Changes in Vegetation Structure after Long-term Grazing in Pinyon-Juniper Ecosystems: Integrating Imaging Spectroscopy and Field Studies

A. Thomas Harris,[1] Gregory P. Asner,[1*] and Mark E. Miller[2]

[1]Department of Global Ecology, Carnegie Institution of Washington, Stanford, University, Stanford, California 94305, USA;
[2]Northern Colorado Plateau Network, National Park Service, 2282 S. West Reserve Blvd., Moab, Utah 84532, USA

ABSTRACT

We used field studies and imaging spectroscopy to investigate the effect of grazing on vegetation cover in historically grazed and ungrazed high-mesa rangelands of the Grand Staircase–Escalante National Monument, Utah, USA. Airborne hyperspectral remote sensing data coupled with spectral mixture analysis uncovered subtle variations in the key biogeophysical properties of these rangelands: the fractional surface cover of photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV), and bare soil. The results show that a high-mesa area with long-term grazing management had significantly higher PV (26.3%), lower NPV (54.5%), and lower bare soil (17.2%) cover fractions in comparison to historically ungrazed high-mesa pinyon-juniper rangelands. Geostatistical analyses of remotely sensed PV, NPV, and bare soil were used to analyze differences in ecosystem structure between grazed and ungrazed regions. They showed that PV was spatially autocorrelated over longer distances on grazed areas, whereas NPV and bare soil were spatially autocorrelated over longer distances on ungrazed areas. Field data on the fractional cover of PV, NPV, and bare soil confirmed these remote sensing results locally. Field studies also showed a significantly higher percentage composition of shrubs (27.3%) and forbs (30.2%) and a significantly lower composition of grasses (34.4%) and cacti (1.1%) in grazed areas. No significant difference between grazed and ungrazed mesas was found in percentage composition of trees or in the number of canopies per hectare. Our combined remote sensing and field-based results suggest that grazing has contributed to woody thickening in these pinyon–juniper ecosystems through an increase in shrubs in the understory and intercanopy spaces. These results improve our understanding of broad-scale changes in pinyon–juniper ecosystem structural composition and variability due to long-term grazing.

Key words: grazing; overgrazing; land use; relict areas; pinyon–juniper ecosystems; imaging spectroscopy; hyperspectral remote sensing; woody encroachment.

INTRODUCTION

Pinyon–juniper woodlands cover 20–30 million ha in western North America (Tueller and others 1979). Like many arid and semiarid ecosystems around the world, pinyon–juniper ecosystems of

the American West have experienced local-scale increases in the spatial extent and density of woody vegetation (Johnsen 1962; Jameson 1962; Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; Tausch and others 1981; West 1984; Miller and Wigand 1994). These increases have been attributed to managed grazing, shifts in fire frequency, climate change, and increases in atmospheric concentrations of carbon dioxide (CO_2) (Isdo 1992; Archer and others 1988, 1995; Scholes and Archer 1997; Bond and Midgley 2000).

Changes in fire frequency, grazing intensity, and climate are inextricably linked as causes of observed increases in the distribution and density of pinyon–juniper woodlands. However, it is generally accepted that intensive livestock grazing was the initial catalyst for the woody thickening seen in many conifer-dominated ecosystems in the Southwestern United States (for example, see Leopold 1924; Swetnam and Baisan 1996). Evidence from fire history reconstructions over broad spatial scales shows that fire recurrence intervals increased dramatically after European colonization and with the subsequent introduction of domesticated livestock (Swetnam and Betancourt 1998). Long-term grazing pressure can lead to increased fire recurrence intervals as the consequent reduction of fine fuels in the understory decreases fire intensity and extent (Madany and West 1983; Savage and Swetnam 1990). Longer fire recurrence intervals have resulted in an increase in the survival of woody plant seedlings. The removal of grasses due to continuous grazing also decreases competition for soil moisture and nutrients, leading to an increase in the germination and survival of tree and shrub seedlings (Madany and West 1983; Karl and Doescher 1993). These processes are constrained by climate: many seedlings become established during extended periods of favorable climatic conditions (Swetnam and Betancourt 1998; Chambers and others 1999). In fact, climatic changes have been responsible for well-documented shifts in plant distributions and forest compositions in the southwestern United States (Wells 1983; Miller and Wigand 1994; Swetnam and others 1999).

Relict areas are regions that have rarely been exposed to land use; therefore, they constitute some of the best available places to study "pristine" ecosystems. Several plot-level studies have used relict areas in the southwestern United States to investigate ecosystem changes associated with grazing (Kleiner and Harper 1972; Brotherson and others 1983; Madany and West 1983; Klopatek and Klopatek 1986; Jeffries and Klopatek 1987; Beymer

and Klopatek 1992). At local scales, long-term managed grazing has been shown to alter species composition (Brady and others 1989; Cole and others 1997), cryptobiotic soil crust cover (Johansen and St. Clair 1986; Jeffries and Klopatek 1987; Beymer and Klopatek 1992; Eldridge and Kinnell 1997), and the fractional cover of photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV), and bare soil (Jeffries and Klopatek 1987; Bastin and others 1993). The local scope of these studies has fostered a detailed understanding of the interactions between grazing and these various environmental conditions. However, plot-level studies are also limited in capability because of the small proportion of total landscape variability they entail. Furthermore, woody thickening and other ecosystem responses to land use are phenomena that occur over broad geographic scales. Regional assessments are therefore needed to evaluate the processes that affect the long-term sustainability of rangelands, fire hazards, land-use effects on carbon sequestration, and ecosystem responses to climate change.

Past efforts aimed at quantifying grazing effects on ecosystems with remote sensing have primarily utilized multispectral spaceborne sensors—such as the Landsat Thematic Mapper (TM)—to assess land degradation around livestock watering points (Pickup and Chewings 1994; Pickup and others 1998). To our knowledge, there have been no studies that investigated the ecosystem structural changes associated with long-term grazing using hyperspectral remote sensing of a relict mesa. To address this we used a combination of field measurements, remote sensing, and geostatistics to develop a detailed analysis of long-term grazing impacts on ecosystem structural attributes on three mesas in the Grand Staircase–Escalante National Monument (GSENM), Utah, USA. At the plot level, we studied community-level indicators of long-term grazing effects, including the fractional cover of PV, NPV, and bare soil; cryptobiotic soil crust cover; and vascular plant community composition. At the regional scale, we used airborne imaging spectroscopy and spectral mixture analysis (SMA) to quantify differences in ecosystem structure that occur at the scale of remotely sensed image pixels (Asner and Heidebrecht 2002). The fractional cover of PV, NPV, and bare soil is the dominant driver of reflectance variability in arid and semi arid ecosystems (Asner and others 2000), and their relative horizontal distributions are closely linked to ecosystem function (Schlesinger and others 1990; Connin and others 1997).
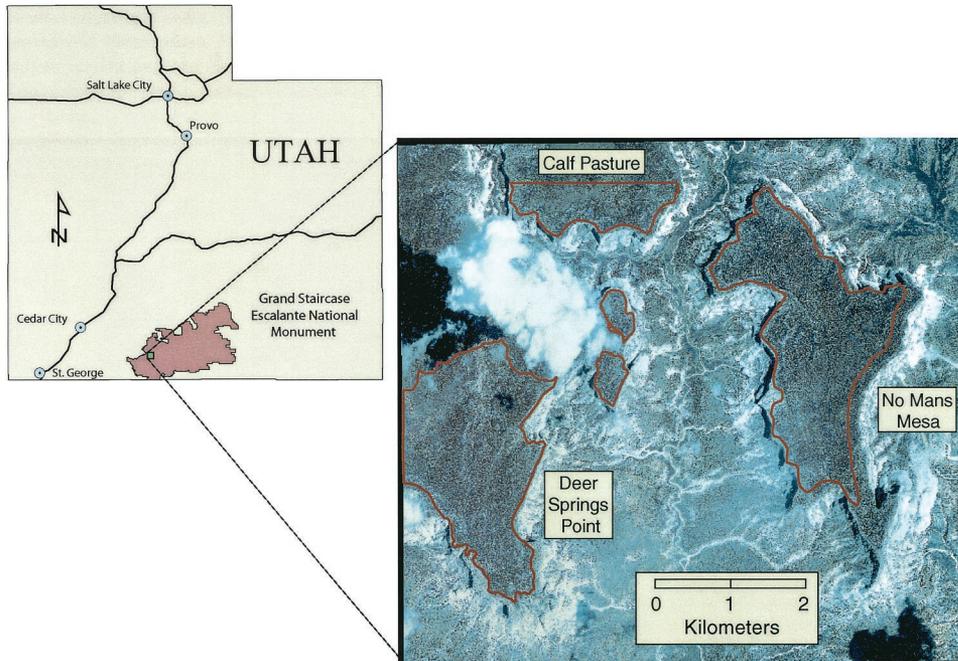
Figure 1. Location of the study area within Grand Staircase–Escalante National Monument, Utah, USA. The image of the study area is a color infrared aerial photo acquired at the time of the AVIRIS overflight. Study area mesas are outlined in red.

