Hysteretic Responses to Grazing in a Semiarid Rangeland

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Abstract

Ecological systems comprise a complex array of interacting processes that manifest across multiple scales. Effective management of natural ecosystems has to be underpinned by an understanding of how the scaling of these processes influences system integrity and stability. This is particularly true in semiarid rangelands, which display strong relationships between pattern and process that are fundamental to maintaining ecosystem function. Grazing can disrupt the scaling of these relationships and the mechanistic coupling between pattern and process, undermining the health of grazed semiarid rangelands. This is due to possible hysteretic responses in key system components to increases and decreases in grazing disturbance. We used data from a semiarid rangeland in northern Australia to test for hysteretic responses in system components after the removal of cattle grazing. We found an uncoupling of spatial linkages between vegetation and soil moisture in a severely degraded plot that was not evident in less intensively grazed or recovering plots. Recovering plots protected from grazing for 20 yr showed a scale of spatial linkage between vegetation and soil moisture, and soil organic matter and mineralization flush, of a scale much coarser than that of degrading plots. These findings provide evidence for hysteretic recovery from grazing and demonstrate that comparison of the spatial patterns of vegetation and soil properties is essential for capturing the true state of ecological functionality in this system. This has important implications for assessing ecological function in systems typified by strong natural environmental variation or in which data for pristine conditions are lacking.

Key Words: cattle grazing, hysteresis, rangeland management, semiarid rangelands, spatial coupling

INTRODUCTION

Spatial and temporal scaling pervade the manifestation of all ecological processes, particularly so in semiarid rangeland systems, where spatial patterns of vegetation and soil resources drive the dynamics of water and nutrient cycles (Kefi et al. 2007; Scanlon et al. 2007). In these systems, pattern and process interact across multiple scales, from the fine-scale distribution of individual grasses up to broad-scale topographic patterns delineating watersheds. Understanding the dynamics of these scale-dependent processes lies at the heart of effective management of rangeland systems around the world.

It is widely recognized that landscape pattern in semiarid rangelands has a profound effect on ecosystem function. While broad-scale patterns of climate, topography, and soil type control landscape-level patterns of vegetation communities (e.g., McNaughton 1983; Ludwig et al. 1999), it is fine-scale processes of resource distribution that drive the ecological functionality responsible for maintaining the integrity of vegetation communities. Fine-scale processes, particularly the resource-concentrating effects of perennial tussock-forming grasses, control the redistribution of water, sediments, and...
nutrients within the landscape, acting to capture and store these limited resources (Tongway and Ludwig 1994; Ryel et al. 1996; Schlesinger et al. 1996; Northup et al. 1999; Ludwig et al. 2000; HilleRisLambers et al. 2001; Northup et al. 2005). Tussocks slow the rate of passage of water runoff, allowing more time for infiltration (Greene et al. 1994; Ludwig and Tongway 1995; McIvor et al. 1995; Rietkerk et al. 2000; Wilcox et al. 2003; Ludwig et al. 2005); microbial activity is concentrated in and near the tussock mounds, promoting effective recycling of organic matter (Northup et al. 1999; Rietkerk et al. 2000). A critical property of this fine-scale patchiness is its tendency to promote a self-reinforcing process—positive feedback between vegetation patches and resource-concentrating processes create self-organizing patterns in the landscape (Ludwig et al. 2000; Rietkerk et al. 2000; Rietkerk et al. 2004; Ludwig et al. 2005), lending the system a degree of stability.

However, grazing by large herbivores can disrupt these fine-scale processes, altering the scaling and heterogeneity of vegetation pattern. Although grazing effects can range over large scales, the direct animal–plant interaction is essentially a local event, and these local events can be highly aggregated when patch grazing occurs. This is particularly true in semiarid landscapes, where selective grazing effects are most evident in the formation of patches in the vegetation on the scale of several meters (Tongway and Ludwig 1994; Ludwig and Tongway 1996; Scanlan et al. 1996; Landsberg et al. 1999; Ludwig et al. 1999; Teague et al. 2004). The formation of patches enhances feedbacks between vegetation and hydrological processes, driving changes in vegetation pattern that can ultimately change the grain and size of patches (Tongway and Ludwig 1994; Ludwig et al. 2000, 2005; Northup et al. 2005), which may result in profound changes to landscape structure and function (Tongway and Ludwig 1994).

