Large-scale impacts of herbivores on the structural diversity of African savannas

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Edited by W. G. Ernst, Stanford University, Stanford, CA, and approved January 26, 2009 (received for review October 22, 2008)

African savannas are undergoing management intensification, and decision makers are increasingly challenged to balance the needs of large herbivore populations with the maintenance of vegetation and ecosystem diversity. Ensuring the sustainability of Africa's natural protected areas requires information on the efficacy of management decisions at large spatial scales, but often neither experimental treatments nor large-scale responses are available for analysis. Using a new airborne remote sensing system, we mapped the three-dimensional (3-D) structure of vegetation at a spatial resolution of 56 cm throughout 1640 ha of savanna after 6, 22, 35, and 41-year exclusions of herbivores, as well as in unprotected areas, across Kruger National Park in South Africa. Areas in which herbivores were excluded over the short term (6 years) contained 38%-80% less bare ground than those that were exposed to mammalian herbivory. In the longer-term (>22 years), the 3-D structure of woody vegetation differed significantly between protected and accessible landscapes, with up to 11-fold greater woody canopy cover in the areas without herbivores. Our maps revealed 2 scales of ecosystem response to herbivore consumption, one broadly mediated by geologic substrate and the other mediated by hillslope-scale variation in soil nutrient availability and moisture conditions. Our results are the first to quantitatively illustrate the extent to which herbivores can affect the 3-D structural diversity of vegetation across large savanna landscapes.

The 3-dimensional (3-D) structure of vegetation is central to the functioning of African savannas, providing habitat for a wide variety of plants and animals (1–4). Like many regions of the world, African savannas are under increasing pressure from humans, and thus increased emphasis is being placed on natural protected areas to preserve biological diversity (5, 6). The sustainability of these protected areas rests on the management plans that affect habitat and wildlife communities, yet most management decisions are formulated with relatively little information on the large-scale ecosystem responses to those decisions. Ground-based ecological monitoring of management outcomes usually lacks regional-scale generality, a problem arising from the enormous vertical complexity and spatial heterogeneity of the vegetation. Nowhere is this deficiency more problematic than in African savannas, where topo-edaphic, climatic, and biological conditions vary at multiple scales, resulting in local, landscape, and regional variability in vegetation 3-D structure (7–9).

The Kruger National Park (KNP) is a premier natural protected area for South Africa and the world, with roughly 2,646 plant and animal species protected on about 2 million ha. KNP has undergone distinct phases in its management history, including periods of elephant culling, large-scale water augmentation, and fire manipulation. Management has recently shifted toward strategic adaptive management approaches that aim to maintain biodiversity and vegetation heterogeneity for the inhabitants of the park (10–12). The efficacy of these management actions has been both highly variable and difficult to quantify over the large geographic areas for which they were intended to serve.

Today in particular, the scales and geographic locations at which KNP's large herbivores impact vegetation and ecosystem processes remain highly uncertain. Herbivores are both a major agent of disturbance and a core focus for conservation (13), so altering herbivore populations in an effort to maintain whole-system biodiversity presents a paradox in a highly managed park such as KNP: Too many or too few herbivores can lead to the loss of ecological functioning through alterations in vegetation composition and structure (14–17). Elephant, buffalo, giraffe, zebra, and many other ungulates contribute to the marked structural changes that have been locally observed in different African landscapes (18–24), yet few experimental studies have been undertaken at a geographic scale that can resolve the impact of herbivores on the overall diversity of the landscape.

