

RAINFALL AND SOILS MODIFY PLANT COMMUNITY RESPONSE TO GRAZING IN SERENGETI NATIONAL PARK

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Abstract. Terrestrial plant community responses to herbivory depend on resource availability, but the separate influences of different resources are difficult to study because they often correlate across natural environmental gradients. We studied the effects of excluding ungulate herbivores on plant species richness and composition, as well as available soil nitrogen (N) and phosphorus (P), across eight grassland sites in Serengeti National Park (SNP), Tanzania. These sites varied independently in rainfall and available soil N and P. Excluding herbivores decreased plant species richness at all sites and by an average of 5.4 species across all plots. Although plant species richness was a unimodal function of rainfall in both grazed and ungrazed plots, fences caused a greater decrease in plant species richness at sites of intermediate rainfall compared to sites of high or low rainfall. In terms of the relative or proportional decreases in plant species richness, excluding herbivores caused the strongest relative decreases at lower rainfall and where exclusion of herbivores increased available soil P. Herbivore exclusion increased among-plot heterogeneity in species composition but decreased coexistence of congeneric grasses. Compositional similarity between grazed and ungrazed treatments decreased with increasing rainfall due to greater forb richness in exclosures and greater sedge richness outside exclosures and was not related to effects of excluding herbivores on soil nutrients. Our results show that plant resources, especially water and P, appear to modulate the effects of herbivores on tropical grassland plant diversity and composition. We show that herbivore effects on soil P may be an important and previously unappreciated mechanism by which herbivores influence plant diversity, at least in tropical grasslands.

Key words: *compositional similarity; congener coexistence; consumer–resource theory; functional types; grazing; plant species richness; Serengeti National Park (Tanzania); soil nitrogen; soil phosphorus.*

INTRODUCTION

Herbivore effects on terrestrial plant species richness and composition can depend on a wide variety of factors, such as annual net primary production (Frank 2005), herbivore size (Olf and Ritchie 1998) and density (Schutz et al. 2003), spatial scale (Stohlgren et al. 1999), and evolutionary history (Milchunas et al. 1988). Variation in these factors undoubtedly causes herbivore effects on plant communities to vary strongly among sites (Gough and Grace 1998, Veski and Westoby 2001), but relatively few studies have explored what explains this variation. One major question is the manner in which herbivore effects depend on the availability of different resources, such as light, water, soil nitrogen (N), or soil phosphorus (P) (Olf and Ritchie 1998, Ritchie and Olf 1999), and, reciprocally, the manner in which herbivore effects on plant resources might control plant communities.

Most previous studies have explored how plant defoliation tolerance, plant palatability, and herbivore selectivity change across environmental gradients and how this might modify herbivore effects on plant communities (McInnes et al. 1992, Augustine and McNaughton 1998, Collins et al. 1998). Studies have often used primary production as a surrogate for resource availability (Frank 2005) or created differences in primary production experimentally through fertilization (Gough and Grace 1998, Gough et al. 2000). Few, if any, studies have measured herbivory effects across different natural resource gradients, such as soil N or P, water, or light, within the same ecosystem. This is despite strong theoretical evidence (Leibold 1996) and empirical data from disparate ecosystems (Proulx and Mazumder 1998) that suggest resource gradients may greatly alter the effects herbivores have on plant species and composition.

Herbivores can modify resource availability (Huntly 1991, Jefferies et al. 1994, Hobbs 1996, McNaughton et al. 1997, Ritchie et al. 1998) and the effects of herbivores on plant communities may also depend on which plant resource herbivores modify and how strongly they modify it (Olf and Ritchie 1998). For example, herbivores can greatly increase light availability (Huisman et al. 1999, Bakker et al. 2004) and alter soil

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available N depending on the vegetation quality, grazing intensity, and nutrient supply (Frank and Evans 1997, Augustine et al. 2003, Bakker et al. 2004), and such modifications of resources may cause associated changes in plant species richness, composition, and vegetation structure through a variety of different mechanisms (Willems et al. 1993, Foster and Gross 1998, Rajaniemi 2002, Stevens et al. 2004). Less well known is that herbivores can also modify soil available P (Hatton and Smart 1984, Chaneton et al. 1996, Lavado et al. 1996, Turner 1998, Augustine 2003) and might consequently alter plant communities by changing P availability. What is almost unknown is how such herbivore effects on plant resources and possible effects on plant communities might depend on background resource availability.

Another important question is how herbivore effects on species richness might differ from their effects on species composition across plant resource gradients. For example, herbivores might cause greater changes in plant species richness than composition when they enhance colonization without increasing local extinction of plant species. This might occur when herbivores reduce the abundance of dominant species, enhance availability of a soil resource such as N, or increase the dispersal rate of species into communities (Hulme 1996). In contrast, grazing might cause greater changes in plant species composition than in richness when herbivores create a balance between rates of local colonization and extinction, so that the numbers of species lost and gained are equal. This might occur when herbivores induce local extinctions by their selective consumption of palatable plant species but change resource availability to favor different functional groups of plants, such as grasses, forbs, or shrubs.