METHODS

Study Region

No Man's Mesa is a relict mesa located in the southwest corner of GSENM, approximately 50 km northeast of Kanab, Utah (Figure 1). Due to its large size, level topography, and close proximity to similar mesas that have been subjected to long-term grazing, it affords a unique opportunity to study the effects of managed grazing on ecosystem structure. Because of the steep cliffs that surround the mesa, domestic livestock have not grazed the area since the late 1920s (Mason and others 1967). In that year, a local rancher drove his goats up a constructed trail to the top, where they grazed successfully for two summers. However, the operation was not sustainable and ultimately failed due to the scarcely of water resources.

To the west and northwest of No Man's Mesa are two mainland mesas, Deer Springs Point and Calf Pasture, which have been accessible to grazing for the past century (Figure 1). These areas have similar topography, vegetation, and soils, and are attached to higher-elevation upland regions. Records indicate that the areas have been grazed since at least 1900 (P. Chapman personal communication). Together, the study mesas encompass 1260 ha.

The dominant vegetation type throughout both areas is mixed pinyon-juniper woodland (*Pinus edulis* and *Juniperus osteosperma*) and big sagebrush shrubland (*Artemisia tridentata*). The herbaceous cover is dominated by C3 grasses, including *Poa* and *Stipa* species. Soils on the study mesas are derived from the same parent material; interior portions of the mesa tops are derived from the Carmel formation and are a loamy fine sand, whereas its margins are derived from Navajo sandstone and are a very fine sandy loam (Mason and others 1967). Mean elevation is 2133 m for No Man's Mesa and 2134 m for Deer Springs Point. Topographically, the study areas are very similar. Flat plains characterize the central portions of both mesas, while their edges have a rolling, channel topography. Due to their proximity, the study mesas have very similar temperature and precipitation regimes. The climate is semiarid, with cold, snowy winters and dry, hot summers. Mean annual precipitation and temperature are approximately 305 mm and 12.3°C, respectively.

Fire histories on the study mesas appear to be similar. No large-scale, stand-replacing fires have occurred on either study area in the past half-century (M.E. Miller unpublished). There are no scientific data on aquifer depth for the mesas. We assumed that water tables in the study mesas are similar given that (a) both mesas are underlain by Navajo sandstone bedrock, and (b) there are few springs emanating from the exposed cliff faces. Large native ungulates (deer and elk) do not appear to be present on No Man's Mesa (A. T. Harris personal observation); no signs of deer were observed during our field studies. In contrast, extensive signs

of deer were observed during field trips to Deer Springs Point.

Field Studies

Permanent transects were established on No Man's and Deer Springs Point mesas in March 2001. Transect endpoints were nonrandomly selected to represent the two dominant vegetation classes present on the mesas and were permanently marked. A global positioning system (GPS) was used to record the starting and ending geographic coordinates for each transect. Two 500-m transects and one 200-m transect were established on Deer Springs Point. Two 400-m transects and one 200-m transect were established on No Man's Mesa.

Measurements of the fractional cover of PV, NPV, and bare soil were collected along transects established on No Man's and Deer Springs Point mesas in March 2001. PV was defined as photosynthetic plant tissue; NPV was defined as dry or senesced leaves, wood, or bark. Fractional cover of PV, NPV, bare soil, and rock, and cryptobiotic soil crust presence–absence were measured at 10-cm intervals along all transects via the line intercept method (Canfield 1941). Within each 10-cm section, the fraction of each cover type intersected by the line was recorded. Species composition data were collected in August 2001. Vegetation composition was tabulated by counting species occurrence along transects whenever an individual intersected the transect tape.

Air Photo Analysis

Aerial photographs acquired by the United States Geological Survey (USGS) in August 1993 were used to estimate the number of tree canopies per hectare on Deer Springs Point and No Man's Mesa. The images were received in digital orthophoto quadrangle (DOQ) format and image processing software (ENVI, v 3.5; Research Systems, Boulder, CO, USA) was used to randomly locate 20 1-ha plots within each study area. The numbers of canopies within each plot were counted visually.

An aerial photograph of the study region taken in 1948 was acquired from the Bureau of Land Management (BLM). Due to poor image quality, the photograph could not be used in a comprehensive digital analysis. However, regions were selected from the ungrazed and grazed mesas which illustrate historical changes in woody vegetation cover.

AVIRIS Imagery

The mesas were imaged on 28 June 2000 by the Airborne Visible Infrared Imaging Spectrometer (AVIRIS) sensor. The AVIRIS sensor measures up-welling radiance in the visible and near-infrared portion of the electromagnetic spectrum (400–2500 nm) in 224 continuous channels (Green and others 1998). AVIRIS was flown on the NASA ER-2 aircraft at an altitude of 20 km, which resulted in an image pixel size of 18 × 18 m. Radiance values were converted to reflectance using an atmospheric correction algorithm (ATREM) (Gao and others 1993) and empirical line fitting (Banin and others 1994). Field spectra of "bright" and "dark" calibration sites in GSENM were collected near in time to the AVIRIS overflight using a portable field spectrometer (Analytical Spectral Devices, Boulder, CO, USA). The bright calibration site was an extensive area of bare soil where all vegetation had been removed. Dark calibration spectra were collected over water at the nearby Lake Powell. High-resolution (DOQ) of the study area were acquired from the State of Utah Automated Geographical Reference Center and used to georectify all AVIRIS imagery. The resulting root mean square (RMS) errors were less than one pixel.

Spectral Mixture Analysis (SMA)

Arid and semiarid ecosystems display high spatial complexity. PV, NPV, and bare soil all vary at scales smaller than the size of the typical remotely sensed pixel, making it difficult to measure these key indicators of ecosystem structure directly and accurately with conventional remote sensing approaches. Spectral mixture analysis (SMA) is a technique for deriving subpixel fractions of surface materials by converting image reflectance values to cover fractions of specified surface constituents, called "endmembers." One of the most successful techniques uses endmember "spectral bundles" that account for the natural variability of endmembers occurring in nature (Bateson and others 2000). Because there are a number of endmember combinations that can produce any spectral signal, a wide range of acceptable unmixing results for any image pixel are possible (Asner and others 2000). To address SMA uncertainty, Asner and Lobell (2000) and Asner and Heidebrecht 2001 provided a detailed description of a general probabilistic linear spectral mixture model based on Monte Carlo analysis, which accounts for natural variability of endmembers through the calculation of uncertainty for each pixel endmember constituent. Employed in this study and described only briefly, the model—known as "Automatic Monte Carlo Unmixing" (AutoMCU)—uses predefined spectral endmember reflectance bundles to calculate fractions of PV, NPV, and bare soil on a per-pixel basis. The method is

ideal for use in arid and semiarid systems where subpixel cover variation is high. Each endmember component contributes to the pixel-level spectral reflectance (ω; $(\sigma)_{pixel}$):

$$\rho(\lambda)_{pixel} = \sum_{e=1}^{n} [C_e \cdot \rho_e(\lambda)] = [C_{pv} \cdot \rho_{pv}(\lambda)$$
$$+ C_{soil} \cdot \rho_{soil}(\lambda) + C_{npv} \cdot \rho_{npv}(\lambda)] + \varepsilon \quad (1)$$

where $\omega_e(\lambda)$ is the reflectance of each land-cover endmember e at wavelength λ, C is the fraction of the pixel composed of e, and ε is the error of the fit. Given an input AVIRIS reflectance measurement ($\rho(\lambda)_{pixel}$) and three endmember reflectance bundles ($\rho(\lambda)_{pv}$, $\rho(\lambda)_{npv}$, $\rho(\lambda)_{soil}$), the model is used to solve for the three subpixel cover fractions (C_{pv}, C_{npv}, C_{soil}).

The atmospherically corrected AVIRIS data were used as input to the AutoMCU spectral unmixing algorithm. Spectral endmember reflectance bundles of PV and NPV were constructed from field spectra collected at GSENM during August 2000. Because the remote location of the study area precluded the use of a field spectrometer, the bare soil endmember bundle was constructed from laboratory spectra of soil samples collected on No Man's Mesa. One soil sample from each of the two soil types present on No Man's Mesa was collected from the top 1 cm of the soil surface.