An important concept in our understanding of vegetation change under grazing in semiarid rangelands is the potential for hysteretic responses in system components following removal of the drivers of degradation (Groffman et al. 2006). Hysteresis in plant communities occurs when the return path to the original state (recovery pathway) is different from that taken during degradation (degradation pathway). Reversibility of this change can be controlled primarily by the alteration or complete loss of key functional processes and linkages within the system. In the case of grazed semiarid rangelands, changes to the spatial pattern of vegetation during degradation can alter soil structure and resources in such a way that recolonization of bare patches by plants may be severely impaired or prevented altogether (Tongway and Ludwig 1994; Ludwig and Tongway 1995; Ludwig et al. 2000; Friedel et al. 2003; Sparrow et al. 2003; Tongway et al. 2003). When this occurs, the recovery pathway may not mirror the degradation pathway but instead follow a new trajectory leading to an alternative and potentially irreversible stable state in which ecological processes operate on a fundamentally different scale to the original, intact state.

Managing systems that display a hysteretic response to disturbance necessitate a sound understanding of the mechanistic coupling between pattern and process. However, traditional approaches for modeling change in semiarid systems, such as state and transition models, have typically classified alternative stable states using only structural characteristics, such as shrub or grass cover (Westoby et al. 1989; Laycock 1991; Ash et al. 1994). This approach relies on the implicit assumption that the classification criteria reflect functional thresholds driven by changes in ecological processes (Bestelmeyer 2006). However, pattern and process relationships are often highly variable in both time and space such that any single value is unlikely to capture the complexities of a specific situation (Fuhlendorf and Smeins 1999; Muradian 2001; Huggett 2005; Bestelmeyer 2006). These issues highlight the need for an empirical approach that can integrate both the structural and the functional properties of the ecological system (Friedel 1991; Friedel et al. 2003; Tongway et al. 2003; Northup et al. 2005). Moreover, this approach must be able to accurately describe pertinent changes in ecological function against a background of high spatial and temporal variability in system components (Northup et al. 2003).

We propose that comparison of the spatial scale of vegetation pattern with that of key soil resources is the most reliable indicator of recovered ecological function in semiarid rangelands. This is because of the potential for hysteretic response of different system components to the application and removal of a disturbance event. We predict that a spatial pattern of more coarse-scale soil resources under a finer-scale vegetation pattern is indicative of a community recovering from disturbance but not yet fully restored to intact ecological function. This prediction is founded on the expectation that functional control of soil resources by vegetation lags behind recovery of vegetation structure because of slower rates of change in soil resources, such as organic matter. The implication of this hypothesis is that hysteretic responses in semiarid rangelands could be hidden within the functional overlap of spatial patterns of key system components and may not be detectable using purely structural vegetation measurements.

We tested this contention by evaluating whether recovered vegetation structure correlated with recovered ecological functionality across a range of grazed and recovering sites in a semiarid rangeland in northern Australia. We predicted that in recovering systems, distribution patterns of soil nutrients would lag behind the restructuring of vegetation pattern when the disturbance event is removed. As a consequence, we expected that functional recovery in this system would lag behind structural recovery and that we would be able to detect this lag using cross correlation of key system components. Given these precepts, we derived the following predictions for the spatial patterns in vegetation, soil moisture, and nutrients at three distinct classes of site:

- **Lightly impacted plots**: Because of the retained dominance of individual tussock grasses in controlling the distribution of limiting resources, we expected to find spatial linkages in vegetation, water, and soil nutrients at directly overlapping sample points.
- **Degraded plots**: Because of the patch scale of alternating vegetation and bare ground, we expected to detect functional linkages between vegetation, water, and soil nutrients that mirrored the new spatial pattern of vegetation and bare ground in these plots.
- **Recovering plots**: We hypothesized recovery of soil components will lag behind recovery of the spatial pattern of vegetation such that spatial linkages between vegetation, water, and soil nutrients will be diffuse because of a larger-scale pattern in soil moisture and nutrients in comparison to the more fine-scale pattern of individual tussock grasses.
METHODS