In contrast to predictions that arise from changes in plant palatability and herbivore selectivity across environmental gradients, an alternate body of theory known as "heterogeneous food webs" (Leibold 1996, Leibold et al. 1997) predicts the effects of consumers on community diversity across a gradient of resource availability. Stated in terms of grassland plant communities, these models assume a trade-off between plants' ability to exploit nutrients and tolerate herbivory across resource gradients (Chase et al. 2000). As resource availability increases, plants that are good resource competitors are substituted for species that are resistant to herbivory. The theory predicts a unimodal relationship between plant species richness and resource availability, a negative relationship between resource availability and compositional similarity between grazed and ungrazed plant communities, and greater coexistence between closely related species in the presence of herbivores.

We explored the effects of excluding herbivores on plant diversity and species composition in Serengeti National Park (SNP) in northern Tanzania, one of the last fully intact grazing ecosystems on earth, featuring 30

species and nearly 3×10^6 grazing animals. We conducted replicated herbivore enclosure experiments at eight different sites that differed in rainfall and soil available N and P. Unlike many temperate grazing ecosystems, the importance of rainfall in determining nutrient availability is often overridden by other soil, biotic, and landscape factors, such that rainfall and nutrient availability can vary independently (McNaughton et al. 1988, Frank et al. 1998; Anderson et al., *in press*). This property makes SNP an ideal system to test hypotheses about the effect of herbivores on plant communities across natural resource gradients. Our eight sites represented a gradient of grassland types, from low rainfall and fertile soils to relatively high rainfall and infertile soils (McNaughton et al. 1988, Ruess and Seagle 1994). We measured responses of plant species richness and compositional similarity at replicate grazing enclosures across these gradients to test several hypotheses about the effects of excluding herbivores on grassland plant species richness and composition across these sites. First, we predicted that herbivore removal would have separate and independent effects on plant species richness and composition and that these effects would change with resource availability. Second, following from predictions of theory on the palatability of dominant species, we hypothesized that the effects of excluding herbivores on plant species richness would shift from positive to negative with greater resource availability. Third, we hypothesized that herbivores would modify nutrient availability, which would be associated with changes in plant species richness and composition. To more completely understand herbivore effects on composition, we assessed whether changes in species richness and composition among grazed and ungrazed plots was explained by shifts in the richness of different functional groups (grasses, sedges, forbs) and altered coexistence among plant congeners.

MATERIALS AND METHODS

Research was conducted at eight grassland sites in Serengeti National Park, Tanzania, which is part of the larger 25 000-km² Serengeti-Mara ecosystem (Fig. 1). Sites were separated by 20–100 km and were chosen to represent variation in annual and seasonal rainfall from 400 to 900 mm/yr (McNaughton 1985) and soil fertility from a variety of soil ages, parent material, and textures (de Wit 1978, Jager 1982, Ruess and Seagle 1994). Sites were located in open grassland swards away from woodland areas; we are relatively confident that herbivore effects were almost entirely attributable to grazers, as browsers and mixed feeders rarely utilize pure grass stands in Serengeti. Mean annual rainfall data for the sites was interpolated from >40 years of rain gauge data at ~50 sites collected by the Serengeti Ecological Monitoring Program (Fig. 1). At each site, a linear array of six plots (4 × 4 m), spaced ~10 m apart, was established in January 1999. Three plots at each site were selected at random and permanently enclosed with