AutoMCU output was used to test for differences in ecosystem structural attributes between grazed and ungrazed mesas. Because the goal of the study was to determine changes in extent and density of the pinyon–juniper ecosystem, pixels with a minimum threshold of 20% PV were extracted for each study mesa. This was done to remove pixels composed of high proportions of bare soil or rock from further analysis. Pixels containing clouds and cloud shadows were removed using supervised classification of AutoMCU output. Because the total number of pixels from the grazed ($n = 17,819$) and ungrazed ($n = 11,908$) study regions was not equivalent, we randomly selected grazed pixels (without replacement) until both sample sizes were equal ($n = 11,908$). Kolmogorov-Smirnov tests for normality of PV, NPV, and bare soil all failed, so the Mann-Whitney rank sum test was used to test for statistical difference between samples.

Geostatistics

To understand how long term grazing has affected the spatial heterogeneity of surface cover on the study mesas, geostatistical analysis was used to cal-
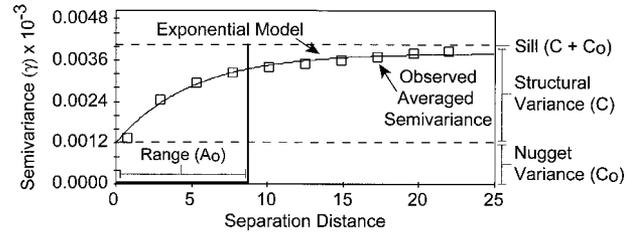
Figure 2. Semivariogram (exponential model) illustrating the nugget, range, and sill. The range in the exponential model is defined as the point at which the model includes 95% of the sill.

culate semivariograms. In the context of remotely sensed data, the semivariogram provides a way to spatially calculate the average variance between pixels as a function of distance (Curran 1988). In this study, we used features of the semivariogram that provide insight into the spatial variability of surface cover on grazed rangelands.

Semivariance is defined as:

$$\gamma(h) = \sum_{i}^{n-h} (X_i - X_{i+h})^2 / 2N(h) \quad (2)$$

where $\gamma(h)$ is semivariance for interval distance h, X_i is the measured sample value at point i, X_{i+h} is the measured sample value at point $i+h$, and $N(h)$ is the total number of sample couples for the lag interval h. Semivariance is evaluated by calculating $\gamma(h)$ for all possible pairs of points in the data set and by assigning each pair to a lag interval class h. The mean semivariance for each lag interval class is then calculated, and a model is fit to the results.

With respect to remotely sensed data, two scales of variability are evident from interpretation of a semivariogram. The first is subpixel variability that occurs at scales smaller than the sampling interval, which is represented in the semivariogram by the "nugget" (Figure 2). Variability occurring at scales larger than the sampling interval is represented by the "range" and "sill" (Figure 2). The range is the distance at which sample pairs are no longer spatially autocorrelated, and it is defined by the point at which the semivariogram reaches the asymptote or sill. The nugget-to-sill ratio (N:S) gives an indication of the percentage of variance described at the subpixel scale.

AutoMCU output from the three-endmember cover fraction images was used as input to a geostatistical software package with advanced visualization capabilities (GS+, v 5.1.1; Gamma Design Software, Plainwell, MI, USA). All fractional cover

Table 1. Field-measured Fractional Cover of Photosynthetic Vegetation (PV), Nonphotosynthetic Vegetation (NPV), and Bare Soil

Fractional Cover Component	Fractional Cover (%)		
	Ungrazed (No Man's Mesa)	Grazed (Deer Springs Point)	*P* Value
PV	21.0(0.01)[b]	28.3(0.08)[a]	< 0.001
NPV	50.0(0.01)[a]	50.4(0.11)[a]	0.545
Soil	26.1(0.02)[b]	20.6(0.14)[a]	0.041

Reported values are means calculated by averaging all convolved values from three transects on each study area.
Values in parentheses are SE. Different lower-case letters between columns denote statistically significant difference (Student's t-test, n = 50).

data were log-transformed to meet the geostatistical assumption that data are normally distributed. We tested for anisotropic effects using directional semivariograms, but none were noted since much of the study area's topography is flat. Semivariance was calculated for PV, NPV, and bare soil across many thousands of pairs of points at each lag distance (for example, for the ungrazed PV data, mean semivariance at lag 2 and 20 pixels is calculated from 43,903 and 922,056 pairs, respectively). We compared the relative degree of spatial autocorrelation of the three cover fractions between the grazed and ungrazed mesas. An iterative process was used to determine the maximum lag for each modeled parameter. Maximum lag was defined when the exponential model fit the observations with an $r^2 > 0.9$ and when the model appeared to reach a true asymptote. The exponential model, commonly used in geostatistical analysis, was chosen to fit all semivariograms because of high r^2 values and for consistency. One property of the exponential model is that it never reaches a true asymptote at the sill. Therefore, the range was defined as the point at which the model included 95% of the semivariance defined by the sill.

RESULTS

Field-based Fractional Cover

Transects established on the grazed study region had significantly higher fractional PV cover (*t*-test, *p* < 0.001) and significantly lower fractional bare soil cover (*t*-test, *P* < 0.05) than on the ungrazed mesa (Table 1). The grazed transects had a mean PV cover of 28.3 ± 0.08% (± SE) and a mean soil cover of 20.6 ± 0.14%, whereas the ungrazed transects had corresponding values of 21.0 ± 0.01% and 26.1 ±

0.02%. No significant difference was found in fractional NPV cover between the grazed and ungrazed transects.

Field-based Vegetation Composition

Vegetation community composition data are presented in Table 2 by lifeform. These data were found to be nonnormally distributed; therefore, Mann-Whitney rank sum tests were used to test for intersite differences. Grazed sites had significantly fewer grasses (*P* < 0.001) and cacti (*P* < 0.01) than the ungrazed sites. Shrubs were encountered more often on grazed than on ungrazed sites (*P* < 0.01). No difference was found between grazed and ungrazed areas in percent tree composition (*P* = 0.16).

Results of tree counts from aerial photography are presented in Table 2 in units of canopies per hectare. We found no significant difference between the study mesas in the number of canopies per hectare (*t*-test, *P* = 0.88). Measurements of cryptobiotic soil crust were significantly higher on ungrazed than grazed areas (Mann-Whitney rank sum test, *P* < 0.001) (Table 2).

Spectral Mixture Analysis

Imaging spectroscopy (AutoMCU) results for the mesas are presented as a red, green, blue (RGB) color composite, where R = PV, G = NPV, and B = bare soil (Figure 3). For clarity, low-lying regions outside the study mesas have been masked, and the mesa tops have been expanded for visualization purposes. General spatial patterns of ground cover are well modeled by the AutoMCU algorithm. For example, high fractions of bare soil (represented in blue) are apparent along the perimeter of No Man's Mesa and in a dry wash on Deer Springs Point. A clear difference in the PV component between study mesas is also apparent: The grazed region is characterized by uniform coverage of PV, whereas the ungrazed region exhibits an irregular pattern typified by patches of PV embedded in a matrix of high NPV.

The AutoMCU output data were extracted and compared to values computed from field measurements. The highly significant correlation between measured and modeled data ($r^2 = 0.94$, *P* < 0.05) indicated that surface biophysical properties were accurately estimated using imaging spectroscopy (Figure 4). Median fractional cover values for PV, NPV, and bare soil for grazed and ungrazed mesas are reported in Figure 5. Grazed and ungrazed mesas had median PV cover fractions of 26.3% and 23.9%; NPV cover fractions of 54.5% and 55.9%; and bare soil cover fractions of 17.2% and 18.5%,

Table 2. Vascular Plant Composition (%), Cryptobiotic Soil Crusts (Observations per Meter), and Tree Canopies (Canopies per Hectare) by Ungrazed (No Man's Mesa) and Grazed (Deer Springs Point) Study Regions

Characteristic	Ungrazed (No Man's Mesa)	Grazed (Deer Springs Point)	*P* value
Vascular plant composition (from transect data) (% of total)			
Grasses	44.3[a]	34.4[b]	0.001
	27.4[a]	30.2[b]	0.001
Shrubs	12.0[a]	27.3[b]	0.004
Cacti	7.0[a]	1.1[b]	0.003
Trees	9.3[a]	7.0[a]	0.164
Cryptobiotic soil crust (observations m^{-1})	0.99[a]	0.58[b]	0.001
Trees (from air photo data) (canopies ha^{-1})	220.1 (8.63)[A]	218.2 (8.53)[A]	0.884