Four hillslope experiments have restricted animal access to large areas of savanna in KNP, providing a chance to compare vegetation 3-D structure with and without the presence of herbivores. Two enclosures, 220 and 230 ha in size, were constructed 36 and 41 years ago, respectively, for the breeding of rare and endangered antelope. In 1986, the larger enclosure was extended by another 72 ha to incorporate more lowland habitat. While protecting small numbers of rare antelope (0.01–0.1 animals ha⁻¹) from predators, the mesh fencing of these enclosures effectively excludes all other mammalian herbivores larger than hares (±5 kg). These 2 enclosures facilitate a large-scale analysis of vegetation structure on both granite and basalt substrates in areas protected from herbivores over the long term (22–41 years). In 2002, KNP constructed 2 additional 129- and 139-ha fenced areas on granite hillslopes adjacent to the Sabie and Letaba Rivers. Although these enclosures have been in place for only 6 years, they complement the 2 long-term enclosures, providing a way to assess the short-term responses of vegetation structure to herbivore exclusion [see supporting information (SI) Table S1].

These large-scale experimental treatments in KNP provide a highly unique opportunity to address many issues surrounding the impact of herbivores on African savannas, but only if the response measurements can be made at a geographic scale commensurate with the broad movements of the animals being manipulated. We deployed a new airborne remote-sensing system to map the 3-D structure of vegetation across the herbivore enclosures and enclosures, as well as the control areas surrounding


The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0810637106/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.0810637106

PNAS | March 24, 2009 | vol. 106 | no. 12 | 4947–4952
ing and adjacent to the treatments. Our total flight coverage for this study was 790 ha of treatment and 850 ha as a comparable control. The data were collected at a spatial resolution of 56 cm, and our analyses explored differences between herbivore treatment and control areas across both upland and lowland hillslope positions (see SI Materials and Methods). We determined the large-scale responses of vegetation and ecosystem structure to herbivore presence/absence using the following remotely sensed measurements: fractional canopy cover of live and senescent/dead herbaceous vegetation, bare soil extent, vegetation height, and the 3-D vertical profile of the woody canopies. These measurements provide a nearly complete structural inventory as defined in classical savanna ecology (25).

Results and Discussion

The impact of herbivores on vegetation structure varied by topographic position, geologic substrate, and treatment age. The most obvious effects were seen in the long-term treatment sites on basalt substrate (Fig. 1A); other sites were more difficult to assess by visual inspection alone (Fig. 1B–D). However, the collection of many thousands of measurements from the air provided a means to explore statistical differences among treatments and topo-edaphic conditions.

Comparing vegetation height distributions using the Kolmogorov–Smirnov (K-S) test, we found a statistically significant effect of herbivore exclusion in all long-term treatment areas and across both lowland and upland areas ($P < .01$) (Fig. 2). Although herbivores were excluded from the long-term granite and basalt substrate sites for similar periods, the differences between protected and accessible landscapes were of significantly greater magnitude in the basalt sites. This was true for woody height distribution (Fig. 2A) and also for the percentage of woody cover, which was 7- to 11-fold greater inside than outside of the protected areas (Table 1). Although height distributions differed significantly between protected and accessible areas in the long-term granite sites, mean canopy height did not (Table S2). Taken together, these findings indicate that the diversity of vegetation structure, expressed here in terms of the distribution of woody canopy heights, rather than the average structure (e.g., mean height), is the primary ecological response to herbivory. Moreover, the differing responses by geologic substrate indicate the potential importance of soil nutrient availability in determining the response of vegetation to herbivores. Herbivores use the landscape in a patch-specific manner, and their impact is greatest in nutrient-rich areas offering the best-quality forage (26, 27). In this landscape, the clay soils in the basalt substrate areas are rich in nutrients and have greater water-holding capacity than the sandy soils on granite substrates (28, 29), predisposing the basalt areas to greater herbivory, driven by higher-quality forage (28).

The influence of nutrient distribution was also evident at the hillslope scale, where the greatest effects of herbivore exclusion were found in the lowland areas (Table 1). Water and nutrients are locally more abundant in lowland areas, giving rise to better-quality forage compared with the adjacent upland areas (28, 30, 31). This topographic effect is obvious in the lowland basalt substrate treatment habitat, even when protected from herbivores for only half as long as the upland habitat (22 vs. 41 years) (Table S1). The lowland basalt areas demonstrated a major change, from mainly short, stunted woody canopies in the areas accessible to herbivores, to canopies in the 4–5 m range above ground in the protected areas (Fig. 2A).