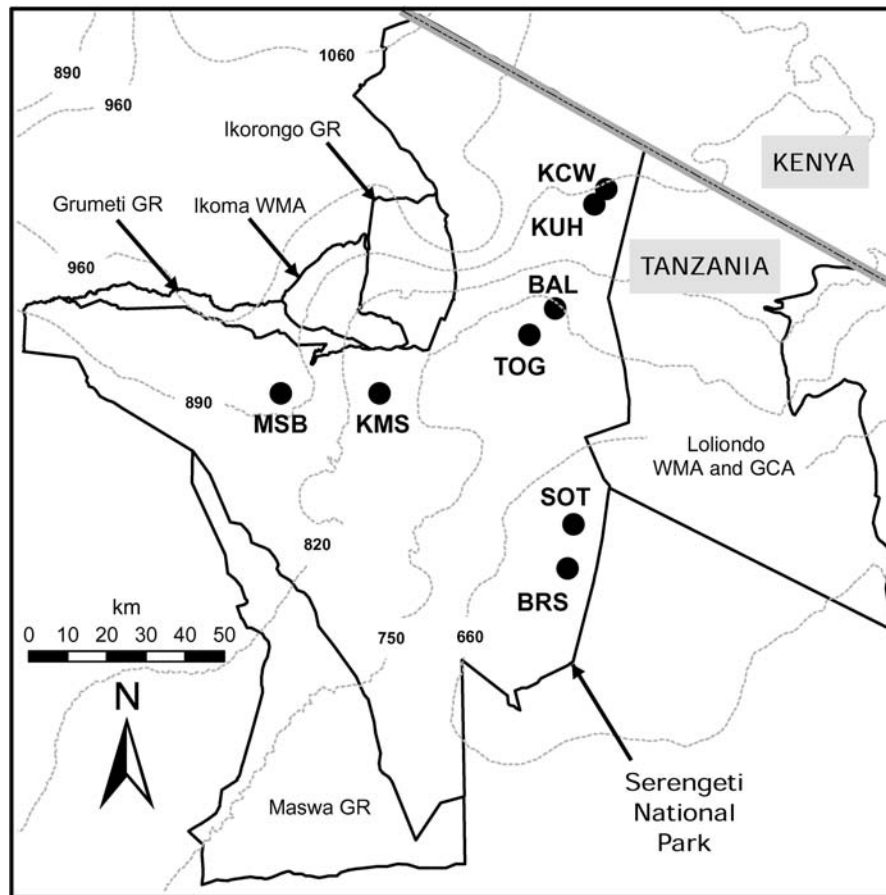


FIG. 1. Map showing the locations of the eight study sites (solid circles) across Serengeti National Park, in Tanzania, East Africa. Each site is labeled with a three-letter code that corresponds to Table 1. Gray dashed lines are isopleths representing mean annual rainfall (mm/yr) over the last 40 years. The surrounding game reserves (GR), game control areas (GCA), and wildlife management areas (WMA) are also shown.

chain-link (8-cm mesh) fence to a height of 2 m while the remaining three plots were left unfenced. Because of their small area, these fences were not jumped by ungulates and effectively excluded all ungulate species. Perhaps because of their small size and relative isolation from other structures, our fences did not attract rodents (Keesing 1998, Shaw et al. 2002, Goheen et al. 2004), as we found no visible signs of herbivorous rodents, such as burrows, trails, feeding stations, or feces.

We measured available soil nutrients and plant biomass in each plot. Extractable soil N and P measurements were repeated a total of seven times between April of 2000 and June 2002. Samples were collected during the growing season, which extends approximately from February to June and temporally spaced by at least one month in all cases. Soil samples (~50 g) were collected from the top 10 cm soil in each plot and processed as follows: ~10 g soil was combined with 50 mL 1 mol/L KCl and preserved with 0.05% phenylmercuric acetate; ~5 g soil was combined with 25 mL of Mehlich's number 3 (Mehlich 1984); ~10 g soil was weighed immediately (wet mass), then transported

to Syracuse University, where it was reweighed after drying at 105°C for 48 h (dry mass) to measure water content. The Mehlich-3 extractant was used because it has been shown to correlate highly with plant-available P across a wide range of soils and pH levels (Mallarino 1997). Soils in KCl and Mehlich's were shaken at 12 h and extracted through Fisher brand P5 medium porosity filter paper (Fisher, Waltham, Massachusetts, USA) at 24 h. Extracts were transported to Syracuse University, where KCl samples were analyzed on a Lachat Quickchem Flow Injection Analyzer (Lachat, Milwaukee, Wisconsin, USA) for extractable mineral N (nitrate + ammonium) and Mehlich's samples were analyzed on a Leeman Inductively Coupled Plasma Spectrophotometer (Leeman, Hudson, New Hampshire, USA) for extractable mineral P. Nutrient concentrations were averaged across the seven growing season samples and are expressed on a milligram per kilogram dry soil mass basis by correcting for soil moisture. Plant biomass was measured by clipping and weighing the dried above-ground biomass inside four replicate 20-cm² wire frames randomly placed within each plot. Biomass samples

were collected at three different times during the study: May 2000, May 2001, and June of 2002. Biomass sampling corresponded with the period of maximal standing biomass during the year and just prior to plant senescence. Grazing intensity (G) was calculated as: $1 - (\text{grazed biomass}/\text{ungrazed biomass}) \times 100$ (McNaughton 1985).