Different lower-case letters between grazed and ungrazed treatments indicate statistical significance utilizing the Mann-Whitney rank sum test; different upper-case letters between treatments indicate statistical significance using Student's t-test.
Numbers in parentheses are SE.
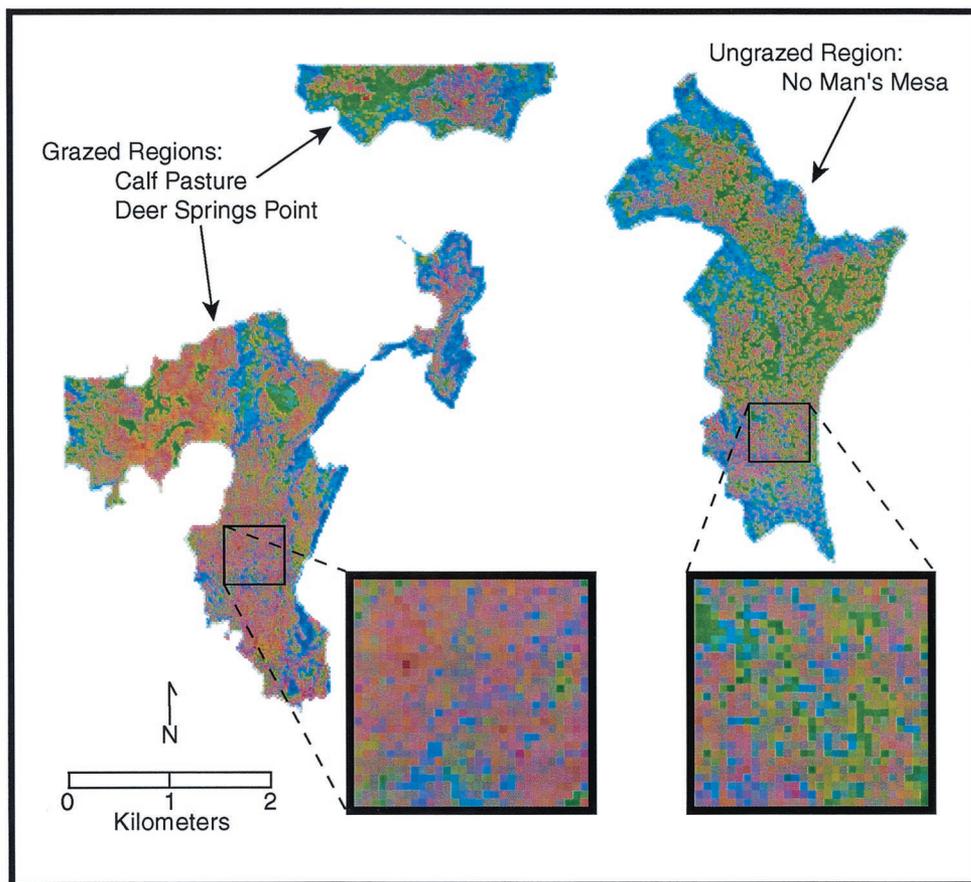
Figure 3. Color RGB image of the study mesas generated from Auto MCU output. Red, photosynthetic vegetation (PV), green, nonphotosynthetic vegetation (NPV), blue, bare soil.

respectively. All cover types were statistically different between grazing treatments (Mann-Whitney rank sum test, $P < 0.001$).

Geostatistics

Figure 6 shows calculated semivariograms for PV, NPV, and bare soil for ungrazed (A–C) and grazed (D–F) mesas, respectively. All semivariograms were fit with the exponential model due to high r^2 values, which were at least 0.98 in all cases (Table 3). To highlight differences in the range statistic of the various cover fractions between mesas, the x-axes of plots B, C, and D were shortened to match those of plots A, E, and F. For example, the x-axis of the
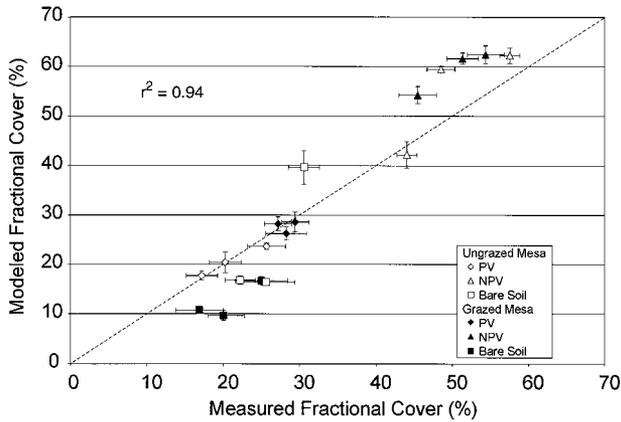
Figure 4. Comparison of measured and modeled cover fractions from grazed (Deer Springs) and ungrazed (No Man's Mesa) field sites.

grazed PV semivariogram plot (Figure 6D) was shortened from a calculated maximum lag of 30 to 20 pixels. Maximum lags used to calculate semivariograms were different within cover fractions on grazed and ungrazed mesas. Maximum lag was 20 and 30 pixels within the PV fraction, 80 and 30 pixels within the NPV fraction, and 70 and 40 pixels within the bare soil fraction for the ungrazed and grazed study areas, respectively (Table 3). Differences in maximum lag reflect dissimilarity in spatial autocorrelation of cover fractions, revealed during iterative fitting of semivariogram models.

The range statistic, depicted in Figure 6 by the vertical black line on each semivariogram plot, shows that PV was spatially autocorrelated to a greater distance on the grazed mesa (6.2 pixels, 111.3 m) than on the ungrazed mesa (3.4 pixels, 60.3 m). NPV was spatially autocorrelated over a longer range of 20.2 pixels (361.6 m) on the ungrazed mesa, in comparison to 3.7 pixels (67.0 m) on the grazed mesa. Bare soil was spatially autocorrelated to a longer distance of 16.5 pixels (295.4 m) on the ungrazed mesa versus 8.4 pixels (150.2 m) on the grazed mesa.

The N:S ratio provides insight into subpixel variability of cover fractions. For PV, NPV, and bare soil, respectively, the ungrazed mesa showed higher subpixel variability, with N:S values of 0.43, 0.43, and 0.42 compared to values of 0.35, 0.19, and 0.32 for the grazed area.

DISCUSSION

The contemporary ecosystem structure of semiarid pinyon–juniper woodlands is the result of historical interactions between climate, vegetation, fire, graz-

ers, browsers, atmospheric CO_2 concentrations, insect outbreaks, and other factors. In this study, the natural experiment afforded by the steep cliffs isolating No Man's Mesa was used to explore the effects of long-term grazing on pinyon–juniper ecosystems. Given that the grazed mesa was exposed to the same long-term atmospheric and climatic conditions as the ungrazed mesa, we infer that differences between the study areas are due primarily to historical grazing. This interpretation relies on successfully discounting other sources of variability between study mesas—such as fire historics and native ungulate population densities—as significant contributors to measured differences between study regions.

A BLM database of fire locations on managed lands of southern Utah shows no occurrences of fire on the study area since recordkeeping began in 1980 (M. E. Miller Personal communication). Fire history before 1980 is unknown. Due to the protected status of No Man's Mesa (BLM Wilderness Study Area), the destructive sampling of tree stem cross-sections, which would be necessary for the reconstruction of the area's fire history, was not permitted. Therefore, we could only use field observations of fire scar, and interviews with BLM personnel to estimate the effects of past fires on present-day ecosystem structure.

During two field trips to the study areas, no signs of fire activity were observed on Deer Springs Point, but a few trees and stumps had fire scars in one area on No Man's Mesa. These fire scars occurred in close proximity to other pinyon and juniper trees without fire scars. We estimate that the few fire scars we observed on No Man's Mesa were the result of a small, localized fire that had little impact on ecosystem structure at the scale of the entire mesa. No signs of large-scale stand-replacing fire, such as numerous large burned snags or quantities of charcoal in the soil, were observed on the mesas.

In a fire history study of pinyon–juniper woodland in Mesa Verde National Monument, Floyd and others (2000) calculated a natural fire turnover time of approximately 400 years. If this turnover time is applicable to other pinyon–juniper woodlands on the Colorado Plateau, and if the absence of large fire-scared snags on our study area is an indication, we infer that large stand-replacing fire has been absent from our study areas for at least the past 100 years.