In contrast to the long-term exclusion sites, the short-term (6-year) sites demonstrated more subtle changes in the distri-
bution of woody vegetation heights (Fig. 2C and D). Total woody canopy cover was greater by an average of 55% in the short-term sites, depending on substrate and topographic position (Table 1). The 6-year-old Letaba exclosure exhibited the most profound changes in the diversity of woody canopy height (Fig. 2D), as well as the greatest difference in woody canopy cover after herbivore exclusion (135%; Table 1). This area is a known hotspot for elephant bulls and entire herds (12), and these exclusion patterns show the major impact of high elephant densities on vegetation height distributions in this landscape.

Our airborne system also provided quantitative measurements of the fractional cover of live photosynthetic vegetation (PV) and dead/senescent nonphotosynthetic vegetation (NPV) among herbaceous plants and their litter, as well as bare soil. Comparisons of the areas protected from and accessible to herbivores showed statistically different fractional cover distributions of the herbaceous layer in upland and lowland areas (P < .01; K-S test) (Fig. S1). In contrast to the woody canopy height distribution results, in which the differences were most pronounced in the long-term treatment areas, some of the...
major differences in the distribution of herbaceous cover were measured in the short-term treatment areas. Moreover, bare soil cover was 38%–80% lower in the areas protected from herbivores (Table 1). The lowland positions contained the highest bare soil fractions in unprotected areas, where herbivores could access an herbaceous layer supported by relatively high nutrient and moisture conditions.

The fractions of NPV and litter were much higher in the areas protected from herbivores. This directly increases fuel load (32), providing a large herbaceous biomass to support hot fires. Over time, the effects of fire on the woody vegetation structure in the protected areas likely will increase significantly as a result of these increased fuel loads. Interestingly, although some research has shown that areas exposed to grazing can experience increased woody establishment and encroachment due to decreased competition with the herbaceous layer and decreased fire intensity (15, 33, 34), we found no evidence of shrub encroachment in the accessible areas. Much debate in savanna ecology has centered on the relative importance of herbivores and fire in shaping vegetation structure (16, 19, 35, 36). Although these 2 key drivers of vegetation dynamics cannot be viewed in isolation from one another, the net effect of herbivore consumption mapped throughout the 4 large savanna areas is lower woody canopy cover and height, not woody encroachment.

Our results suggest at least 2 scales of ecosystem response to herbivore consumption, one broadly mediated by geologic substrate and the other mediated by hillslope-scale variation in soil nutrient availability and moisture conditions. Despite these scale-dependent mediators of herbivore impact, combining our data across all sites revealed that herbivore exclusion universally increased the height of woody canopies (Fig. 3A). The greatest absolute increases were observed in vegetation ranging from 1 to 5 m in height, although relative differences were greatest among taller trees. Independent of substrate, topographic position, or treatment age, there was also a universal increase in woody canopy cover after herbivore exclusion (Fig. 3B); relative increases ranged from 50% to 800%, depending on vegetation height class. Thus, although herbivores are often considered to be locally selective in their foraging strategies, their impacts on the 3-D structure and diversity of vegetation are clearly evident at much broader scales.