Plant species richness was measured by counting all species in each plot during the growing season and peak flowering at the sites in February 2005, thereby increasing the probability of encountering rare species. It is unlikely that major qualitative differences in species richness existed between the sampling dates for soil nutrient measurement and species richness (Anderson et al. 2004). Species names and taxonomic authorities were verified with *Flora of Tropical East Africa* (Beentje 2001) and the Missouri Botanical Garden's Vascular Tropics nomenclature database and associated World Wide Web authority files (VAST 2004). We calculated relative effect of herbivore removal on species richness as $(\text{ungrazed richness} - \text{grazed richness})/\text{grazed richness}$. When randomly placed grazed and ungrazed plots occurred next to one another at a site, we also calculated the relative effect of herbivores between the paired adjacent plots. The locations of randomized plots allowed for three paired comparisons at two sites and two comparisons at six sites ($n = 18$). This analysis reduced within-site variation that may influence estimates of herbivore exclusion. Absolute species richness was analyzed with ANOVA with site and grazing (TRT) as main treatment effects. We used ANCOVA to analyze absolute species richness response to variation in mean annual rainfall (RAIN) and soil nutrients with RAIN, N, and P as covariates substituted for site. $N \times \text{TRT}$ and $P \times \text{TRT}$ interactions were used to test the hypothesis that grazing had different effects on plant species richness at different levels of soil nutrients. A $\text{RAIN} \times \text{RAIN} \times \text{TRT}$ interaction term was used to test whether a quadratic effect of rainfall on species richness was dependent on grazing. To analyze relative herbivore effects on richness (i.e., percentage of change) we used multiple regressions to analyze relative difference in species richness between grazed and ungrazed plots with RAIN and average differences in N and P between grazed and ungrazed plots as independent variables. Variation in N and P between grazed and ungrazed treatments among sites was attributed to the effects of excluding herbivores. Multiple regression fit was assessed with Mallows C_p statistic and the maximum R^2 improvement method (Freund and Littell 2000). All statistics in this and remaining sections were conducted with version 9.1 of SAS (SAS Institute 2003) unless otherwise specified.

Jaccard's index (J) was used to quantify plant species compositional similarity among plots across sites using $J = A/(A + B + C)$, where A was the number of species shared by two samples, B was the number of species found in only one sample, and C was the number of

species found only in the other sample. Two types of compositional similarity were calculated: among-plot and among-treatment. Among-plot similarity at each site was the mean of all three pairwise comparisons among plots within a treatment. Among-treatment similarity at each site was calculated where A was the number of species shared by grazed and ungrazed plots, B was the total number of species found across all three grazed plots, and C was the total number of species found across all three ungrazed plots and A was the species shared between B and C .

To more fully explore how herbivores changed plant species richness and composition, we analyzed two different types of patterns across sites, namely, coexistence among congeneric species and changes in plant functional types between grazed and ungrazed plots. To explore the coexistence of congeneric species, we compared the number of species per genus (hereafter species:genus ratio) in grazed and ungrazed plots across sites with Friedman's test (Sokal and Rohlf 1995) for all species and for each functional type. To investigate how herbivory affected species richness of plant functional types, we conducted nonmetric multidimensional scaling (NMS) in version 4.01 of PC-ORD (McCune and Medford 1999) and discrimination analysis using PROC DISCRIM in SAS on the relative species richness of six functional types in grazed and ungrazed plots. These functional types were grasses, sedges, forbs, shrubs, trees, and succulents and were chosen to reflect differences in growth rate, herbivory tolerance, and resource requirements. Matrix values were the mean proportion of total species richness accounted for by each of the six functional group in grazed and ungrazed plots according to site ($8 \text{ sites} \times 2 \text{ treatments} = 16 \text{ data points}$). Axis significance in NMS was tested with Monte Carlo randomization procedures in PCORD. Results of discrimination analysis were evaluated with the Hotelling-Lawley Trace statistic.

RESULTS

Sites displayed variation in rainfall and soil available P, but relatively little variation in soil available N (Table 1, Appendix A). As a result, sites did not differ in soil available N ($F_{7,32} = 1.65$, $P = 0.16$) but differed in soil P ($F_{7,32} = 113.86$, $P < 0.0001$), with 22 significant differences out of a possible 28 pairwise comparisons. There were no significant relationships between rainfall, plant biomass, and soil available N and P in either the fenced or unfenced grasslands among sites (all correlations $P > 0.18$; Appendix B). Grazing intensity at the sites ranged from 11.9% to 55.8% and showed no relation to rainfall or latitude. Despite these considerable site differences, all sites had mean ungrazed productivity of $\sim 600 \text{ g/m}^2$ or greater (mean = 721.8 g/m^2 ; Appendix A). Finally, the exclusion of herbivores had no consistent main effect on soil available N ($F_{1,32} = 0.02$, $P = 0.90$), P ($F_{1,32} = 0.22$, $P = 0.65$), or the N:P ratio ($F_{1,32} = 0.22$, $P = 0.64$), and there was no site \times

TABLE 1. Site characteristics (mean \pm SE) in Serengeti National Park where species richness (S) of sites and plots in grazed (G) and ungrazed (UG) grassland were studied.