We found no evidence of native ungulate presence on No Man's Mesa. It is not known with certainty what effects the lack of large mammal browsers have had on vegetation structure on the
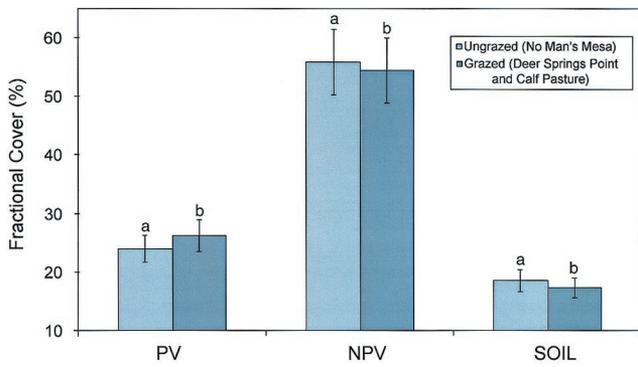
Figure 5. Median fractional cover of photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV), and soil from grazed and ungrazed study regions derived from the AutoMCU method. All fractional cover values are statistically different (Mann-Whitney rank sum test, $P < 0.001$) between grazing treatments, as noted by lower-case letters. Error bars are 10% of the range.
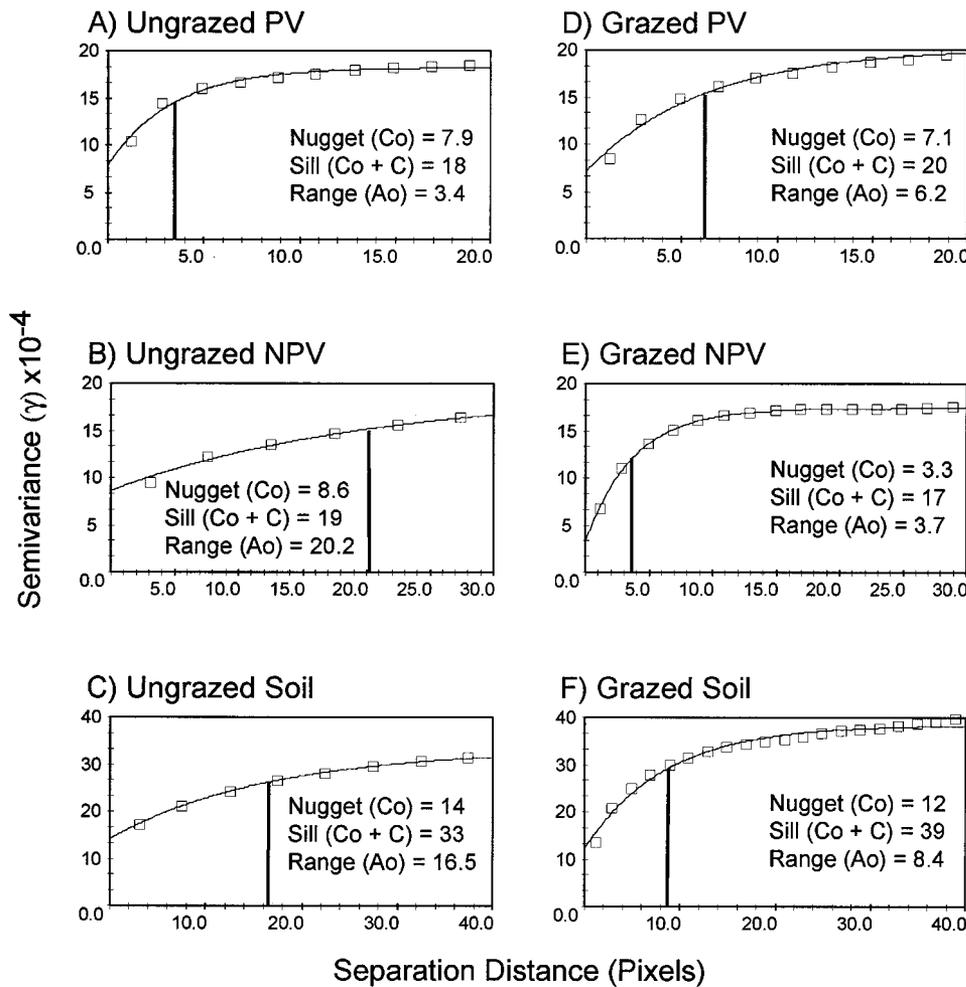
Figure 6. Exponential model isotropic semivariograms generated from ungrazed (**A–C**) and grazed (**D–F**) AutoMCU output polygons: (□), observed; (-), modeled. X-axis dimensions have been adjusted to the shortest maximum lag on plots B, C, and D for visualization purposes. The range statistic is depicted with the vertical black line on each plot.

mesas. However, vegetation structure in an exclosure near No Man's Mesa indicates that native ungulates, such as mule deer, limit rather than facilitate *Artemisia* recruitment (M. E. Miller unpublished). Similar patterns also are found in exclosures located on BLM land in southeastern Utah. These observations suggest that mule deer have had a limited impact on the observed differences between the study areas.

Field Studies

Analysis of field transect data showed no significant difference in percentage composition of trees between the grazed and ungrazed study sites (Table 2). To test whether our transect data suffered from inadequate sampling density, tree cover was investigated by visually counting canopies on panchromatic air photographs. This technique was useful

Table 3. Semivariogram Statistics (Exponential Model) for Photosynthetic Vegetation (PV), Nonphotosynthetic Vegetation (NPV), and Soil Fractional Cover Images from Grazed and Ungrazed Study Regions

Variable	Ungrazed PV	Grazed PV	Ungrazed NPV	Grazed NPV	Ungrazed Soil	Grazed Soil
Nugget (C_o) ((γ) $\times 10^{-4}$)	7.9	7.1	8.6	3.3	14	12
Sill ($C + C_o$) ((γ) $\times 10^{-4}$)	18	20	19	17	33	39
Range (A_o) (pixels)	3.4	6.2	20.2	3.7	16.5	8.4
Range (A_O) (m)	60.3	111.3	361.6	67.0	295.4	150.2
r^2	0.98	0.99	0.99	1.0	1.0	0.98
N:S	0.43	0.35	0.43	0.19	0.42	0.32
Lag class interval (pixels)	2	2	5	2	5	2
Maximum lag (pixels)	20	30	80	30	70	40

N, nugget; S, sill
The range statistic is presented in units of pixels and meters calculated from an average pixel size of 17.9 m on the study mesas.

because individual canopies were distinguishable from surrounding vegetation, allowing an estimate of the number of canopies per hectare. This is distinct from the number of stems or individual trees per hectare because of the way in which pinyon–juniper trees grow: Two or more individuals often grow in close association and share the same canopy volume. Results from the air photo canopy count showed no significant difference between the grazed and ungrazed regions in number of pinyon–juniper canopies (Table 2). These findings are inconsistent with the generally accepted notion that grazing has resulted in greater densities of trees in semiarid pinyon–juniper ecosystems of the American Southwest (Johnsen 1962; Blackburn and Tueller 1970; West 1984).

Figure 7 shows panchromatic aerial photographs of two areas on No Man's and Calf Pasture mesas acquired in 1948 (A and C) and 1993 (B and D) and illustrates the recruitment of pinyon pine and juniper trees into both regions. Results of our air photo analysis suggest that the relative densities of the canopies in the grazed and ungrazed mesas are similar. This finding implies that a process other than managed grazing has led to the recruitment of pinyon and juniper trees into areas where they did not previously exist.

Field data presented in Table 2 show that grasses were significantly more common on the ungrazed mesa (Mann-Whitney rank sum test, $P < 0.001$). This finding is consistent with previous studies comparing grazed and ungrazed rangelands in the southwestern United States. For example, several studies have indicated that ungrazed relict areas support more vegetative cover than grazed areas (Kleiner and Harper 1972; Brotherson and others 1983; Madany and West 1983; Jeffries and Klopatek 1987; Beymer and Klopatek 1992).

Our field data also show that grazed areas support significantly fewer cacti of the genus *Opuntia* than the ungrazed relict mesa (Table 2). In agreement with Kleiner and Harper (1972), we attribute the lower occurrence of cacti on the grazed area to mechanical damage from cattle trampling. Canfield (1948) found that 25 years of protection from grazing increased the fractional ground cover of cacti (*Opuntia* spp.) on an experimental range dominated by grasses and mesquite (*Prosopis* spp.) in southern Arizona.

Our finding that grazed areas have a significantly lower fractional cover of cryptobiotic soil crusts (Table 2) is consistent with reports from other authors showing a lower cover of cryptobiotic soil crusts on grazed than on ungrazed rangelands (Kleiner and Harper 1972; Anderson and others 1982; Brotherson and others 1983; Beymer and Klopatek 1992). Cryptobiotic soil crusts are important for soil stability and resistance to wind and water erosion in arid and semiarid ecosystems (Eldridge and Kinnell 1997; Belnap and Gillette 1998). They also contribute significant biomass to soils (Beymer and Klopatek 1991) and are essential contributors to the nitrogen cycle (Evans and Ehleringer 1993).