Our findings concur in part with those of Pringle et al. (37), who reported a greater impact of herbivores on vegetation in low-productivity areas. Plant productivity is driven primarily by rainfall in savanna systems (25, 38–40); we found greater differences in vegetation structure at the long-term basalt site, which receives ≈30% less rainfall than the long-term granite site that had the least

### Table 1. Total percentage cover of woody canopies, live and dead/senescent herbaceous canopies, and bare soil across the four treatments in both lowland and upland landscape positions in KNP

<table>
<thead>
<tr>
<th>Site</th>
<th>Woody cover (%)</th>
<th>Live herbaceous canopy (%)</th>
<th>Dead/senescent herbaceous canopy (%)</th>
<th>Bare soil (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lowland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nwashitsumbe</td>
<td>15.6</td>
<td>32.4</td>
<td>56.7</td>
<td>10.9</td>
</tr>
<tr>
<td>Long-term granite</td>
<td>12.7</td>
<td>26.7</td>
<td>69.8</td>
<td>3.6</td>
</tr>
<tr>
<td>Lowland</td>
<td>25.5</td>
<td>39.3</td>
<td>60.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Hiangwini</td>
<td>12.7</td>
<td>42.2</td>
<td>57.3</td>
<td>0.4</td>
</tr>
<tr>
<td>Short-term granite</td>
<td>26.9</td>
<td>25.1</td>
<td>67.7</td>
<td>7.1</td>
</tr>
<tr>
<td>Lowland</td>
<td>10.0</td>
<td>22.7</td>
<td>69.6</td>
<td>6.8</td>
</tr>
<tr>
<td>Short-term granite</td>
<td>48.4</td>
<td>33.9</td>
<td>60.0</td>
<td>6.1</td>
</tr>
<tr>
<td>Lowland</td>
<td>18.2</td>
<td>29.6</td>
<td>65.2</td>
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<tr>
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<td>12.7</td>
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<tr>
<td>Lowland</td>
<td>18.2</td>
<td>29.6</td>
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<tr>
<td>Lowland</td>
<td>22.3</td>
<td>32.1</td>
<td>64.3</td>
<td>3.6</td>
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<tr>
<td>Lowland</td>
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<td>30.0</td>
<td>65.2</td>
<td>4.8</td>
</tr>
<tr>
<td>Total</td>
<td>15.6</td>
<td>32.4</td>
<td>56.7</td>
<td>10.9</td>
</tr>
<tr>
<td>Accessible to herbivores</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Lowland</td>
<td>1.4</td>
<td>26.4</td>
<td>64.2</td>
<td>9.3</td>
</tr>
<tr>
<td>Lowland</td>
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<td>53.1</td>
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<td>Lowland</td>
<td>5.8</td>
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<td>Lowland</td>
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<td>63.5</td>
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<td>Lowland</td>
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<td>Lowland</td>
<td>13.2</td>
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<td>53.1</td>
<td>17.9</td>
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<tr>
<td>Lowland</td>
<td>11.8</td>
<td>30.3</td>
<td>55.6</td>
<td>14.1</td>
</tr>
</tbody>
</table>

*Protected* and *accessible* indicate portions of the landscape without and with herbivore activity, respectively. Woody canopy cover values are the mean percentage cover of vegetation > 1 m tall, as defined through airborne laser point cloud classification. Other values are the fractional contribution of live herbaceous, dead or senescent herbaceous, and bare soil cover, as defined from the spectral mixture analysis of hyperspectral imagery (see SI Materials and Methods).

*Fig. 3.* Large-scale effects of herbivores on vegetation 3-D structure and structural diversity. (A) Frequency histograms of vegetation canopy height derived from 1640 ha (56-cm resolution) of airborne LiDAR observations showing significant differences between protected and accessible areas (*P* < .01; K-S test). (B) Height class-specific differences between protected and accessible areas.
structural differences. Similarly, of the 2 granite sites, the Letaba is drier than the Nkulu (Table S1) and exhibited a greater structural response to herbivore exclusion. Our findings thus support the trend toward greater herbivore impact in areas of low rainfall and/or productivity, yet these high-impact areas are where substrate nutrient availability is highest (28). Moreover, our findings at the hillslope scale contradict the highimpact-low-productivity pattern reported by Pringle et al. (37), because the greatest impact of herbivores was apparent in the productive lowlands, where water and nutrient availability is high. Thus, we posit that the impact of herbivores on vegetation structure is most strongly mediated by the distribution of nutrients on the landscape at different scales, rather than by rainfall or productivity.