We compared spatial relationships between plants and key ecohydrological and soil processes at plots subjected to a range of cattle grazing intensities at one site in a semiarid rangeland. To test our hypotheses, we located plots exposed to heavy grazing intensity (within 250 m of a water point), plots subjected to light grazing intensity (280–600 m from nearest water point), and plots removed from grazing for 20 yr. We first established the nature of the structural pattern of vegetation in each plot. Using geostatistics, we then captured the degree of spatial linkage between vegetation, soil moisture, and soil nutrients at each plot. We then compared these scales of spatial linkage in vegetation and soil patterns to the predictions derived previously.

The site is a commercially leased cattle grazing operation situated in the Burdekin river catchment in northern Queensland, Australia (lat 19°45′36″, long 146°30′00″). This region lies within the seasonally wet–dry tropics, typified by a distinct hot, wet summer and a mild, dry winter. Rainfall is highly variable from year to year, receiving on average 600 mm. The region contains six water points, with Narrow-Leafed Ironbark (Eucalyptus crebra F. Muell.) and Bloodwood (Corymbia erythrophloia Blakely) forming the main vegetation unit. Understory herbage vegetation is a mixture of native perennial tussock grasses, including Heteropogon contortus L., Bothriochloa eurwartus Domin., Dicanthium sericeum R. Br., and Chrysopogon fallax S. T. Blake, although areas of introduced Indian couch (Bothriochloa pertusa L.) do occur. The paddock has been moderately stocked at around 8–9 ha/head in recent years (Ash et al. 2001; Roth et al. 2003). Mean paddock annual dry matter production is around 1.500–1.800 kg·ha⁻¹ (Roth et al. 2003). Seven plots were established at the site. We located four plots within grazed areas radiating out from two water points. The grazed plots were located at various distances from the water points to capture a gradient in grazing intensity from intense (100–200 m from water point) to very low (>400 m from water point). All the grazed plots (hereafter referred to as D₁–D₄) were located on the same Charters Towers soil type, consisting of dark brown clay loams over alkaline-structured red to reddish brown clay (Rogers et al. 1999). The recovering plots (hereafter referred to as R₁–R₃) were located in an adjacent area that has been removed from gazing pressure by cattle and macropods for approximately 20 yr. These plots were located within a 4-ha cattle and macropod spp. exclusion established in 1985 (Scanlan et al. 1996). This site had previously been heavily grazed (Scanlan et al. 1996). At that time, alternating areas of bare soil with very little evidence of plant establishment, and remaining vegetation were present (Scanlan et al. 1996)—conditions that are typical of rangelands in this region that have undergone severe overgrazing by cattle (Tongway and Ludwig 1994; Ludwig and Tongway 1995; Ludwig et al. 2000, 2005; Northup et al. 2005). The soil at this site is red chromosol Dalrymple series (eroded phase) consisting of reddish brown to dark brown loamy sand to sandy loam over structured red to reddish brown clay (Rogers et al. 1999).

Each 5 × 5 m plot was divided into 225 33 × 33 cm quadrats. Vegetation measurements were made at the end of the wet season in June 2006. All soil measurements were taken on 3 consecutive days in May 2006. Basal area of each tussock present per quadrat was determined as the area of an ellipse using two diameters. These basal areas were then summed to give total basal area per quadrant (cm²). Soil cores were taken from 60 quadrats within each plot; each of these quadrats was assigned using a spatial grid generated in ArcMap (Environmental Systems Research Institute 1999) to facilitate geometric analysis of spatial patterns (i.e., points were dispersed within the plot to encompass a range of between-sample distances). Two soil cores (3-cm diameter by 10-cm depth) were taken from the center of the quadrant unless there was a tussock present, in which case the soil cores were taken on the edge of the tussock. The two cores forming a pair were taken within approximately 5 cm of each other and then bulked together to form the soil sample for each quadrant. Any litter on the soil surface was removed before taking soil cores.