Issues with Local Assessments

In their analysis of a sagebrush steppe, Anderson and Inouye (2001) concluded that a large-scale perspective was required to understand vegetation dynamics, arguing that it was not possible to infer trends accurately from one or a few plots. Our remote sensing approach allowed highly accurate analysis of large regions: 23,816 20 $\times$ 20 m "plots" were analyzed for fractional cover of the fundamental ecosystem structural parameters of PV, NPV, and bare soil cover (Figure 4). This approach offers unique insight into ecosystem composition across

A) Ungrazed - 1948
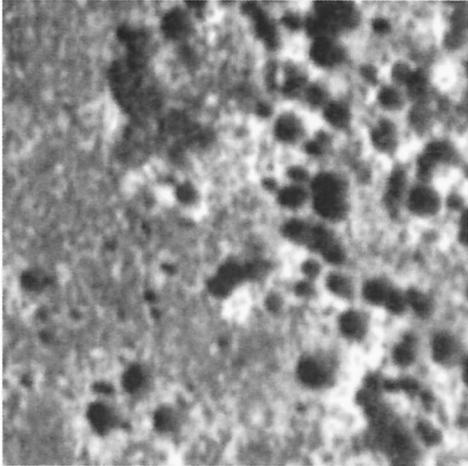
B) Ungrazed - 1993
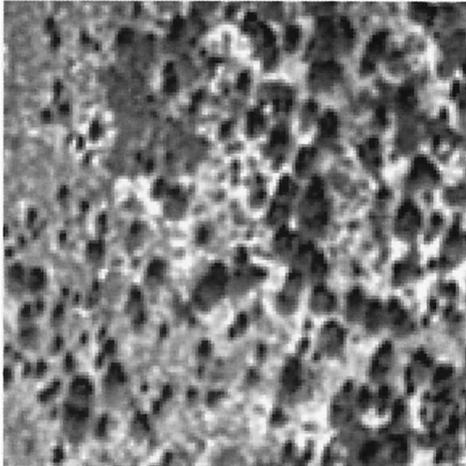
C) Grazed - 1948
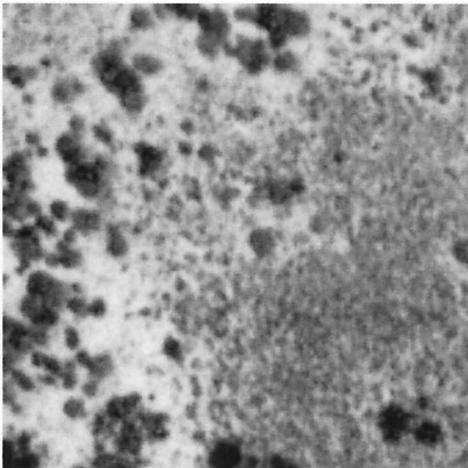
D) Grazed - 1993
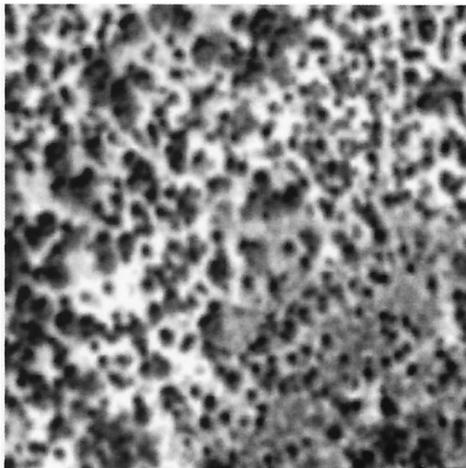
Figure 7. Panchromatic air photographs of identical regions on grazed (Calf Pasture) and ungrazed (No Man's Mesa) mesas acquired in 1948 (**A** and **C**) and 1993 (**B** and **D**).

substantial geographic regions. However, the processes responsible for observed large-scale structural differences between grazed and ungrazed mesas occur at scales smaller than the size of a typical remotely sensed pixel; thus, they can be better understood via field investigation. By combining large-scale hyperspectral remote sensing observations with fine-scale field observations, we can realize the greatest utility of both approaches.

Imaging spectroscopy indicated that significantly higher fractional PV cover occurred on the grazed relative to the ungrazed mesas (Figure 5). We used an array of scale-dependent results to interpret this finding. At the time of spectroscopic imaging in late June 2000, herbaceous cover was senescent due to normal phenological patterns (A. T. Harris and G. P. Asner personal observation). The PV cover fraction was therefore comprised almost exclusively of shrub and tree canopy foliage, while senescent grasses were spectrally identified as NPV. Aerial photography showed that there was no significant difference in the density of tree crowns between grazed and ungrazed mesas, yet field data showed that there was a significant difference in percent composition of shrubs (Table 2). Additionally, field data showed that grasses were significantly less abundant on the grazed transects (Table 2), suggesting that herbaceous vegetation was not contributing to the observed higher concentration of PV on the grazed region. Combining these separate lines of evidence, we conclude that greater PV fractional cover on grazed mesas can best be attributed to historical increases in shrub percentage composition. These results are supported by Kleiner and Harper (1972), who found that several species of shrubs increased in abundance on grazed rangeland relative to a protected relict area, and by Schmutz and others (1967), who found that sagebrush (*Artemisia* sp.) made up 82% and 37% of the vegetation cover on grazed and relict study areas, respectively.

NPV is an important component of ecosystem function, contributing nutrients to soils via decay and their influence on water interception, infiltration, and retention (Boeken and Orenstein 2001). NPV cover was significantly lower on grazed areas (Figure 5). The NPV component included senescent grasses, forbs, and leaf litter, in addition to woody debris such as logs and stumps. Bark and exposed wood within canopies also contributed to the overall NPV signal. Previous studies have shown that relationships between grazing and NPV differ for grazed, ungrazed rangelands. Jones (2000) analyzed 54 studies conducted in the western United States for the effects of grazing on a host of ecosystem response variables, including NPV cover. She found a significant statistical difference then ($P = 0.046$) between the fractional cover of NPV on grazed and ungrazed sites. In studies specific to the arid US Southwest, there is also a consistent relationship between grazing intensity and surface litter. When Gamougoun and others (1984) studied surface litter under a variety of grazing treatments, they found a statistically significant decrease in litter under moderate and rested rotation grazing treatments. Beymer and Klopatek (1992) showed a 5% increase in surface litter between a heavily grazed pasture and a ungrazed relict area; and Johansen and St. Clair (1986) and Pieper (1968) found that surface litter decreases with grazing.

We attribute the decreases in NPV throughout the grazed mesas (Figure 5) to consumption by domesticated grazers over short- and long-term scales. We consider a significant portion of the NPV signal to be composed of grasses. This view is consistent with the field data, which showed a significant decrease in grasses between grazed and ungrazed mesas (Table 2). Interestingly, analysis of field-based fractional NPV cover showed no significant difference between grazing treatments (Table 1). This result underscores the importance of the detailed landscape-scale perspective provided by airborne imaging spectroscopy. Whereas an entirely field-based study might not have detected NPV differences between the study areas, imaging spectroscopy provided the geographic scale and spectral resolution necessary to detect subtle but clear and significant differences.

We recognize that observed differences in NPV between out study regions could be due to the short-term effects of grazing at Deer Springs Point. Deer Springs Point is a summer pasture that is generally grazed from the beginning of June until mid-October. At the time of the vegetation survey, during the first week of August 2001, cattle had been actively grazing the pasture for 2 months. Observed differences in numbers of grasses and forbs between No Man's Mesa and Deer Springs Point may be only temporary and not symptomatic of long-term changes in community composition.

Our local-scale results show that bare soil cover was significantly lower in the grazed region (Table 1 and Figure 5). Changes in bare soil cover correspond and are opposite in sign to changes in fractional PV cover. This result is contrary to studies by Johansen and St. Clair (1986) and Beymer and Klopatek (1992), which found a significantly higher percentage of bare soil cover in grazed areas. However, these researchers were primarily interested in quantifying the effects of grazing on the fractional cover of cryptobiotic soil crusts; thus, they assigned soil surfaces covered with crusts to a separate fractional cover category. Our study made no such distinction, due to the difficulty of separating bare soil from senescent biological soil crusts in remotely sensed data. When the fractional cover values reported by Johansen and St. Clair (1986) and Beymer and Klopatek (1992) for bare soil and cryptobiotic soil crusts are combined, they show only slightly higher bare soil on grazed sites.