Conclusion

Herbivores are key agents of vegetation change in savannas, but their impact ranges from subtle to obvious at any given locale and is very challenging to measure at the landscape level because of the great vegetation structural heterogeneity of these areas. Like many natural protected areas, KNP is mandated to maintain biodiversity in all its facets and fluxes (11). Biodiversity in this sense encompasses 3 core components: composition, structure, and function (41). We combined a unique airborne mapping system with the KNP large-scale herbivore treatment areas to quantify the effects of herbivore exclusion on 3-D vegetation structure, one of the 3 core components of biodiversity.

In the short term (6 years), the effects of herbivore exclusion appear as greater herbaceous cover, with a few measurable differences in the 3-D structure of woody plants, particularly in lowland, nutrient-rich areas. In the longer term (22–41 years), however, herbivore exclusion manifests at a much larger scale, with both upland and lowland areas experiencing increased woody canopy cover and 3-D structural diversity. These differences in turn affect the diversity and richness of animal species, as well as the ecological functioning of these systems. Greater canopy structural diversity enhances the habitat available for a wide range of organisms beyond the herbivore communities (2, 3, 37, 42) and alters such ecological processes as nutrient cycling, seed dispersal, and germination (2, 4, 43, 44). Our findings highlight the trade-offs that managers must grapple with when attempting to sustain biodiversity among plant and vertebrate communities.

In both the long- and short-term treatment areas, the effects of herbivore exclusion on vegetation structure were greatest in loca-

Supporting Information

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SI Materials and Methods

Remote-Sensing System. Large-scale analysis of forest 3-D structure and biological composition requires a combination of advanced airborne imaging technologies that simultaneously resolve the horizontal and vertical characteristics of the vegetation, as well as the type of vegetation. No airborne (or space-based) technologies were available to make these simultaneous measurements, so we developed the CAO, a new system designed specifically for mapping the biochemical, taxonomic, and structural properties of vegetation and ecosystems (http://cao.stanford.edu) (1). The CAO combines 3 major instrument subsystems—HiFIS, waveform LiDAR scanner, and global positioning system—inertial measuring unit (GPS-IMU)—into a single airborne package.

The CAO HiFIS subsystem provides spectroscopic images of the land surface. The CAO-Alpha configuration uses a pushbroom imaging array with 1500 cross-track pixels, with sampling done across the 367–1058 nm range at a spectral resolution of up to 2.4 nm. The spectrometer subsystem is fully integrated with a waveform LiDAR subsystem with an adjustable laser pulse repetition rate of up to 100 kHz (1). The GPS-IMU subsystem provides 3-D positioning and attitude data for the sensor package on board the aircraft, allowing for highly precise and accurate projection of HiFIS and LiDAR observations on the ground (1). The CAO-Alpha configuration provides coaligned HiFIS and LiDAR data at a spatial resolution of 0.4–1.0 m, depending on the aircraft’s altitude above the ground.

Airborne Data Collection. In April–May 2008, we operated the CAO-Alpha system over KNP. The CAO-Alpha data were collected at 1,000 m above ground level, providing combined HiFIS and LiDAR measurements at a spatial resolution of 56 cm. All flights were conducted within 2.5 h of solar noon. For this study, the airborne data were collected over 790 ha of herbivore enclosure-exclosure areas and an additional 850 ha of surrounding savanna region.

Data Processing and Analysis. Fusion of the imaging spectroscopy and LiDAR data requires a processing stream that maximizes the sharing of information between data products. Given the enormous data volumes involved, the processing stream must be highly automated. Fig. S2 shows the processing stream for this study, in which raw spectral, laser, and trajectory data are integrated and analyzed in a series of higher-order products and results. The following sections briefly describe the major steps in the process.