Extensive research in this rangeland system has demonstrated that soil organic matter (SOM) and mineralizable nitrogen (N) are good soil fertility indicators that are directly linked to processes such as plant growth, soil surface stability, and rates of mineralization and soil respiration (Tongway and Ludwig 1997). Therefore, each soil sample was analyzed for SOM, percent soil moisture, and mineralizable N. SOM was determined by calculating the weight lost on ignition overnight in a furnace, after samples had been dried in an oven overnight at 40°C. Percent soil moisture was calculated using pre- and post-air-drying weights. Potentially mineralizable N (PMN) was calculated using aerobic incubation periods of 2 wk at standardized temperature (30°C) and moisture (field capacity). Prior to incubation, the amount of NO₃-N and NH₄-N in each soil sample was determined, and these values were subtracted from the values obtained during incubation. Production of NO₃-N and NH₄-N was measured using leaching after 7 d and 14 d using a KCl extraction followed by automatic colorimetric determination (Bremner 1965; Stanford and Smith 1972; Wang et al. 2003). PMN was then calculated as the difference in mineral-nitrogen before and after the period of incubation. We split results from the nitrogen mineralization incubations to examine the dynamics of PMN over time. Calculation of the rate of production of NO₃-N over the first 7 d of incubation provides an indication of the ability of the system to respond to rain events during the first flush of activity immediately following precipitation (e.g., Schimel and Parton 1986). Flush rates of NO₃-N production (N mineralization flush) were calculated as

\[
\text{flush rate} = \frac{(\text{NO}_3-N \text{ after } 7 \text{ d}) - (\text{NO}_3-N \text{ after } 0 \text{ d})}{7}
\]

Geometric Analysis

Because of the wide range of vegetation pattern in our plots (from very sparse to relatively dense), we applied two techniques to assess vegetation pattern in our seven plots. Using more than one geostatistical technique to compare patterns in data is recommended because methods respond
differently to data characteristics (Dale 2000). We expected that in the more densely vegetated plots, semivariance analysis would detect spatial patterning of vegetation due to the positions of individual tussocks within each plot. However, because the degraded plots contained very sparse vegetation, it was unlikely that semivariance analysis would be able to detect a repetitive pattern in the vegetation. Therefore, we also used lacunarity analysis, which examines patterns in the dispersion of points over a range of spatial scales (Dale 2000). We expected that lacunarity analysis would more effectively detect vegetation pattern in the more degraded plots where vegetation tended to be dispersed into sparse, irregular clumps interspersed by bare ground.

Experimental semivariograms were calculated as a function of distance (0.33–2.5 m) on the value of summed basal area per quadrat. Semivariance was estimated using

\[ \gamma(h) = \frac{1}{2N_h} \sum_{i=1}^{N_h} [y(i + h) - y(i)]^2 \]  

where \( N_h \) is the number of pairs of points located at distance \( h \) from one another (VARIOWIN; Pannatier 1996).

For the lacunarity analysis, we transformed measurements of summed basal area of tussocks per quadrant to binary presence/absence data. A moving window was then used to calculate the first and second moments of the frequency distribution of events (presence of tussock) for each box size (0.08–2.5 m). Lacunarity (Lac) was then calculated as

\[ Lac = \frac{\text{second moment}}{\text{first moment}} \]  

where

\[ \text{first moment} = \sum_{s=1}^{(\text{biggest box})^2} s^2 Q(s, r) \]  

and

\[ \text{second moment} = \sum_{s=1}^{(\text{biggest box})^2} s^2 Q(s, r) \]  

and \( Q(s, r) \) is the proportion of boxes of size \( r \) containing \( s \) occupied sites (APACK; Mladenoff and DeZonia 2004).

Spatial patterns of functional relationships between vegetation and soil variables were examined using cross correlograms. The cross correlogram plots the cross correlation \( r_{ab}(h) \) between two variables as a function of the distance \( h \) between sample points.