Site	Rain (cm)	N (mg/kg soil)		P (mg/kg soil)		S_{site}	S_{plot}		J_{AP}		J_{AT}
		G	UG	G	UG		G	UG	G	UG	
KUH	77.9	7.3 \pm 1.1	7.1 \pm 0.2	11.0 \pm 0.5	10.2 \pm 0.1	51	25.3 \pm 1.9	20.7 \pm 1.7	55.5 \pm 3.3	38.7 \pm 3.1	43.1
KCW	76.6	6.8 \pm 1.2	7.1 \pm 0.8	10.0 \pm 0.6	14.1 \pm 3.5	62	30.3 \pm 3.8	27.0 \pm 2.1	49.0 \pm 1.8	43.6 \pm 3.2	50.0
BAL	71.1	6.0 \pm 0.4	5.7 \pm 0.6	91.2 \pm 12.6	105.3 \pm 7.1	66	34.3 \pm 5.8	23.7 \pm 3.5	42.6 \pm 4.2	35.9 \pm 4.9	52.3
TOG	67.6	8.4 \pm 2.5	5.2 \pm 0.2	165.3 \pm 1.6	158.6 \pm 5.5	42	26.3 \pm 0.9	19.7 \pm 0.7	67.8 \pm 3.4	55.3 \pm 1.5	53.7
MSB	89.1	7.0 \pm 0.1	9.2 \pm 0.9	126.7 \pm 5.0	111.5 \pm 2.9	31	16.0 \pm 0.6	15.0 \pm 1.2	61.6 \pm 10.4	57.8 \pm 1.3	41.9
KMS	79.9	6.7 \pm 0.7	6.2 \pm 0.4	101.1 \pm 12.1	82.2 \pm 10.5	36	20.7 \pm 2.2	12.3 \pm 2.2	47.5 \pm 3.3	60.4 \pm 5.2	38.9
SOT	53.8	7.4 \pm 0.3	7.5 \pm 1.2	62.2 \pm 1.6	72.9 \pm 10.3	32	18.7 \pm 0.7	15.3 \pm 1.2	57.9 \pm 3.9	51.3 \pm 4.2	59.4
BRS	49.8	7.5 \pm 0.3	9.4 \pm 0.9	74.9 \pm 2.2	100.4 \pm 9.0	22	15.7 \pm 0.9	10.7 \pm 1.5	68.3 \pm 8.2	52.1 \pm 4.1	63.6

Notes: Definitions: Rain, mean annual precipitation; N, soil extractable nitrogen; P, soil extractable phosphorus; J_{AP} is the among-plot Jaccard's index (J); J_{AT} is the among-treatment J comparing grazed with ungrazed plots at a site. Plot-level species richness was estimated from three replicate 4 \times 4 m plots for both fenced and unfenced treatments at each of the eight sites. Site-level species richness was determined by summing the total number of species found in both the fenced and unfenced plots at each site. Sites are listed from north (top) to south (bottom). Sites names are as follows: KUH, Kuka hills; KCW, Klein's camp west; BAL, Balanites; TOG, Togoro plain; MSB, Musabi plain; KMS, Kemarishe; SOT, Soit le Moytoni; BRS, Barafu south.

treatment interaction for soil available N ($F_{7,32} = 1.58$, $P = 0.18$) or the N:P ratio ($F_{7,32} = 0.51$, $P = 0.82$). There was, however, a significant treatment \times interaction for soil P ($F_{7,32} = 2.46$, $P = 0.039$), indicating that the effects of fences on soil P depended on site.

Excluding herbivores decreased mean species richness across all sites (grazed, 23.4 ± 2.7 > ungrazed, 18.0 ± 2.2 [mean \pm SE]; $F_{1,32} = 20.8$, $P < 0.0001$), and sites themselves differed significantly in species richness ($F_{7,32} = 13.5$, $P < 0.0001$). The effect of grazing on species richness did not depend on site per se, as indicated by a nonsignificant grazing \times site interaction ($F_{7,32} = 0.86$, $P = 0.55$). Plant species richness in both grazed and ungrazed plots was a unimodal function of rainfall (Fig. 2). The ANCOVA result demonstrated a highly significant RAIN \times RAIN \times TRT interaction term ($F_{2,38} = 16.06$, $P < 0.0001$), indicating that the quadratic relationship was different for grazed and ungrazed plots. The bivariate plot shows that grasslands sites of intermediate rainfall lost numerous species inside fences, while the decrease in species richness due to fencing was lower at high and low rainfall (Fig. 2). There was no evidence that the absolute decrease in plant species richness due to herbivore exclusion differed across the range of soil N and P, as demonstrated by the nonsignificant N \times TRT and P \times TRT in the ANCOVA (N \times TRT, $F_{1,32} = 0.00$, $P = 0.95$; P \times TRT, $F_{1,32} = 0.65$, $P = 0.42$).

In contrast, when effects of excluding herbivores on the relative change in species richness between paired fenced and unfenced plots at each site were analyzed with a multiple regression, we found a strong effect of herbivore-induced changes in soil P (Fig. 3, $F_{1,16} = 8.50$, $P = 0.01$, variance contributed to total $R^2 = 0.35$) and to a lesser extent RAIN ($F_{1,16} = 3.16$, $P = 0.096$, variance contributed to total $R^2 = 0.11$) on relative changes in plant species richness. The resulting regression shows that the reduction in plant species richness from excluding herbivores was greater when herbivore removal increased soil available P and at sites with lower

rainfall: percentage change in richness = $(-0.26 \times \Delta P) + (0.29 \times \text{RAIN}) - 42.15$ ($R^2 = 0.46$).