Aircraft Positioning. The CAO uses in-flight and postflight data integration approaches to precisely match HiFIS and LiDAR data in 3-D space. The in-flight step is achieved by providing a common mount with measured offsets between instrument optical centers, as well as time-stamping of spectral and LiDAR data collection streams with shared position and trajectory data. The LiDAR has a custom-designed laser beam divergence to precisely match the field of view of the CAO-Alpha spectrometer. The GPS-IMU data provide the common link for the detailed ray-tracing of the photons between aircraft sensors and the ground. The point-for-point alignment of the LiDAR and HiFIS data are complicated by inherent differences in the scanning geometries of the 2 systems and further distortions of the ground sampling grid due to topography. Our approach is to recover the best estimates for each pixel center location in 3 dimensions for both the LiDAR and HiFIS data (1), then use these pixel centers to render the 2 data sets into a single, integrated grid of HiFIS and LiDAR data for subsequent processing, analysis, and product generation.

LiDAR Data Processing. The GPS-IMU data are combined with the laser ranging data to determine the 3-D location of the laser returns. From the laser “point cloud” data, a physical model is used to estimate top-of-canopy and ground surfaces [digital elevation models (DEMs)], using the REALM (Optech) and Terrascan/Terramatch (Terrasolid) software packages. Vegetation height is then estimated by differentiating the top-of-canopy and ground surface DEMs (2, 3).

HiFIS Data Processing. The HiFIS data are converted to at-sensor radiances by applying radiometric corrections developed during sensor calibration in the laboratory. Apparent surface reflectance is then derived from the radiance data using an automated atmospheric correction model (ACORN SLIBatch; Imspec). Inputs to the atmospheric correction algorithm include ground elevation (from the LiDAR), aircraft altitude (from GPS-IMU), solar and viewing geometry, atmosphere type (e.g., tropical), and estimated visibility (in km). The code uses a MODTRAN look-up table to correct for Rayleigh scattering and aerosols. Water vapor is estimated directly from the 940-nm water vapor feature in the radiance data.

Once the HiFIS and LiDAR data have been prepared, the spectral images are masked based on illumination conditions between the sensors and canopies (Fig. S2). The LiDAR and GPS-IMU data provide 3-D maps of precise illumination conditions on each canopy, allowing for the automatic identification and masking of shaded portions of the vegetation.

The masked HiFIS images are passed to an automated spectral mixture analysis model, AutoMCU (4). This algorithm uses spectroscopic signatures to quantify the fractional cover of PV, NPV, and bare substrate within each image pixel, and Monte Carlo unmixing to derive mean estimates of fractional cover along with standard deviation and root mean squared error data on a per-pixel basis.

Landscape Stratification. Savanna landscapes are heterogeneous systems in both space and time (5, 6), so careful consideration must be given to landscape stratification for analysis purposes. Catenal development (7), whereby soil and vegetation associations vary down slope, is evident throughout much of KNP (8). The distinction between the nutrient-poor sandy soils of the upland positions and the more nutrient-rich clay soils of the lowland positions provides an ecologically meaningful basis upon which to dissect the landscape.

High-resolution (56 cm) DEMs, derived from the LiDAR data, were used in conjunction with available soil maps (KNP GIS database; http://www.sanparks.org/parks/kruger/conervation/scientific/gis/gisrsdataview.php) to delineate upland and lowland patch types at each site in both protected and accessible areas. From within each of these patches, the most comparable areas of similar size were selected based on topography. Comparisons between the herbivore exclusion treatments and the accessible areas at each site were conducted on a patch-specific basis.

At Nkuhlu and Letaba, 2 different enclosure types are present: full enclosure, consisting of mesh fencing that excludes all herbivores larger than hares, and partial enclosure, consisting of 2 strands of wire that exclude only elephants and giraffes. For the purposes of this analysis, only the full enclosures were sampled with their respective accessible areas, because these are more
similar to the design of the longer-term sites, where mesh fencing is also used.

