Impact of grazing on the species richness, diversity and composition of temperate grassland in Kunjapuri Hills of Garhwal Himalaya, Uttarakhand

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Abstract: Disturbance plays a critical role in maintaining diversity, structure and function of an ecosystem. Grazing is a significant disturbance spread worldwide in natural grasslands. In the present study, we evaluated the effects of grazing on the species richness, diversity, and composition of grassland ecosystems of Kunjapuri Hills. Total 34 species were present in protected site (ungrazed) and 47 species in grazed site. Poaceae and Asteraceae were the most dominant families in protected and grazed sites, respectively. Grazed site accounted for higher species richness, diversity and number of non–palatable species in comparison to the protected site. We found that grazing is facilitating the invasion of non-palatable weeds and woody species that is ultimately altering the composition and affecting the diversity of the grassland.

Key words: Grazing, diversity, composition, species richness, non-palatable, Kunjapuri.

1. Introduction

Grasslands have been valued for their open, treeless expanses, low-relief topography, dark, rich fertile soils, excellent moisture regime sufficient to support rich plant growth, abundant wildlife populations, abundant natural forage and their relative ease of use, especially in comparison with heavily-forested environments¹. But, similar attributes of value, cumulatively and synergistically has opened up grassland for exploitation and have led to their extreme vulnerability for anthropogenic disturbance. Today grasslands, the world over, are the most threatened biome of the earth's ecosystem and several studies reported the decreased extent of grasslands and their status as most threatened ecological $community^{2-6}$.

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Department of Ecology and Environmental Sciences, Forest Research Institute, Dehradun- 248006, Uttarakhand, India. Email: The unprecedented cumulative and synergistic factors are manipulating the inherent properties of the grassland ecosystem by disturbing the structure and functioning of the grassland ecosystems. Some of the major factors that are forerunner in this modifications are conversion to and expansion of agriculture and agricultural activities inclusive of which is livestock farming (and associated grazing), traditional grazing, associated human settlements and concomitant urbanization, mega hydro–projects and expanding rail/road network lead fragmentation, fire (disturbance induced increased intensity), surface mining, desertification and introduction of exotic species and weeds.

The biotic disturbances such as grazing play an important role in change, loss or maintenance of plant diversity of a region. Grazing animals may influence plant composition and community structure both directly via physical means and indirectly via biogeochemical and biotic feedbacks⁷. Garhwal region of Uttarakhand is famous for its grasslands like Valley of Flowers, Har-Ki-Doon, Dayara, Hemkund Sahib, etc. but the unprecedented grazing is slowly and steadily reducing these grasslands. The grazing is changing the composition of these regions by favouring weeds and unpalatable species, reducing scenic beauty of grasslands as well as affecting their ecology. Present study was carried out in Kunjapuri hills of Garhwal Himalaya with an objective to evaluate the amount of changes in the species richness, diversity and vegetation composition of grassland ecosystem in response to cattle grazing.

2. Material and Methods

2.1 Study site

Present study site (Kunjapuri) is situated between latitude 30° 11' N and longitude 78° 28' E and at an altitude of 1,645 m. It falls in Shivpuri Forest Range of the Narendra Nagar Forest Division at about 35 Km from Rishikesh on Rishikesh–Gangotri road. The total area of this range is approximately 19,427.56 ha, which accounts for 31% of the total area of the Forest Division. The entire forest division is mountainous hilly with precipitous slopes.

Protected grassland site is located in the community lands of the village Badera of Kunjapuri and is maintained and managed by the local people. Local people do not allow their cattle to enter in this region. A fence cuts across the habitat boundaries of these two sites and is effective in preventing cattle's movement in protected grassland area. Grazed site is located adjacent to the protected site and is heavily grazed by the cattle throughout the year. These grassland sites (protected and grazed) along with the similarity in height also have homogeneity in some other physiographic features i.e., slope and aspect.

Climate of the study area is warm–temperate with moderate summers and severe winters. The mean maximum temperature varies from 13.9 °C (January) to 25.7 °C (June) and the mean minimum from 2.6 °C (January) to 17.0 °C (July). Total annual rainfall was 1170.5 mm with a minimum rainfall of 1.70 mm in November and a maximum rainfall of 325.9 mm in July (Fig., 1).