Herbivore removal interacted with plant resources in different ways to affect plant species composition. Removing herbivores weakly decreased among-plot, within-site compositional similarity (ungrazed, $49.4 \pm 3.2 <$ grazed, 56.3 ± 3.4 ; $t_7 = 1.89$, $P = 0.077$, from a paired t test). When the quantitative effects of RAIN, N, and P on among-plot compositional similarity were analyzed with ANCOVA, the overall model was not significant ($F_{8,15} = 2.03$, $P = 0.17$), indicating that neither resources nor resource \times treatment interactions explained variation in among-plot compositional similarity. For compositional similarity among grazed and ungrazed treatments, neither N nor P were significant explanatory variables in the multiple regression ($P > 0.7$

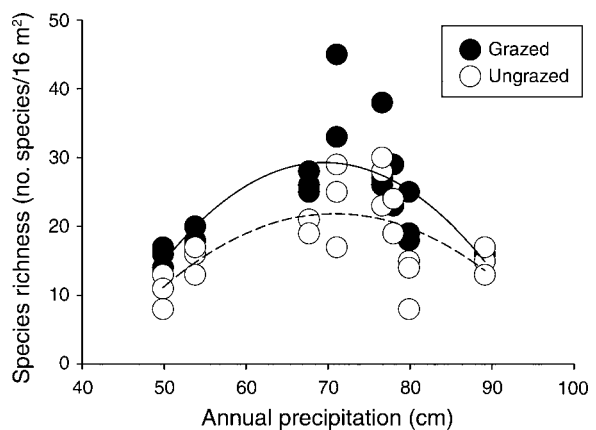


FIG. 2. Mean species richness in grazed and ungrazed 16-m² plots vs. mean annual rainfall at eight sites across Serengeti National Park. Lines for grazed (solid) and ungrazed (dashed) were fit with quadratic equations estimated in SigmaPlot version 8.02 (SYSTAT Software, San Jose, California, USA). Equations are: grazed, $-679.6 + (1.8 \times \text{RAIN}) - (0.0011 \times \text{RAIN}^2)$ ($R^2 = 0.95$, $F_{2,6} = 37.1$, $P = 0.003$); ungrazed, $-620.5 + (1.6 \times \text{RAIN}) - (0.0010 \times \text{RAIN}^2)$ ($R^2 = 0.81$, $F_{2,6} = 8.3$, $P = 0.04$).

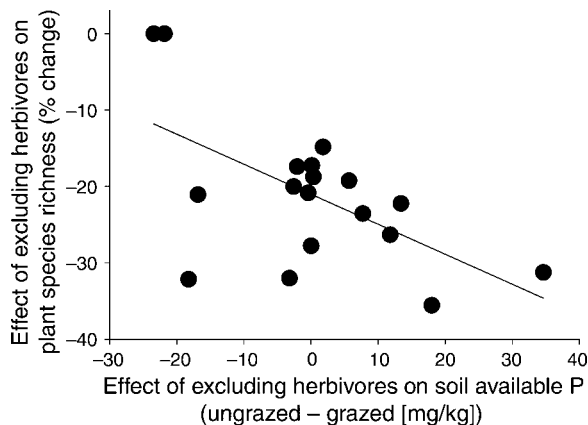


FIG. 3. Bivariate relationship between the effects of herbivore removal on plant species richness in 16-m² plots (measured as the percentage change due to fencing) regressed against the effects of herbivore removal on soil available P (measured as the difference between soil available P in ungrazed plots and grazed plots). Each point represents the difference between a paired grazed and ungrazed plot; the random location of adjacent plots allowed for three paired comparisons at two sites and two paired comparisons at six sites ($n = 18$). The equation for the effect of herbivore-induced changes in P on herbivore-induced changes in plant species richness is: Δ plant species richness = $-0.39 \times \Delta$ soil P - 21.0 ($R^2 = 0.34$, $F_{1,16} = 8.5$, $P = 0.01$).

in both cases), but we found a strong negative relationship of among-treatment compositional similarity with rainfall (Fig. 4). Thus, excluding herbivores led to greater species turnover at sites with higher rainfall.

This turnover in species reflected significant differences in the effects of herbivore removal on plant functional composition across the rainfall gradient. Sedge species

richness was greater in grazed compared to ungrazed plots at all sites, while forb richness was greater in ungrazed plots at six of the eight sites, lower at one site, and not different at another site (Fig. 5). Discrimination analysis showed the grazed and ungrazed treatments were indeed significantly grouped in multivariate space based on functional type richness ($T = 2.07$, $F_{5,10} = 4.14$, $P = 0.027$). The NMS analysis explained 97.8% of the variation in the data on two axes (final stress = 14.5%) and confirmed that higher sedge richness in grazed plots and increased forb richness in the ungrazed plots explained much of the separation between treatments. The first axis ($R^2 = 55.3\%$) was most strongly correlated with an increase in forb richness and decrease in sedge richness. The second axis ($R^2 = 42.6\%$) was most strongly correlated with an increase in grass richness and a decrease in forb richness. Finally, more congeneric grass species were found in grazed vs. ungrazed plots over all sites; the grass species:genus ratio in grazed plots was 1.20 ± 0.06 compared to 1.09 ± 0.05 in ungrazed plots ($Q = 4.5$, $df = 1$, $P = 0.034$). However, the relationship was unique to the graminoids, as species:genus ratios were not different among grazed and ungrazed plots for any other functional type (all $P > 0.20$).