Whereas both of the long-term sites are burned in conjunction with the KNP fire management policy, fire is excluded from half of the treatment area at the short-term sites, with the other half is allowed to burn under natural conditions. Since its establishment, no fires have occurred at the Letaba site, but the southern portion of the full exclosure at Nkuhlu was burned in 2007. We sampled only the nonburned areas in our analysis, to remove fire as a covariate.

**Statistical Analysis.** After identifying the most suitable areas for our comparisons, we further subsampled them (66% of the smallest region of interest), to dampen the potential influences of spatial autocorrelation. This procedure resulted in the random sampling of 27,000 pixels (summing to 8,467 m²) in both upland and lowland hillslope positions, with and without herbivores at each of the 4 sites. Statistical differences in vegetation 3-D structure and fractional cover were determined using the K-S test. This nonparametric test is well suited to such analyses, because it is sensitive to differences in both the location and shape of the empirical cumulative distribution functions (9). We also pooled data from different areas to evaluate the general effects of herbivore presence/absence independent of substrate. Comparisons of means for protected and unprotected areas were conducted using standard r tests. We considered this approach to be robust because of the near-normal nature of the data and the large sample size.

**Field Validation of Airborne Vegetation Heights and Fractional Cover.** LiDAR-derived vegetation height from the CAO was validated in forested settings in previous work (10), but had yet to be evaluated in a semiarid savanna system. Thus, we carried out a field campaign to assess the accuracy of the vegetation height estimates in KNP. We collected 350 randomly selected field points for woody canopies ranging in height from 1 to 16 m and including a wide range of the common plant species found throughout the park. The data were collected with an extendable, graduated range pole or a handheld laser range finder (Impulse200; Laser Technologies). The geographic coordinate of each point was logged on a survey-grade GPS receiver (GeoXT; Trimble) and later differentially corrected to submeter accuracy using a local GPS base station (http://www.trignet.co.za/). The individual tree crowns of the field-measured trees were digitized as polygons in the LiDAR-derived canopy height model. The maximum canopy height for each polygon was then calculated and regressed against the field data for that particular tree. Linear regression indicated a strong positive relationship between field-measured and remotely sensed vegetation height (Fig. 53), with $r^2 = 0.92$, $P < .01$, and a standard error of the estimate of 1.17 m.

Fractional canopy cover mapping methods have been heavily validated in previous studies across a range of arid to humid ecosystems (4, 11–13); however, the imaging sensors used in those studies covered a broader range of the solar-reflected spectrum that incorporated the shortwave infrared (SWIR: 1300–2500 nm). Because the CAO HiFIS system does not extend past 1064 nm, we measured fractional cover in the field to validate the AutoMCU results in the absence of SWIR. We sampled 7 field transects ~1 km in length. Fractional cover was visually classified as PV, NPV, or bare ground on a patch-by-patch basis (11). The locations of the leading and trailing edges of each patch were recorded with the GPS, and the points were later differentially corrected to submeter accuracy for comparison against the outputs from AutoMCU. We used a simple classification accuracy technique in which lateral cover estimates from spectral unmixing were considered to be correct for each patch when the field declaration matched the spectral unmixing classification. Despite the lack of SWIR coverage, we achieved an overall classification accuracy of 74%, derived from 658 patches across the 7 transects.