For pairs of observations \( a(x_i) \) and \( b(x_i + h) \), the experimental cross correlogram for the separation vector \( h \) was calculated as

\[ r_{ab}(h) = \frac{\sum_{i=1}^{N_h} a(x_i)b(x_i + h) - m_a m_b}{s_a s_b} \]  

where \( m_a \) and \( m_b \) are the sample mean of variables \( a \) and \( b \), \( s_a \) and \( s_b \) are the corresponding standard deviations, and \( N_h \) is the number of pairs of observations. This measure of spatial continuity ranges between −1 and +1. If patterns of the two variables are completely overlapping, \( r_{ab}(0) \) is equal to 1. If patterns are completely opposite and overlapping \( r_{ab}(0) \) is equal to −1. For totally unrelated patterns, \( r_{ab}(h) \) is equal to zero. The value of the cross correlogram at lag distance \( h = 0 \) yields the statistical correlation coefficient, \( r \) (VARIOWIN; Pannatier 1996).

### RESULTS

**Structural Vegetation Pattern**

We first looked at structural patterns in vegetation in the four plots subjected to cattle grazing. These four plots encompassed a structural vegetation gradient from few grass tussocks of small basal area to many large tussocks (Table 1; Fig. 1). The most intensively grazed plots (D1 and D2) were dominated by *B. pertusa* plants of small basal area and contained significant areas of bare ground, indicating considerable degradation of fine-scale vegetation structure (Table 2; Fig. 1). Lacunarity analysis revealed a scale of patchiness in plant cover in the most intensively grazed plot (D1) at a scale of around 0.4 m (Fig. 2). Patchiness in plant cover in the other intensively grazed plot (D2) occurred on the scale of 0.4–0.75 m (Fig. 2). The scale of patches of bare ground in the most intensively grazed plots were approximately 0.75–1.25 m (plot D1) and around 0.75 m in plot D2 (Fig. 2). Semivariance analysis detected weak spatial patterning in the most degraded plot (D1) on a scale of approximately 1.0 m (Table 1; Fig. 2). In contrast, the less intensively grazed plots (D3 and D4) within the grazed area had many plants of large tussock basal area, dominated by the perennial species *B. ewartiana*, and had high percent ground cover (Fig. 2). We were unable to detect any patchiness in the vegetation in these two less intensively grazed plots.

The recovering plots were dominated by many large tussocks of similar size, cover, and distribution as the less intensively grazed plots within the grazed area (Table 1; Fig. 1). However, while the less intensively grazed plots were dominated by *B. ewartiana*, the recovering plots were dominated by *H. contortus* of large basal area (Table 2), with little bare ground.

### Table 1. Structural characteristics of vegetation in each plot and percent of total variance explained structural variance.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mean basal area (SD), cm²</th>
<th>Percent of surface cover</th>
<th>Structural variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1</td>
<td>3.7 (8.3)</td>
<td>0.34</td>
<td>0.25</td>
</tr>
<tr>
<td>D2</td>
<td>33.9 (63.4)</td>
<td>3.0</td>
<td>None</td>
</tr>
<tr>
<td>D3</td>
<td>72.8 (81.5)</td>
<td>6.7</td>
<td>None</td>
</tr>
<tr>
<td>D4</td>
<td>97.6 (83.0)</td>
<td>8.8</td>
<td>None</td>
</tr>
<tr>
<td>R1</td>
<td>79.9 (49.0)</td>
<td>7.2</td>
<td>0.20</td>
</tr>
<tr>
<td>R2</td>
<td>89.0 (63.4)</td>
<td>8.0</td>
<td>None</td>
</tr>
<tr>
<td>R3</td>
<td>65.09 (57.65)</td>
<td>5.98</td>
<td>None</td>
</tr>
</tbody>
</table>
Figure 1. Relative dimensions of summed tussock basal area per quadrat in each of the grazed plots (D1–D4), and the three recovering plots (R1, R2, and R3). The points are scaled to represent summed basal area of tussocks per quadrat (square is 5 × 5 m).