We suggest that the higher fractional PV cover on the grazed study region is responsible for the lower observed bare soil cover fraction relative to the ungrazed mesa. Moreover, we hypothesize that the process responsible for the observed differences between grazed and ungrazed mesas in the fractional cover of PV, NPV, and bare soil is the increased survival of shrub seedlings, which, in turn, is due to reduced fire frequencies and decreased competition from grasses. These two phenomena are caused by the removal of grasses from the understory due to grazing. Further investigation is needed to test this hypothesis.

Geostatistical Analysis of Surface Cover

Traditionally, geostatistical analysis has taken strong spatial dependence between variables as an analogue for spatial heterogeneity and, conversely, spatial independence as an analogue for homogeneity. For example, Schlesinger and others (1996) and Schlesinger and Pilmanis (1998) cited spatial autocorrelation of measured nutrients beneath shrub canopies as evidence for greater soil resource heterogeneity in shrublands. In this study, we were primarily interested in the "range" of the observed spatial autocorrelation as an indicator of structural homogeneity. We therefore treated spatially autocorrelated lags up to the range as having a homogeneous spatial structure. For example, as shown in Figure 6 and Table 3, PV on the grazed mesas was spatially autocorrelated to a range almost twice that

of PV on the ungrazed mesa (111.3 versus 60.3 m, respectively). We interpreted this finding as evidence that PV homogeneity occurs to a longer maximum lag on the grazed mesas, and that this results from increased shrub cover. The difference in the percentage cover of shrubs (Table 2) could be responsible for this observed-modeled difference by decreasing local, fine-scale variability through the process of filling spaces on the landscape that had formerly been occupied by bare soil. This interpretation is supported by the finding of lower subpixel variability on the grazed mesa, as indicated by a lower N:S ratio of 35% versus 43% for the ungrazed mesa (Table 3).

Range statistic measurements of spatial autocorrelation distance for NPV showed the greatest differences of all fractional cover measurements. We interpret the result that NPV was spatially dependent at shorter distances on the grazed mesa (67.0 versus 361.6 m) (Table 3) as an indication that grazing pressure has decreased NPV homogeneity at landscape to regional scales. We believe that this effect is due to the consumption of forage by cattle on the grazed mesa. This idea is supported by our finding of a significantly lower percentage composition of grasses on Deer Springs Point mesa (Table 2). Additionally, the N:S ratio for the grazed mesas was lower than that for the ungrazed mesa (19% and 43%, respectively), indicating lower subpixel, spatially dependent variability of NPV. We contend that the decrease in the percentage composition of grasses, coupled with an increase in the numbers of shrubs on the grazed mesas, has increased the spatial heterogeneity of NPV across the region.

Bare soil was spatially autocorrelated to 150.2 m on the grazed mesas and 295.4 m on the ungrazed mesa. Bare soil also exhibited lower subpixel variation (N:S ratio of 32% versus 42%) on the grazed mesa. Coupled with the finding that bare soil was significantly less abundant on the grazed mesa (Figure 5 and Table 1), we conclude that an increase in the number of shrubs in the landscape has reduced the amount of exposed bare soil. At the subpixel scale, this same process of woody thickening has resulted in lower variability of the bare soil cover fraction.

The three remotely sensed cover fractions are not independent of one another at any scale. At the pixel scale, all cover fractions sum to unity; a change in one cover fraction necessarily results in changes in one or both of the others. At the landscape scale, cover fraction dependence is demonstrated by directional changes in semivariance range values relative to regional median cover values. For example, a higher maximum range statistic

for PV on the grazed mesa (as illustrated by the calculated semivariogram) tracked a higher median PV value for the grazed relative to the ungrazed mesa. Similar patterns were seen for the other two surface cover classes.

Geostatistical analyses add to our understanding of the problem of woody thickening due to grazing. Absolute median differences in cover fractions between grazed and ungrazed mesas, while significant, may not prove the existence of large relative differences. However, when analyzed with geostatistical methods, we found major differences in spatial variability of cover fractions. This trend is especially striking in the analysis of regional NPV: median values were significantly different between mesas, but they were nonetheless rather similar. Geostatistical analysis revealed that NPV cover on the ungrazed mesa was spatially autocorrelated to a distance almost four times that of the grazed mesa, indicating significant differences between the study areas in ecosystem structure.

In sum, our findings highlighted significant differences in several biophysical and structural attributes of the mesas that have undergone long-term grazing while the relict mesa has been almost completely protected. What do the observed differences in vegetation structure indicate about the functioning of pinyon–juniper ecosystems? There is widespread recognition that arid and semiarid ecosystem function is closely linked to vegetation structure (Belsky and others 1989; Breshears and Barnes 1999; Schlesinger and others 1990). In systems with a large woody vegetation component, the spatial organization of tree canopies and interspaces mediates nutrient cycling (Barth 1980; Klopatek and Klopatek 1986; Schlesinger and others 1996), energy balance (Belsky and others 1989; Breshears and others 1998; Martens and others 2000), erosion rates (Leopold 1924; Wilcox 1994; Davenport and others 1998; Reid and others 1999), local hydrology (Breshears and others 1997; Malek and others 1997), and trace gas exchange with the atmosphere (Hartley and Schlesinger 2000). Changes in ecosystem structure therefore affect these processes and have implications for sustainable rangeland and fire management, soil conservation, regional biogeochemistry, and hydrology. In the specific case presented here, the economic viability of ranching may be reduced over the long term by decreases in range quality brought about by woody thickening and encroachment. The findings presented here indicate that this study needs to be extended over a much larger area of southern Utah and beyond to assess the long-term effects of grazing in pinyon–juniper ecosystems.

CONCLUSIONS

We used an automatic Monte Carlo spectral unmixing technique with airborne imaging spectroscopy data to investigate differences in pinyon–juniper ecosystems on grazed and ungrazed mesas in southern Utah. Integration of fine-scale field observations with regional-scale remote sensing proved useful for interpretation of ecosystem structural variation.

Spectral mixture analysis (AutoMCU) revealed significantly higher PV, lower NPV, and lower bare soil fractional cover on the grazed than on the ungrazed mesas. Field measurements subsequently confirmed the accuracy of the AutoMCU results. Field investigation of vascular plant composition by lifeform also showed that there were significantly fewer grasses and cacti and more forbs and shrubs on the grazed than on the ungrazed areas. Moreover, aerial photographic analyses showed no significant difference in the numbers of tree canopies per hectare between the grazed and ungrazed mesas—a result that contrasts with other studies that found increases in the numbers and density of pinyon and juniper trees in these systems (Johnsen 1962; Blackburn and Tueller 1970; West 1984). Our findings thus raise the question of whether the increase in pinyon pine and juniper recruitment can be attributed solely to managed grazing.

Geostatistical analysis was used to determine the effects of grazing on the spatial variability of surface cover fractions. We found that the fractional cover of PV on the grazed mesa was more homogeneous, whereas the cover fractions of NPV and bare soil were more heterogeneous. These analyses also revealed that there were substantial differences between the study mesas in the spatial variability of cover fractions, a conclusion that could not have been reached using only parametric statistics.

The higher fractional cover of PV on the grazed mesas was interpreted as the result of the woody thickening of shrubs into regions formerly occupied by bare soil. This change has increased the spatial homogeneity of PV on the grazed mesas in conjunction with decreased herbaceous cover due to consumption, and it has also increased the heterogeneity of NPV and bare soil.

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REFERENCES

Anderson DC, Harper KT, Holmgren RC. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. J Range Manag 35(2):180–5.

Anderson JE, Inouye RS. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol Monogr 71(4):531–56.

Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2?. Clim Change 29:91–9.

Archer SR, Scifres C, Bassham C, Maggio R. 1988. Autogenic succession in a subtropical savanna: rates, dynamics and processes in the conversion of grassland to thorn woodland. Ecol Monogr 58:111–27.

Asner GP, Heidebrecht KB. 2002. Spectral unmixing of vegetation, soil and dry carbon cover in arid regions: comparing multi-spectral and hyperspectral observations. Int J Remote Sensing. 23,19:3939–3950.

Asner GP, Lobell DB. 2000. A biogeophysical approach for automated SWIR unmixing of soils and vegetation. Remote Sens Environ 74:99–112.

Asner GP, Wessman CA, Bateson CA, Privette JL. 2000. Impact of tissue, canopy, and landscape factors on the hyperspectral reflectance variability of arid ecosystems. Remote Sens Environ 74:69–84.

Banin A, Ben-dor E, Kruse FA. 1994. Comparison of three calibration techniques for utilization of GER 63-channel aircraft scanner data of Makhtesh Ramon, Negev, Israel. Photogram Eng Remote Sens 60:1339–46.

Barth RC. 1980. Influence of pinyon pine trees on soil chemical and physical properties. Soil Sci Soci Am J 44:112–4.