Fig. 1: Ombrothermic diagram of the study site.

2.2 Methods

Phytosociological studies were carried out in the year 2006 during the months of August and September. Random sampling method was followed for collecting the data. Quadrats of 5m \times 5m and 1m \times 1m sizes were laid for shrub and herb layers, respectively in all the sites of the study area. Each shoot of herb and shrub was considered as an individual plant⁸. The saplings and seedlings of trees and shrubs were considered under shrub and herb layers, respectively. Importance values of species were calculated

following Curtis and McIntosh⁹. Richness of species was estimated as the number of species present in the site. Simpson's index¹⁰ was calculated to assess the heterogeneity and Shannon–Wiener's diversity index¹¹ to find out the diversity of the site. All the diversity indices were calculated using SPDIVERS.BAS software (Ludwig and Reynolds¹²). The significance of difference between the protected and grazed sites was analysed statistically using Mann–Whitney U–test. The test was performed by XLStat–Pro[®] (Addinsoft, New York).

3. Results

Total 34 species belonging to 21 families and 34 genera, comprising 7 grasses, 21 forbs, 11 shrubs, and 2 saplings of tree species were present in the protected site (Table 1).

 Table 1. Taxonomic diversity of protected and grazed sites at Kunjapuri

	Protected Site	Grazed site
Number of families	21	21
Total genera	34	44
Total species	34	47
Dominant family	Poaceae	Asteraceae
Co-dominant family	Fabaceae	Poaceae
Dominant genera	_	Cyperus
Number of saplings	2	_
Number of shrubs	11	19
Number of herbs	21	28
(a) Forbs	14	20
(b) Grasses	7	6
(c) Sedges	-	2

In the grazed site, a total of 47 species belonging to 21 families and 44 genera were recorded. The contribution of different lifeforms was; 6 grasses, 28 forbs, 2 sedges and 19 shrub species (Table 1).Poaceae (7 genera/ 7 species) was the most dominant family followed by Fabaceae (4 species), Lamiaceae (3 species), and Acanthaceae and Rubiaceae (2 species each), whereas remaining 16 families were represented by only one species each (Table 2). Taxonomically, most dominant family was Asteraceae (9 general 9 species), followed by Poaceae (5 general 6 species), Acanthaceae (5 general 5 species), Lamiaceae (4 general/5 species), Fabaceae (4 genera/ 4 species), Rubiaceae (2 genera/ 2 species) and Cyperaceae (1 general 2 species), whereas the remaining 14 families were represented by only one genera and species each (Table 2).

In the protected site, *Debregeasia hypoleuca* (IVI, 121.1) was the most dominant and *Aechmanthera gossypina* (IVI, 96.3) the co-dominant shrub. Grazed site was dominated by *Aechmanthera gossypina* having 83.4 IVI and the co-dominants were *Eupatorium glandulosum*

(IVI, 60.2) and *Debregeasia hypoleuca* (IVI, 53.1). The percentage contribution of palatable species was 81.8% in protected and 68.8% in grazed site (Table 3).

Table	2.	Family-wise	$\operatorname{contribution}$	of	genera	and
		species in the	e two sites			

a •	Protected site		Grazed site		
Species –	Genus	Species	Genus	Species	
Acanthaceae	2	2	5	5	
Agavaceae	-	_	1	1	
Amaranthaceae	1	1	1	1	
Anacardiaceae	-	_	1	1	
Apiaceae	-	_	1	1	
Asteraceae	1	1	9	9	
Berberidaceae	1	1	1	1	
Cyperaceae	-	_	1	2	
Dioscoreaceae	1	1	-	_	
Dipsacaceae	1	1	_	_	
Euphorbiaceae	1	1	_	_	
Fabaceae	4	4	4	4	
Gentianaceae	1	1	1	1	
Haemodoraceae	1	1	_	_	
Hypericaceae	1	1	1	1	
Lamiaceae	3	3	4	5	
Liliaceae	1	1	-	_	
Lythraceae	1	1	1	1	
Menispermaceae	_	-	1	1	
Oxalidaceae	1	1	1	1	
Poaceae	7	7	5	6	
Ranunculaceae	1	1	_	_	
Rhamnaceae	_	-	1	1	
Rubiaceae	2	2	2	2	
Scrophulariaceae	1	1	1	1	
Solanaceae	-	-	1	1	
Tiliaceae	1	1	_	-	
Urticaceae	1	1	1	1	

