil at sites 1 and 2 is autocorrelated at a range similar
418 to that of vegetation. Nitrate is autocorrelated at 1.8 m at site 3, while no autocorrelation is
419 observable at site 4, even though significant differences are observable in the soil-nitrate
420 content of non-vegetated and shrub-covered soil ($p \leq 0.0005$). The soil C:N ratio is
421 autocorrelated at the same range as vegetation at site 1, but at ranges much greater than
422 vegetation at the other sites. Similarly, soil $\delta^{15}\text{N}$ is autocorrelated at the same range as
423 vegetation at site 1, but at ranges much greater than vegetation at sites 2, 3 and 4. At sites 1
424 and 2, the nitrate content of the soil is autocorrelated at a range slightly greater than that
425 range at which vegetation was autocorrelated. The strength of spatial dependence of soil-
426 nitrate content is greater over site 2 than site 1.

427

428 **4 Discussion**

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

437

438

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

442 The soil under shrubs has a greater store of SOM, and therefore has a greater store of
443 mineralizable nutrients leading to increased potential nutrient. Since microbial biomass is
444 greatest in soil underneath shrub canopies and lower in the intershrub areas (Ewing et al.,
445 2007), the increase in SOM underneath shrubs increases the potential for enhanced nutrient
446 availability, compared to grasses (Ewing et al., 2007; Gallardo and Schlesinger, 1992). The
447 nitrate content of the soil at sites 2 and 3 is greater under creosotebush than black grama,
448 which is indicative of the onset of resource-island development from the earliest stages of

449 shrub encroachment. The higher nitrate content of the soil under the shrubs is likely to give
450 shrubs a competitive advantage over the grasses in times when nutrient availability is
451 reduced. Although creosotebush vegetation has a lower C:N ratio than black grama grass,
452 the soil C:N ratio under creosotebush is higher than the soil C:N ratio under black grama.
453 Typically, the soil C:N ratio has an influence on N mineralization rates (Booth et al., 2005)
454 with higher C:N ratios (such as those under creosotebush) exerting a negative influence on
455 N mineralization rates (Hart et al., 1994; Mack and D'Antonio, 2003). However, in spite of
456 the potential negative influence of higher C:N ratios under creosotebush, the nitrate content
457 of soil is higher which suggests that microbial populations in soil under creosotebush are
458 more readily able to mineralize nitrogen, or that the nitrogen in soil under shrubs is in a
459 more bioavailable form that can be mineralized more readily. The $\delta^{15}\text{N}$ of soil under grasses
460 was also lower than non-vegetated surface soil and soil under shrubs, which may be due to
461 the lower $\delta^{15}\text{N}$ in black grama compared with creosotebush or the overall change in gross
462 soil N dynamics and losses under these two distinct vegetation systems (Amundson and
463 Baisden, 2000; Robinson, 2001; Bol et al. 2005 and 2008; Senbayram et al. 2008).

464

465 The overall increase in soil bulk density over the shrub-encroachment gradient is due to an
466 increase in the both the area of non-vegetated surfaces that have a higher bulk density due
467 to an increase in the amount of rock fragments in the soil and increased compaction of non-
468 vegetated surfaces since these soils are more exposed to raindrop impact (Parsons et al,
469 1992; Wainwright et al, 2000). The higher percentage of stone pavement cover at sites 3
470 and 4 increases runoff generation and the connectivity of runoff over these surfaces
471 (Turnbull et al, 2010a), leading to further changes in soil structure due to soil erosion.

472

473 From a biotic perspective, the greater proportion of pebbles (and thus a decrease in fine
474 soil) that make up the soil matrix in non-vegetated areas in combination with the increase
475 in non-vegetated area over the shrub-encroachment gradient has great implications for
476 biogeochemical cycling, since fine soil has a greater surface area and therefore has a higher
477 cation exchange capacity than coarse soil (Lister, 2007). This effect is reinforced by the
478 (typically) higher water availability beneath shrubs because of higher infiltration rates
479 associated with reduced stone pavement cover under vegetation (Turnbull et al, 2010a).
480 Gallardo and Schlesinger (1992) found that soils with higher clay content may have a direct
481 effect on microbial communities since soils with higher clay content have the capacity to

482 preserve or protect the microbial biomass. Therefore, it is possible that the observed
483 difference in the particle-size distribution between non-vegetated and vegetated areas over
484 each site can further affect the release of nutrients into plant-available forms by microbial
485 activity, due to a feedback between soil particle size and the resilience of microbial
486 populations. Therefore, the reduced SOM content and reduced proportion of fine sediment
487 in non-vegetated, intershrub soil greatly reduces the potential for the release of plant-
488 available forms of nitrogen.

489

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

493 Results show an overall decrease in vegetation cover over the shrub-encroachment
494 gradient, since the increase in shrub cover does not compensate for the decrease in grass
495 cover. These results contrast with a previous study at Walnut Gulch, Arizona, where an
496 overall increase in the percent vegetation cover between grassland to shrubland vegetation
497 was observed, but are comparable with those from the Jornada LTER site, New Mexico
498 (Wainwright et al., 2000). Concurrent with a change in dominance from grass to shrub over
499 the shrub-encroachment gradient, is a change in the structure of grass patches over the
500 transition with the patch-size frequency distribution varying significantly between sites ($p \leq$
501 0.05), which is indicative of a reduction in the structural connectivity of grass patches over
502 the shrub-encroachment gradient. The observed changes in the percent cover and spatial
503 distribution of grass patches over the shrub-encroachment gradient are likely to disrupt
504 intra-patch processes and the integrity of the remaining grass patches, by producing a net
505 imbalance between resource inputs and outputs (Wiens et al., 1985). The effect of such
506 destabilization in one patch may spread into adjacent areas (Wiens et al., 1985), the extent
507 of which will be determined by the strength of interactions and connectivity between biotic
508 and abiotic and structural and functional components of the ecosystem. For example, in a
509 comparable ecosystem at the Jornada Experimental Range, Li et al. (2007) found that
510 sparsely distributed shrubs with the same fractional cover as grasses provided much less
511 protection from wind erosion than grasses of the same fractional cover value, because of a
512 change in the distribution of vegetation and the reduced effect of shrubs on decreasing the
513 momentum of wind-eroded, saltating soil particles. Similarly, at Walnut Gulch higher shrub
514 cover than grass cover promotes more water erosion because of the development of more