(Fig. 1). We detected no spatial structure in two of the recovering plots (R1 and R3). These two plots showed a fine-scale distribution of tussocks such that no spatial vegetation structure could be detected by our sample size, similar to the less intensively grazed sites in the grazed area. However, semivariance analysis of the other recovering plot (R2) revealed patchiness in vegetation at a scale of approximately 1.0 m, though much of the variance in summed basal area per quadrat remained unexplained (Table 1; Fig. 2; structural variance 0.2).

**Linking Structure and Function to Determine Ecological Functionality**

In the most degraded plot (D1) we were unable to detect any cross correlations between tussock basal area and percent soil moisture (Fig. 3A). However, in the three other grazed plots (plots D2, D3, and D4), we found positive correlations between basal area and percent soil moisture at overlapping sample points, with cross correlation decreasing rapidly with lag distance (Fig. 3A). We also found spatial correlation between summed basal area and PMN in the most structurally degraded plot (D1). In this plot, PMN was negatively correlated with summed basal area out to distances of approximately 1.0 m, corresponding to the scale of patchiness in bare ground in this plot (Fig. 3B). Basal area and PMN were not spatially correlated in the less intensively grazed plots (D1 and D4), where we found no evidence for spatial linkages between basal area and PMN (Fig. 3B). Strong positive correlations between SOM and the flush rate of NO3-N (N mineralization flush) were found in all the grazed plots, and this correlation dropped sharply as lag distance increased (Fig. 3C).

In contrast, in two of the recovering plots (R2 and R3), we found a positive correlation between basal area and percent soil moisture that was maintained out to lag distances of approximately 1.0 m, while the other plot showed no detectable correlation between vegetation and soil pattern at any scale (Fig. 3D). Two of the recovering plots (R1 and R2) also showed significant positive correlations between SOM and the flush rate of NO3-N that were maintained over lag

<table>
<thead>
<tr>
<th>Species</th>
<th>D1</th>
<th>D2</th>
<th>D3</th>
<th>D4</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bothriochloa pertusa</td>
<td>32.9</td>
<td>90.7</td>
<td>14.2</td>
<td>54.2</td>
<td>15.5</td>
<td>8.4</td>
<td>12.9</td>
</tr>
<tr>
<td>Bothriochloa ewartiana</td>
<td>0.4</td>
<td>32.4</td>
<td>88.0</td>
<td>64.9</td>
<td>0.4</td>
<td>1.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>77.8</td>
<td>86.7</td>
<td>76.0</td>
</tr>
<tr>
<td>Aristida spp.</td>
<td>0.4</td>
<td>0.0</td>
<td>0.0</td>
<td>0.4</td>
<td>9.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Other perennials</td>
<td>5.6</td>
<td>8.4</td>
<td>0.0</td>
<td>0.0</td>
<td>11.6</td>
<td>17.8</td>
<td>7.5</td>
</tr>
</tbody>
</table>
distances up to approximately 1.0 m, suggesting a functional scale of patchiness in these plots of larger scale than found in the grazed plots (Fig. 3F). Only one of the recovering plots (R2) showed cross correlation between basal area and PMN on a scale matching the scale of patchiness in vegetation (~1.0 m) in this plot (Fig. 3E).

**DISCUSSION**

Evaluating relationships between spatial patterns of key features within a community enables inferences to be drawn about the nature of ecosystem function (Rietkerk et al. 2000; Maestre et al. 2005). Comparing overlap between spatial patterns of vegetation and surrogates for ecosystem function, such as soil moisture and nutrients, gives an indication of the strength and stability of linkages between community components—linkages that are so crucial to the resilience of ecological communities in semiarid systems. Using geostatistics, we identified the structural and functional scales of dominant ecological processes in plots subjected to a range of cattle-grazing intensities and in plots that had been recovering from grazing for approximately 20 yr. We used these observations to look for hysteretic recovery of system components, which we hypothesized would lead to mismatches in the scale of patterns of vegetation and soil nutrients.