Species	Family	Protected site	Grazed site
Palatable species			
Aechmanthera gossypina (Nees) Nees	Acanthaceae	96.3	83.4
Asparagus racemosus Willd.	Liliaceae	5.6	-
Berberis asiatica Roxb. ex. DC.	Berberidaceae	12.7	15.8
Cissampelos pariera L.	Menispermaceae	_	3.4
Craniotome versicolor Reich.	Lamiaceae	-	5.5
Debregeasia hypoleuca Wedd.	Urticaceae	121.1	53.1
Desmodium tilaefolium D. Don	Fabaceae	5.1	4.5
Grewia optiva Drum ex. Burret	Tiliaceae	5.1	_
Hamiltonia suaveolens Roxb.	Rubiaceae	5.1	_
Lepidagathis cuspidata Nees	Acanthaceae	_	4.0
Leptodermis lanceolata Wall.	Rubiaceae	20.4	4.6
Lespedeza sericea (Thunb.) Miq.	Fabaceae	13.5	18.1
Plectranthus rugosus Wall.	Lamiaceae	_	5.4
Randia tetrasperma Benth. & Hook. f	Rubiaceae	_	10.9
Non-palatable species			
Eupatorium glandulosum HBK. non. Michx	Asteraceae	_	60.2
Hypericum patulum non Thunb.	Hypericaceae	5.1	3.4
Inula cuspidata (DC.) Clarke	Asteraceae	_	3.7
Rhus parviflora Roxb.	Anacardiaceae	_	19.7
Woodfordia fruiticosa (L.) Kurz.	Lythraceae	10.1	3.9

Table 3. Species composition and IVI of species of shrub layer in grazed and protected sites of Kunjapuri

Herbaceous layer of both protected and grazed sites was dominated by *Chrysopogon serrulates* with 164.2 and 144.0 importance value index, respectively. The percentage contribution of non-palatable species or increasers was 24% in protected and 50% in grazed site (Table 4). We also found that the vegetation of grazed site was mostly cushioned whereas in protected site it was erect.

Table 4. Species composition and IVI of species of herb layer in grazed and protected sites of Kunjapuri

Species	Family	Protected site	Grazed site
Palatable species			
Achyranthes aspera L.	Amaranthaceae	3.4	3.3
Aechmanthera gossypina (Nees) Nees	Acanthaceae	3.9	_
Apluda mutica L.	Poaceae	10.7	7.9
Arthraxon lancifolius (Trin.) Hochst.	Poaceae	4.7	1.2
Arundinella nepalensis Trin.	Poaceae	12.9	-
Astragalus leucocephalus Grah. ex. Benth.	Fabaceae	-	1.1
Atylosia scarabaeoides (L.) Benth	Fabaceae	15.3	4.7
Bothriochloa bladhii (Retz.) Blake	Poaceae	8.9	_
Chrysopogon serrulatus Trin.	Poaceae	164.2	144.0
Debregeasia hypoleuca Wedd.	Urticaceae	-	2.2
Dicliptera roxburghiana Nees	Acanthaceae	10.8	6.5