DISCUSSION

Herbivory and plant species richness

Hypotheses based on a theory of the palatability of dominant plant species across environmental gradients (Olf and Ritchie 1998, Ritchie and Olf 1999) suggest that herbivores should have negative impacts on vegetation species richness in dry savannas on fertile soils but positive effects on plant species richness in wetter savannas on infertile soils. Based on these

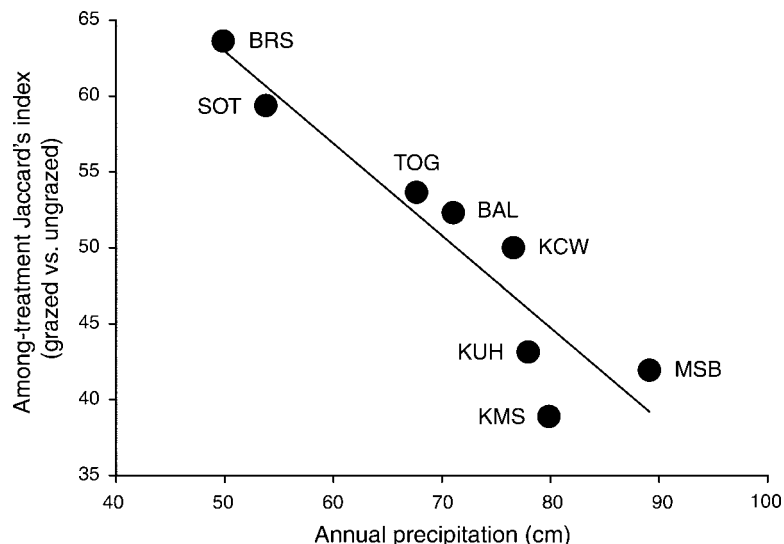


FIG. 4. Relationship between among-treatment Jaccard's index (J_{AT}) and mean annual precipitation (RAIN) at eight sites in Serengeti National Park. The index provides an estimate of plant compositional similarity between grazed and ungrazed plots at each site (see *Materials and Methods* for full description). RAIN was the only significant coefficient in the multiple regression: $J_{AT} = 93.3 - (0.61 \times \text{RAIN})$ ($R^2 = 0.87$, $F_{1,6} = 39.5$, $P = 0.0008$). See Table 1 for an explanation of the site abbreviations.

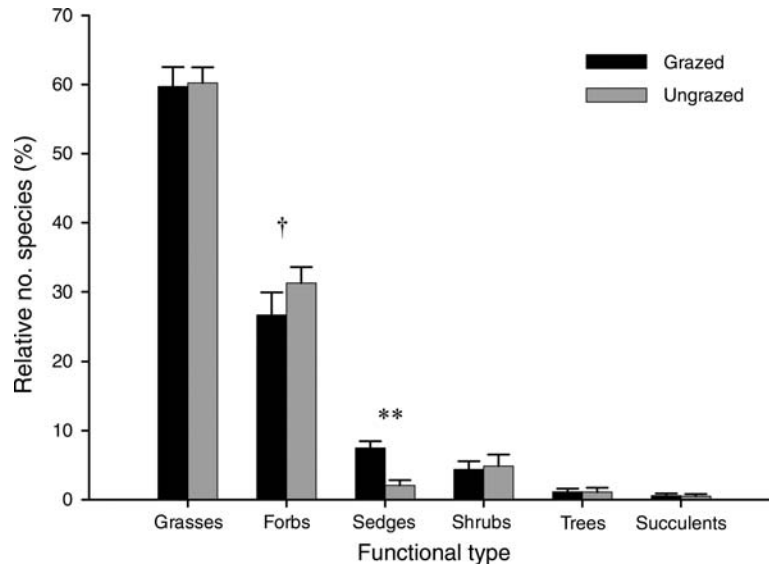


FIG. 5. Relative species richness (mean + SE) of six plant functional types in grazed and ungrazed treatments across eight grassland sites in Serengeti National Park. Univariate paired *t* tests between grazed and ungrazed plots suggested differences for forbs and sedges († $P < 0.08$; ** $P < 0.001$). More comprehensive multivariate comparisons including nonmetric multidimensional scaling and discrimination analysis confirmed that species functional-type richness was influenced by excluding grazers.

predictions and the results from other studies (Proulx and Mazumder 1998, Austrheim and Eriksson 2001, Frank 2005), we hypothesized that herbivore removal effects on plant species richness would change from positive in dry regions on fertile soils to negative in wet regions on infertile soil. This hypothesis was not supported by responses of absolute plant species richness. In contrast, we found that absolute plant species richness decreased more when herbivores were removed at intermediate rainfall than at either high or low rainfall. This finding was despite major differences among sites in terms of soils, climate, plant species composition, grazing intensity, and regional affiliation (Fig. 1; McNaughton 1983, 1985, Ruess and Seagle 1994).