The species composition differed between the plots subjected to grazing and those undergoing recovery. Grazed plots were dominated by *B. pertusa* and *B. ewartiana*, and although the recovering plots contained these two species, they were composed predominantly of *H. contortus*. Data on species-specific relationships between perennial grass tussocks and soil variables are sparse in this system; however, one study has shown that *B. ewartiana* tussocks had a stronger (but spatially limited to ~30 cm) effect on microbial biomass than *H. contortus* tussocks, although both species had significantly higher microbial biomass around tussocks than that found in bare interspaces (Northup et al. 1999). It is likely, therefore, that the specific values for some soil components may well have been differentially affected by the variation in species composition between plots. However, because we compared patterns of spatial overlap between system components, not absolute

![Figure 2. Lacunarity slope functions (right panels) for bare ground and vegetation patches in the two most intensively grazed plots (D1 and D2). Semivariance graphs for plots in which structural vegetation patterns were detected are shown in the left panels.](image-url)
values, we do not expect that the relative dominance of these two species in grazed versus recovering plots would have significantly altered the scaling of functional relationships.

Vegetation Structure

Intense grazing in two plots (D1 and D2) had significantly altered the spatial pattern of vegetation creating larger, clumped patches of tussocks (~50–75-cm diameter) that were interspersed by patches of bare ground (75–125 cm). These findings are consistent with previous observations for degraded pastures in this system (e.g., Northup et al. 2005). High-intensity grazing also greatly reduced tussock basal area, in line with previous research in this system that has recorded declines of 40% and 70% in tussock basal area in degrading and degraded paddocks (Northup et al. 2005).

We were unable to detect patchiness in vegetation at the less intensively grazed plots (D3 and D4); this was likely due to the scale of measurement (33 × 33 cm) being too coarse to capture the fine-scale variation in basal area and bare ground between the closely aggregated individual tussocks. The relatively even distribution of tussocks and larger basal area in the less intensively grazed plots may have rendered variation in vegetation structure too fine for our measurements to capture. The same was likely also true for two of the three recovering plots, where we were also unable to detect patchiness in vegetation. However, in one of the recovering plots, we found evidence that, in line with hysteresis theory, patchy accentuation of resource capture during recovery had led to the development of a coarser scale of structural variation in vegetation, characterized by clumps of tussocks aggregated into larger patches (~1.0 m). These findings highlight the importance of sampling at appropriate spatial scales.

Linking Structure and Function

Given these structural measurements of vegetation pattern, traditional theory would suggest that only the most intensively grazed plots (D1 and D2), where vegetation pattern had been altered by grazing, would show significant disruption of ecological function. The assumption that ecological function mirrors structural recovery of vegetation in this system leads to the conclusion that the five plots with high ground cover and tussocks of large basal area (D3, D4, and R1–3) should display relatively tight spatial linkages between vegetation and soil pattern, as has been demonstrated in intact areas (Northup et al. 1999, 2005). Alternatively, if this system follows a hysteretic response such that some system components lag behind recovery of others, we expect to find mismatches in the scale of vegetation pattern and the scale of soil resources in the recovering plots that indicate incomplete recovery of ecological function.

In line with these expectations, the most degraded plot (D1) showed no spatial linkages between patterns of basal area and percent soil moisture. It is likely that the much-reduced size of tussocks in the heavily grazed area (mean area of tussocks in the most degraded plot was 11 cm²) had decreased the ability of tussocks to capture overland flows of water and enhance infiltration (Northup et al. 2005). We also found negative cross correlations between vegetation and PMN in the most degraded plot. This negative cross correlation between spatial patterns of basal area and PMN found at the scale of patchiness

Figure 3. Spatial cross correlograms for summed basal area and percent soil moisture (A, D), summed basal area and potentially mineralizable nitrogen (PMN; B, E), and soil organic matter and NO₃-N flush (C, F), and in the plots subjected to cattle grazing (top row) and those removed from cattle grazing for 21 yr (bottom row).
in bare ground (~1 m) in the most degraded plot may be due to impaired hydrologic function. It is possible that the bare patches were unable to maintain sufficient moisture to permit breakdown of organic nitrogen. This could have resulted in accumulation of SOM in the bare interpatch areas and resulted in our analyses of PMN showing negative cross correlations with vegetation pattern. Spatial linkages in vegetation pattern and PMN were not detected in the less degraded or recovering plots; other studies have also failed to find cross correlation in plant and soil variables at overlapping sample points in intact semiarid systems (e.g., Reitkerk et al. 2000). A possible explanation for this result is that tussocks act in concert to maintain soil nutrients relatively evenly throughout the soil when vegetation is densely distributed at fine scales (Tongway and Ludwig 1994; Northup et al. 1999, 2005).