515 concentrated flow pathways (and thus functional connectivity) and because of feedbacks
516 leading to the development of enhanced microtopography (and thus higher structural
517 connectivity) in the intershrub areas (Parsons et al 1996). Therefore, the observed changes
518 in the type and distribution of vegetation over the shrub-encroachment gradient may cause
519 changes in the dynamics of wind and water erosion, which is likely to reinforce the changing
520 structure and consequently the function of the ecosystem and the distribution of soil
521 nutrients, since it is the fine, nutrient-rich soil particles that are preferably eroded by wind
522 (Okin et al., 2004; Okin, 2005) and water (Wainwright et al., 2000; Turnbull et al., 2010a;
523 Lister, 2007). The observed hydrologic function of site 2 does not differ significantly from
524 site 1 (Turnbull et al, 2010a), which suggests that irreversible changes in ecosystem
525 structure only occur beyond a threshold level of grass loss. At present, it is only possible to
526 suggest that this threshold occurs somewhere between the conditions observed on site 2
527 and those observed on site 3.

528

529 Concurrent with changes in the vegetation characteristics over the shrub-encroachment
530 gradient, there are changes in the structural and resource characteristics of the soil. The
531 greater store of SOM under shrubs is an important factor in soil fertility as a store of
532 potentially mineralizable nutrients in the soil. Differences in the microbial communities
533 beneath grasses and shrubs may also accentuate differences in nutrient processing between
534 these different vegetation types (Booth et al, 2005; Herman et al, 1993; Whitford et al,
535 2002). The release of nutrients from SOM is strongly linked to the quality of litter inputs and
536 to the nature and abundance of the microbial decomposer community (Sjögersten and
537 Wookey, 2005). The higher TN content of soil underneath shrubs compared to soil
538 underneath grasses indicates stronger vegetation-soil feedbacks associated with shrubs,
539 which may be exacerbated further by faunal feedbacks such as higher termite colonization
540 beneath the shrubs which have been noted to be a significant cause of the mechanical
541 breakdown of litter (Whitford et al, 1988), as a precursor to full decomposition. The
542 observed overall decrease in the $\delta^{15}\text{N}$ signature of non-vegetated surface soil over the
543 shrub-encroachment gradient corroborates this interpretation. In whole soil, the $\delta^{15}\text{N}$
544 signature is positively correlated to the degree of humification (Nadelhoffer and Fry, 1988).
545 Therefore, the reduction in non-vegetated soil- $\delta^{15}\text{N}$ signatures over the shrub-
546 encroachment gradient indicates a reduction in humification in non-vegetated surface soil,
547 from the grass-dominated state to the shrub-dominated state, which is likely to be due to a

548 reduction in the clay fraction of soil which reduces the capacity of the soil to sustain
549 microbial biomass (Gallardo and Schlesinger, 1992).

550

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

557

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

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

581 in runoff (Turnbull et al., 2010a) that may, in turn, increase the preferential erosion of fine
582 particles and modify further the spatial distribution of soil bulk density and soil particle-
583 size characteristics.

584

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

600

601 **5 Conclusions**

602 This study has considered three hypotheses to evaluate the conceptual model of Turnbull et
603 al. (2008a) that the development of structural connectivity due to biotic-abiotic structural-
604 functional feedbacks is critical in explaining shrub encroachment into semi-arid grasslands.
605 It was found that there are significant differences in soil properties between non-vegetated
606 and vegetated surfaces, but for grass and shrub patches, there are only significant
607 differences for biotic soil properties. Vegetation cover was found to decrease as shrub
608 encroachment continued, but vegetation-patch size increased, as did the spatial
609 heterogeneity of soil properties. The disparity between the range at which soil properties
610 and vegetation are spatially autocorrelated suggests that other processes are in operation
611 that modify soil characteristics at spatial scales which differ from the scale of the individual
612 plant, superimposing a broader spatial structure of soil properties across the landscape.
613 This result suggests that although some feedbacks are driven by the vegetation change, it is

614 the development of larger, more connected bare patches that is most important in driving
615 the overall behaviour of shrub-dominated sites. It appears that changes in the spatial
616 autocorrelation of biotic and abiotic soil properties over the shrub-encroachment gradient
617 do not follow a linear trajectory which indicates that processes other than changes in
618 vegetation cover and distribution have a significant effect on changes in ecosystem
619 structure. Results of this study support the hypothesis that feedbacks of functional
620 connectivity reinforce the development of structural connectivity, which increase the
621 resilience of the shrub-dominated state, and thus make it harder for grasses to re-establish
622 and reverse the vegetation change.

623

624

625

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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 cm³)										
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 cm³)										
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 cm³)										
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 cm³)										
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
δ¹⁵N (‰)										
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	a	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)	$\delta^{15}\text{N}$ (‰)
% 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		
$\delta^{15}\text{N}$ (‰)	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						
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
$\delta^{15}\text{N}$	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