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Dioscorea belophylla Voigt.	Dioscoreaceae	8.1	_
Indigofera heterantha Wall. ex. Brandis	Fabaceae	1.9	_
Lepidagathis cuspidata Nees	Acanthaceae	_	3.2
Leucas lanata Benth.	Lamiaceae	3.7	8.0
Micromeria biflora (BuchHam. ex. DDon) Benth.	Lamiaceae	9.4	17.0
Ophiopogon intermedius D. Don.	Haemodoraceae	1.9	_
Oxalis corniculata L.	Oxalidaceae	2.3	3.0
Pennisetum orientale L. C. Rich.	Poaceae	3.4	_
Plectranthus coesta BuchHam. ex. D. Don	Lamiaceae	4.6	1.3
Randia tetrasperma Benth. & Hook. f	Rubiaceae	_	5.1
Rungia pectinata (L.) Nees	Acanthaceae	1.9	6.6
Setaria glauca P. Beauv.	Poaceae	_	20.9
Setaria homonyma (Steud.) Chiov	Poaceae	_	2.0
Solanum nigrum L.	Solanaceae	_	1.1
Strobilanthes atropurpureus Nees	Acanthaceae	_	2.1
Thallictrum foliosum DC.	Ranunculaceae	5.6	_
Non-palatable species			
Agave cantula (Haw.) Roxb.	Agavaceae	_	1.1
Ageratum conyzoides Linn.	Asteraceae	_	1.1
Anaphalis contorta (D. Don) Hook. f.	Asteraceae	_	1.1
Bidens biternata (Lour.) Merr. & Sherff ex. Sherff	Asteraceae	_	1.1
Bupleurum falcatum L.	Apiaceae	_	2.1
Conyza stricta Willd.	Asteraceae	_	2.3
Cymbopogon distans (Nees ex. Steud) W. Wats	Poaceae	4.1	15.2
Cyperus iria (L.)	Cyperaceae	_	5.0
Cyperus niveus Retz.	Cyperaceae	_	8.7
Dipsacus inermis Wall.	Dipsacaceae	1.9	_
Embilica officinalis Gaertn.	Euphorbiaceae	3.7	_
Eupatorium glandulosum HBK. non. Michx	Asteraceae	_	2.1
Gerbera lanuginosa (Wall. ex. DC.) B. & Hook. f.	Asteraceae	_	1.1
Hypericum patulum non Thunb.	Hypericaceae	9.3	_
Inula cuspidata (DC.) Clarke	Asteraceae	_	2.5
Launaea nudicaulis (L.) Hook. f.	Asteraceae	_	1.2
Rhus parviflora Roxb.	Anacardiaceae	_	3.8
Sageretia filiformis (Roth. Ex. Schult) G. Don	Rhamnaceae	_	1.1
Saussurea heteromalla (D. Don) Hand.–Mazz.	Asteraceae	_	4.4
Striga asiatica (L.) O. Kuntze	Scrophulariaceae	1.9	1.1
Swertia chirayita (Roxb. ex. Fleming) Karsten	Gentianaceae	1.9	3.6
Woodfordia fruiticosa (L.) Kurz.	Lythraceae	_	1.1

The values of species richness (N) and Shannon–Wiener index were higher in grazed site for bothe shrub and herb layers. Simpson's index was however higher in protected site. The higher values of Simpson's index and low Shannon–Wiener's index shows that the protected site is dominated by a few species. The values of species richness and both the indices varied significantly (P < 0.05) between protected and grazed sites for both shrub and herb layers (Table 5).

4. Discussion

Dominance of Poaceae in protected site may be ascribed to various management practices applied by the locals to enhance the production of grasses in this area. Whereas, the dominance of Asteraceae family with nine genera (all non– palatable) in grazed site clearly indicates towards the existence of disturbance in the region. Dominance of members of Asteraceae further indicates their better invasive adaptation as most of them are not affected by grazing due to non–palatability.

Table 5. Diversity indices, richness and evenness of herb and shrub layers in the study sites at Kunjapuri

	Protected site	Grazed site	Р
Shrub layer			
Species richness (N)	11	16	0.017
Shannon-Weiner index (H')	0.63	0.94	0.013
Simpson's index (Cd)	0.28	0.17	0.004
Herb layer			
Species richness (N)	25	38	0.034
Shannon-Weiner index (H')	1.48	2.25	0.017
Simpson's index (Cd)	0.35	0.27	0.007

(Mann–Whitney U–test; n = 10)

Grazed site had significantly higher species richness and diversity in comparison to the protected site. High species richness in grazed site may be attributed to the grazing, which has increased the number of weeds and non– palatable species and thereby increased the total number of species in the area. The reduced vegetation due to grazing facilitates space for the direct invasion of weeds and non–palatable species. Higher species richness of grazed area is supported by the findings of Sankaran¹³ who reported that plant species richness, diversity and evenness were significantly lower in ungrazed plots compared to those that were grazed.