Bastin GN, Sparrow AD, Pearce G. 1993. Grazing gradients in central Australian rangelands: ground verification of remote sensing-based approaches. Rangeland J 15(2):217–33.

Bateson CA, Asner GP, Wessman CA. 2000. Endmember bundles: a new approach to incorporating endmember variability into spectral mixture analysis. IEEE Trans Geosc Remote Sen 38(2):1083–94.

Belnap J, Gillette DA. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. J Arid Environ 39:133–42.

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J Appl Ecol 26:1005–24.

Beymer RJ, Klopatek JM. 1991. Potential contribution of carbon by microphytic crusts in pinyon–juniper woodlands. Arid Soil Res Rehabil 5:187–98.

Beymer RJ, Klopatek JM. 1992. Effects of grazing on cryptogamic crusts in pinyon–juniper woodlands in Grand Canyon National Park. Am Midl Nat 127:139–48.

Blackburn WH, Tueller PT. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51(5):841–8.

Boeken B, Orenstein D. 2001. The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. J Veget Sci 12(6):825–32.

Bond WJ, Midgley GF. 2000. A proposed CO_2-controlled mech-

anism of woody plant invasion in grasslands and savannas. Global Change Biol 6:865–9.

Brady WW, Stromberg MR, Aldon EF, Bonham CD, Henry SH. 1989. Response of a semiarid grassland to 16 years of rest from grazing. J Range Manag 42(4):284–8.

Breshears DD, Barnes FJ. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecol 14:465–78.

Breshears DD, Nyhan JW, Heil CE, Wilcox BP. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int J Plant Sci 159(6):1010–7.

Breshears DD, Rich PM, Barnes FJ, Campbell K. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol Appl 7(4):1201–15.

Brotherson JD, Rushforth SR, Johansen JR. 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument, Ariz. J Range Manag 36(5):579–81.

Burkhardt JW, Tisdale EW. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472–84.

Canfield RH. 1941. Application of the line intercept method in sampling range vegetation. J For 39:388–94.

Canfield RH. 1948. Perennial grass composition as an indicator of condition of southwestern mixed grass ranges. Ecology 29(2):190–204.

Chambers JC, Vander Wall SB, Schupp EW. 1999. Seed and seedling ecology of pinyon and juniper species in the pygmy woodlands of western North America. Bot Rev 65(1):1–38.

Cole KL, Henderson N, Shafer DS. 1997. Holocene vegetation and historic grazing impacts at Capital Reef National Park reconstructed using packrat middens. Great Basin Nat 57(4): 315–26.

Connin S, Virginia RA, Chamberlain CP. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. Oecologia 110:374–86.

Curran PJ. 1988. The semivariogram in remote sensing: an introduction. Remote Sensing Environ 24:493–507.

Davenport DW, Breshears DD, Wilcox BP, Allen CD. 1998. Viewpoint: sustainability of pinyon–juniper ecosystems—a unifying perspective of soil erosion thresholds. J Range Manag 51:231–40.

Eldridge D, Kinnell PIA. 1997. Assessment of erosion rates from microphyte-dominated calcareous soils under rain-impacted flow. Aus J Soil Res 35:475–89.

Evans RD, Ehleringer JR. 1993. A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}N$ of soils. Oecologia 94:314–7.

Floyd ML, Romme WH, Hanna DD. 2000. Fire history and vegetation pattern in Mesa Verde National Park, Colorado, USA. Ecol App 10(6):1666–80.

Gamougoun ND, Smith RP, Wood MK, Pieper RD. 1984. Soil, vegetation, and hydrologic responses to grazing management at Fort Stanton, New Mexico. J Range Manag 37(6):538–41.

Gao B, Heidebrecht KB, Goetz AFH. 1993. Derivation of scaled surface reflectance from AVIRIS data. Remote Sens Environ 44:165–78.

Green RO, Eastwood ML, Sarture CM, Chrien TG, Aronsson M, Chippendale JA, Pavri BE, Chovit CJ, Solis M, Olah MR, and others. 1998. Imaging spectroscopy and the Airborne Visible/ Infrared Imaging Spectrometer (AVIRIS). Remote Sens Environ **65**:227–48.

Hartley AE, Schlesinger WH. 2000. Experimental controls on nitric oxide emission from northern Chihuahuan desert soils. Biogeochemistry 50:279–300.

Isdo SB. 1992. Shrubland expansion in the American Southwest. Clim Change 22:85–6.

Jameson DA. 1962. Effects of burning on a galleta-black grama range invaded by juniper. Ecology 43(4):760–3.

Jeffries DL, Klopatek JM. 1987. Effects of grazing on the vegetation of the blackbrush association. J Range Manag 40:390–2.

Johansen JR, St. Clair LL. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. Great Basin Nat 46(4):632–40.

Johnsen TN. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecol Monogr 32(3):187–207.

Jones A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. West North Am Nat 60(2): 155–64.

Karl MG, Doescher PS. 1993. Regulating competition on conifer plantations with prescribed cattle grazing. For Sci 39(3):405–18.

Kleiner EF, Harper KT. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecology 53(2):299–309.

Klopatek CC, Klopatek JM. 1986. Mycorrhizae, microbes and nutrient cycling processes in pinyon–juniper systems. General Technical Report **INT-215:**Reno (NV): USDA Forest Service, Pinyon–Juniper Conference. p 360–4.

Leopold A. 1924. Grass, brush, timber, and fire in southern Arizona. J For 22:2–10.

Madany MH, West NE. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64(4):661–7.

Malek E, Bingham GE, Or D, McCurdy G. 1997. Annual mesoscale study of water balance in a Great Basin heterogeneous desert valley. J Hydrol 191:223–44.

Martens SN, Breshears DD, Meyer CW. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecol Model 126:79–93.

Mason LR, Andrew HM, Carley JA, Haacke ED. 1967. Vegetation and soils of No Man's Land Mesa relict area, Utah. Journal Range Manag 20(1):45–9.

Miller RF, Wigand PE. 1994. Holocene changes in semiarid pinyon–juniper woodlands: response to climate, fire, and human activities in the U.S. Great Basin. BioScience 44:465–74.

Pickup G, Bastin GN, Chewings VH. 1998. Identifying trends in land degradation in non-equilibrium rangelands. J Appl Ecol 35:365–77.

Pickup G, Chewings VH. 1994. A grazing gradient approach to land degradation assessment in arid areas from remotely-sensed data. Int J Remote Sens 15(3):597–617.

Pieper RD. 1968. Comparison of vegetation on grazed and ungrazed pinyon–juniper grassland sites in south-central New Mexico. J Range Manag 21:51–3.

Reid KD, Wilcox BP, Breshears DD, MacDonald L. 1999. Runoff and erosion in a pinyon-juniper woodland: influence of vegetation patches. Soil Sci Soc Am J 63(6):1869–79.

Savage M, Swetnam TW. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71(6):2374–8.

Schlesinger WH, Pilmanis AM. 1998. Plant–soil interactions in deserts. Biogeochemistry 42:169–87.

Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77(2):364–74.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science 247:1043–8.

Schmutz EM, Michaels CC, Judd BI. 1967. Boysag Point: a relict area on the North Rim of Grand Canyon in Arizona. J Range Manag 20:363–9.

Scholes RJ, Archer SR. 1997. Tree-grass interactions in savannas. Annu Rev Ecol Syst 28:517–44.

Swetnam TW, Allen CD, Betancourt JL. 1999. Applied historical ecology: using the past to manage for the future. Ecol Appl 9(4):1189–206.

Swetnam TW, Baisan CH. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen CD, editor. Fire effects in southwestern forests. Proceedings of the Second La Mesa Fire Symposium, Los Alamos, NM. General Technical Report **RM-GTR-286.** USDA Forest Service. p 11–32.

Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. J Clim 11:3128–47.

Tausch RJ, West NE, Nabi AA. 1981. Tree age and dominance patterns in Great Basin pinyon–juniper woodlands. J Range Manag 34(4):259–64.

Tueller PT, Beeson CD, Tausch RJ, West NE, Rea KH. 1979. Pinyon–juniper woodlands of the Great Basin: distribution, flora, vegetal cover. Research Paper **INT-229.** Ogden (UT): USDA Forest Service, Intermountain Research Station. p 22.

Wells PV. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecol Monogr 53:341–82.

West NE. 1984. Successional patterns and productivity potentials of pinyon–juniper ecosystems. In: , editor. Developing strategies for rangeland management. Boulder (CO): Westview Press. p 1301–32.

Wilcox BP. 1994. Runoff and erosion in intercanopy zones of pinyon–juniper woodlands. J Range Manag 47:285–95.