We found tight spatial linkages between basal area and percent soil moisture at directly overlapping sample points in the less intensively grazed plots. This indicates that hydrological function in these plots had been maintained under fine-scale tussock control despite the grazing disturbance. This correlation decreased rapidly with increasing lag distance, in line with previous work that demonstrated influence of individual tussock grasses on soil moisture out to approximately 30 cm (Northup et al. 1999). We also found tight spatial linkages between SOM and mineralization flush rates at the scale of individual tussocks in the four degraded plots.

In contrast, in the recovering area we found positive spatial linkages in vegetation and soil moisture pattern in two plots at scales greater than that of individual tussocks. This is evidence for a larger scale of ecohydrological linkage between vegetation and soil moisture in areas of the system that have experienced recovery over several decades. Similarly, we detected cross correlations between SOM and nitrogen mineralization flush rates in the recovering plots that demonstrated a coarser scale of spatial linkage than that found in the degrading plots. In combination, these results indicate a hysteretic recovery pathway in this system. Patchy structural recovery of vegetation in the protected area had likely led to the development of a more coarse scale of ecohydrological linkage that still persisted after more than 20 yr of protection from grazing.

In summary, comparing the results from the three recovering plots with those subjected to cattle grazing indicates that alterations to the spatial pattern of vegetation during degradation and recovery can lead to a new scale of functional coupling between plants, soil moisture, and nutrient dynamics. We found evidence that in parts of the recovering area, despite the apparent recovery of vegetation to a state similar to that typical of intact areas, the spatial pattern of soil moisture and nutrients still retained a more coarse-scale distribution. These results suggest that although the structural nature of vegetation had returned to a state very similar to that found in undisturbed locations, the system had failed to recover functional links typical of intact areas (Northup et al. 1999, 2005). This highlights the need for assessments of recovery in this system to involve measurements of functional linkages, not just structural measurements of vegetation pattern. After 20 yr of complete protection from grazing, it remains unclear as to whether the recovery of degraded areas in this system can approach a fully intact system, given sufficient time and appropriate conditions.

**IMPLICATIONS**

We aimed to provide evidence that comparing spatial patterns of vegetation, soil moisture, and nutrients in this system provides a robust measure of ecological function along degradation and recovery pathways under cattle grazing. The results from this study do suggest that the changes to ecosystem structure and function during degradation and recovery can be captured empirically. Hysteresis appears to be an important derivative of degradation and recovery processes in this grazed semiarid rangeland system, and its effects have far-reaching implications for system stability and resource management. Our findings suggest that the spatial comparison of structural elements is better able to reveal the ecological function of a system in a variable environment than simple structural measurements of vegetation. The advantage of this method is that it may be used to reveal a site that has recovered vegetation structure but not ecological function. Importantly, this method may obviate the need to compare recovered sites to intact or predegradation sites to reliably evaluate structure and function. This is especially valuable in systems where there is no information about initial conditions (e.g., pre-European colonization). Understanding the role of hysteretic responses to grazing disturbance in semiarid rangelands remains an important challenge to effective management. We believe that the ideas and methodology outlined here will be important tools for refining current methods for assessing ecological function in this biologically and economically important system.

**ACKNOWLEDGMENTS**

We thank Mr and Mrs R. Whitney at Fanning River Station and J. Ramsay at Meadowvale Station for their generosity in allowing us to implement this study on their land. We thank L. Whiteman, J. Corfield, A. Way, A. Bishop, P. Wiegand, and A. Zull for their invaluable assistance with fieldwork. S. Berthelson and M. Tink conducted analyses of soil variables. B. Abbot provided insightful assistance with spatial analyses. We thank M. Haddix, R. Lawes, B. Abbott, and P. Nelson for their numerous discussions over the theory and content of this manuscript.

**LITERATURE CITED**