Result obtained from the present study showed that in grazed site the population of highly palatable native grass species such as *Chrysopogon serrulatus* and *Apluda muitica* reduced whereas, the population of nonpalatable species i.e. *Hypericum patulum*, *Swertia chirayita* and *Cymbopogon distans* increased in response to grazing. Noy–Meir *et al.*¹⁴ stated that the population of some plants in a community decreases (*decreasers*), while that of others increases (*increasers*) in response to grazing. Decreasers are the plants with attributes that favour them in competition for space and resources but disfavour them under differential defoliation, and these are readily palatable and available to grazers. Increasers are the plants with at least some of converse attributes and have lower palatability to grazers due to chemical and morphological defensive characters (invaders).

The contribution of grasses decreased with grazing. A large number of invasive forbs species such as Striga asiatica and Bidens biternata and other non-palatable species such as Ageratum convzoides, Anaphalis contorta, Conyza stricta, Cyperus iria, Cyperus niveus, Launaea nudicaulis, Saussurea heteromalla, Agave cantula and Inula cuspidata were also reported only in the grazed site. Similar findings have also been reported by Billings¹⁵ and McNaughton¹⁶. In over-grazed areas near mid and high-elevation villages in Nepal, decrease in grasses and an increase in the non-palatable species has also been noticed by Numata¹⁷. Kucera¹⁸ also reported a large reduction of vegetation cover of native grasses in the grazed site while studying grazing effects on virgin prairie in north-central Missouri.

Grazing was also found responsible for the invasion of exotic species like Eupatorium glandulosum in grazed site. These results parallel a number of other studies^{18–20} that show how grazing can allow species invasion, as the dominant native species are most sensitive to grazing pressure. Gilliam²¹ stated that once exotic plants get established in the herb layer of a forest, they could rapidly become the dominant species, not only altering the species composition of the herb layer but also decreasing overall biodiversity. Mechanisms for this response include strong tendency of nonnative species to compete more successfully than native species; their ability to escape herbivory in their new environment, and their tendency to alter soil resources. Thus, an environment is created which is more conducive for exotic species.

In the present study, the grazed site had higher number of weeds and woody shrubs than the protected site. Invasion of woody plants into grassland communities in many parts of the world have been attributed to grazing pressure^{22–25}, which is hypothesized to reduce competitive interaction between grasses and woody seedlings²². Watkinson and Ormerod²⁶ stated that grazing leads to two types of invasions: (1) there is the invasion of grassland by woody species with the consequent loss of the grassland system, and (2) the invasion of grasslands by weeds and typically unpalatable species.

In grassland, topography, edaphic factors, and disturbances produce regional variations in composition and structure of vegetation^{27, 28} and increase or decrease diversity and heterogeneity within communities as well²⁹. In the present study, disturbance in the form of grazing was significantly responsible for difference in the diversity, composition and structure of vegetation between protected and grazed sites. It also increased relative abundance of certain species in grazed site. Degradation of vegetation in grassland due to grazing will ultimately cause changes in its microclimatic conditions like decline of resource availability, especially fodder, soil moisture and nutrients. These changes altogether will pose a serious threat to the stability of the ecosystem.