Fig. S1. Frequency histograms of live PV, dead/senescent NPV, and bare soil for upland and lowland areas protected from or accessible to herbivores. (A and B) Long-term treatment areas. (C and D) Short-term treatment areas. In all panels, the left columns are for uplands and the right columns are for lowlands. All comparisons between treatments were statistically different using the K-S test ($P < .01$).
Fig. S2. The processing stream for in-flight and postflight integration of airborne imaging spectrometry and LiDAR observations, shade masking, and fractional canopy cover mapping. Raw data inputs from the CAO are shown in red; computer algorithms are depicted in gray. Final outputs are shown in green.
Fig. S3. Field validation of woody canopy height from 350 randomly selected points measured throughout KNP during the mapping campaign in April–May 2008.
Table S1. Descriptions of 4 large-scale herbivore treatments in KNP

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<thead>
<tr>
<th>Site</th>
<th>Age, years</th>
<th>Ecosystem</th>
<th>Substrate</th>
<th>Precipitation, mm year$^{-1}$</th>
<th>Area, ha</th>
<th>Fire return interval since establishment, years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nwashitsumbe</td>
<td>41*</td>
<td>Northern plains</td>
<td>Basalt</td>
<td>425</td>
<td>230 (302)*</td>
<td>4.0†</td>
</tr>
<tr>
<td>Hlangwine</td>
<td>36</td>
<td>Southern hills</td>
<td>Granite</td>
<td>625</td>
<td>220</td>
<td>3.6†</td>
</tr>
<tr>
<td>Nkuhlu</td>
<td>6</td>
<td>Sabie River hillslope</td>
<td>Granite</td>
<td>525</td>
<td>139</td>
<td>n/a‡</td>
</tr>
<tr>
<td>Letaba</td>
<td>6</td>
<td>Letaba River hillslope</td>
<td>Granite</td>
<td>475</td>
<td>129</td>
<td>n/a‡</td>
</tr>
</tbody>
</table>

*The Nwashitsumbe exclosure was extended by 72 ha into the lowland habitat in 1986, providing a total of 302 ha for our analysis.
†Calculated from the KNP GIS database (http://www.sanparks.org/parks/kruger/conservation/scientific/gis/gisrsdataview.php)
‡A portion of Nkuhlu was burned in 2002 and 2007, but this portion was excluded from the study, leaving the analysis without fire as a covariate. Letaba has not been burned since the treatment was established in 2002.
### Table S2. Height of woody canopies across the 4 treatment landscapes in both lowland and upland topographic positions in KNP

<table>
<thead>
<tr>
<th>Site</th>
<th>Upland</th>
<th>Lowland</th>
<th>Protected, m</th>
<th>Accessible, m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long-term basalt (Nwashitsumbe)</td>
<td>2.6 ± 2.1</td>
<td>3.3 ± 1.7</td>
<td>1.7 ± 1.2</td>
<td>1.6 ± 1.4</td>
</tr>
<tr>
<td>Long-term granite (Hlangwine)</td>
<td>3.9 ± 2.0*</td>
<td>3.4 ± 2.5*</td>
<td>3.9 ± 2.2*</td>
<td>3.4 ± 2.5*</td>
</tr>
<tr>
<td>Short-term granite (Nkuhlu)</td>
<td>3.5 ± 2.3</td>
<td>3.1 ± 2.2</td>
<td>3.0 ± 2.1</td>
<td>3.0 ± 2.0</td>
</tr>
<tr>
<td>Short-term granite (Letaba)</td>
<td>2.2 ± 1.3*</td>
<td>4.6 ± 2.8</td>
<td>2.2 ± 1.1*</td>
<td>3.4 ± 2.4</td>
</tr>
<tr>
<td>Hillslope comparison</td>
<td>2.9 ± 2.0</td>
<td>3.5 ± 2.3</td>
<td>2.7 ± 2.1</td>
<td>2.7 ± 2.2</td>
</tr>
<tr>
<td>Total</td>
<td>3.3 ± 2.2</td>
<td></td>
<td>2.7 ± 2.1</td>
<td></td>
</tr>
</tbody>
</table>

*No significant difference in mean height between protected and accessible areas (P < .05; t test; n = 27,000).

Protected and accessible indicate portions of the landscape without and with herbivore activity, respectively. Canopy height values are the mean canopy height ± SD derived from airborne laser returns.