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References

- 1. Henwood, W.D., An overview of protected areas in the temperate grasslands biome. *Parks*, 1998, **8**(3), 1–9.
- Bernes, C., *Biological diversity in Sweden*. Swedish Environmental Protection Agency, Monitor 14, Solna, SE, 1994.
- Samson, F.B., Knopf, F.L. and Ostlie, W.R., Grasslands. In Mac, M.J., Opler, P.A., Puckett, C.E. and Doran P.D. (eds.), *Status* and Trends of the Nation's Biological Resources, Vol. 2, Reston, VA: U.S. Department of the Interior, U.S. Geological Survey,1998, pp. 437–472.
- 4. WRI (World resources 2000–2001), *People* and Ecosystems: The Fraying Web of Life. World Resources Institute, New York, 2000.
- White, R. P., Murray, S. and Rohweder, M., *PAGE: Pilot Analysis of Global Ecosystems: Grassland Ecosystems.* World Resources Institute, Washington, DC, 2000, pp 81.
- 6. Vera, F.W.M., *Grazing Ecology and Forest History.* CABI Publ., Wallingford, UK, 2000.
- Allen–Diaz, B. and Jackson, R. D., Herbaceous Responses to Livestock Grazing in Californian Oak Woodlands: A Review for Habitat Improvement and Conservation Potential. USDA Forest Service Gen. Tech. Rep. PSW–GTR–195, 2005.
- Singh, J. S. and Yadav, P. S., Seasonal variation in composition, plant biomass and net primary productivity of tropical grassland at Kurukshetra, India. *Ecological Monographs*, 1974, 44, 351–376.
- Curtis, J. J. and McIntosh, R. P., The interrelations of certain analytical and synthetic phytosociological characters. *Ecology*, 1950, 31, 434–455.
- 10. Simpson, E. M., Measurement of diversity. *Nature*, 1949, **163**, 688.
- 11. Shannon, C. E. and Wiener, W., *The Mathematical Theory of Communication*. Univ. Illinois Press, Urbana, 1963.
- 12. Ludwig, J. A. and Reynolds, J. F. Statistical Ecology– A Primer on Methods and Computing. John Wiley and Sons, New York, 1988.
- 13. Sankaran, M., Fire, grazing and the

dynamics of tall–grass savannas in the Kalakad–Mundanthurai Tiger Reserve, South India. *Conservation and Society*, 2005, **3**(1), 4–25.

- Noy–Meir, I., Gutman, M. and Kalplan, Y., Responses of Mediterranean grassland plant to grazing and protection. *J. Ecol.*, 1989, 77, 290–310.
- 15. Billings, W. D., Alpine phytogeography across the Great Basin. In Harper, K. T. and Reveals, J. L. (eds.), *High Altitude Geology AAAS Selected Symposium 12*. West View Press Inc. Boulder. Colo., 1978, pp. 105– 117.
- McNaugton, S. J., Ecology of grazing ecosystem: The Serengeti. *Ecological Monographs*, 1985, 55, 259–295.
- 17. Numata, M., Conditions of semi-natural pastures in the humid Himalayas. *Intecol Bulletin*, 1986, **13**, 65–68.
- Kucera, C. L., Grazing effects on composition of virgin prairie in north– central Missouri. *Ecology*, 1956, **37**, 389– 391.
- Beebe, J. D. and Hoffman, G. R., Effects of grazing on vegetation and soils in southeastern South Dakota. *American Midland Naturalist*, 1968, **80**, 96–110.
- 20. Milchunas, D. G. and Lauenroth, W. K., Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 1993, **63(4)**, 327–366.
- 21. Gilliam, F. S., The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience*, 2007, **57**(10), 845–858.
- 22. Debain, S., Curt, T. and Lepart, J., Indirect effects of grazing on the establishment of

Pinus sylvestris and *Pinus nigra* seedlings in calcareous grasslands in relation to resource level. *Ecoscience*, 2005, **12**(2), 192–201.

- Tamartash, R., Jalilvand, H. and Tatian, M. R., Effects of grazing on chemical soil properties and vegetation cover (Case Study: Kojour Rangelands, Noushahr, Islamic Republic of Iran). *Pakistan Journal of Biological Sciences*, 2007, **10(24)**, 4391– 4398.
- 24. Savadogo, P., Savadogo, L. and Tiveau, D., Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savanna woodlands of Burkina Faso. *Agric. Ecosyst. Environ.*, 2007, **118**, 80–92.
- Williams, W. D., Dormaar, J. F. and Smoliak, S., Vegetation responses to time controlled grazing on mixed and fescue prairie. *Journal of Range Management*, 1990, 43, 513–517.
- 26. Watkinson, A. R. and Ormerod, S. J., Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology*, 2001, **38**, 233–237.
- Belsky, A. J., The effect of grazing: confounding of ecosystem community and organism scales. *American Naturalist*, 1987, 129, 777–783.
- Gibson, N. and Hulbert, L. C., Effects of fire, topography and year to year climatic variation on the species composition in tall grass prairie. *Vegetatio*, 1987, **72**, 175–185.
- 29. Milchunas, D. G., Sala, D. E. and Lauenroth, W. K., A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, 1988, **132**, 87–106.