The relative change in plant species richness with herbivore removal also differed from our initial predictions in several ways. Herbivore-induced changes in soil P emerged with rainfall as an important correlate of changes in plant species richness in the absence of herbivores. Specifically, herbivore removal led to a relatively greater loss of species in the form of greater local extinctions and fewer colonizations of new species at lower rainfall sites and where herbivore removal also caused increases in soil P. In contrast, at sites with higher rainfall and where herbivore removal reduced soil available P, herbivore removal led to relatively little change in species richness but dramatic turnover of plant species and functional groups.

Herbivore modification of plant diversity was associated more strongly with rainfall and herbivore effects on soil nutrients, particularly P, than with modification of competition for light. The fact that sites had either high

rainfall or high soil nutrient availability explains why sites were all highly productive ($>600 \text{ g/m}^2$) in the absence of herbivores. Grazing intensities varied, but herbivores reduced biomass on average by 30% and at most by 56% across sites, which was not enough to reduce plant biomass to $<300 \text{ g/m}^2$ or enough to provide plant species major relief from light competition (Collins et al. 1998, Ritchie and Olf 1999, Bakker et al. 2004). Instead, herbivore removal induced rather large proportional increases in soil available P, of over twice as much between paired exclosures within a site and 41% averaged across a site (Fig. 3, Table 1), which may be large enough to prevent P limitation and decrease plant species richness (Willems et al. 1993, Kirkham et al. 1996, Janssens et al. 1998, Güsewell 2004). These results are consistent with observational studies of pastures in the northeastern United States (Tracy and Sanderson 2000), Ottawa River wetlands in Canada (Weiher et al. 1998), European grasslands (Janssens et al. 1998), and experimental additions of P in Dutch chalk grasslands (Willems et al. 1993), in which higher soil available P was associated with lower plant species richness.

The alteration of P by herbivores is less well known than the alteration of soil N (Pastor et al. 1988, McNaughton et al. 1997, Frank and Groffman 1998), but is not without precedent. Exclusion of red deer in Scottish highlands changed an N-limited system to P-limited, although the authors hypothesized the shift was due to increased N mineralization rather than decreased P mineralization (Carline et al. 2005). Local herbivore-induced P losses can result from increased P cycling rates from plant tissue consumption and turnover and P accumulation in animal biomass (particularly in bones)

that outstrip soil P mineralization (Chaneton et al. 1996). Given the potential for tropical soils to be lower in P than in glaciated or otherwise younger North American and European soils (Vitousek 2004), it is possible that variation in herbivore effects on soil nutrients may explain previous reports of both positive and negative effects of herbivores on plant richness in tropical savannas (McNaughton 1983, Noy-Meir et al. 1989, Mwendera et al. 1997, Todd and Hoffman 1999, Oba et al. 2001, Taddese et al. 2002).

There are several possible explanations for the observed variation in herbivore effects on soil available P across sites. Phosphorus availability is strongly influenced by pH, and herbivores can influence soil pH via several mechanisms, including stimulation of plant root exudates, influencing organic matter content through dung deposition, and modifying the soil moisture regime and decomposition rates (Augustine and Frank 2001, Hamilton and Frank 2001, Bardgett and Wardle 2003). Moreover, microbial mineralization of P can play an important role in P availability (Stewart and Tiessen 1987, Bardgett 2005), and the effects of herbivory on microbial processes and dynamics are well known (Ruess and McNaughton 1987, Frank et al. 2000). Therefore, if the effects of herbivory on soil pH and microbial processes differ across the wide variety of soil types sampled in our study (Ruess and Seagle 1994), then one would expect fencing to produce variation in P availability across SNP; we feel this untested hypothesis is deserving of further examination in future studies.

Herbivory and plant species composition

We observed a strong rainfall \times grazing interaction on species compositional turnover between treatments. The resulting slope suggested that for every increase in mean annual precipitation of 10 cm the compositional similarity declines by $\sim 6\%$ (Fig. 5). These results indicate the contribution of new unshared species inside exclosures in northern higher rainfall, lower P sites compared to the lower availability of species adapted to high-biomass, low-light exclosure conditions in the drier Serengeti plains sites. Grazing at higher rainfall sites may selectively reduce the abundance of preferred plant species such as forbs and increase more tolerant species such as grasses and sedges. Such selective grazing might have eliminated species that may be strong light competitors at high water availability and productivities $>600 \text{ g/m}^2$, but not as tolerant of grazing.

The results of the among-plot compositional similarity demonstrated that herbivore removal led to more heterogeneous species composition within a site. Adler et al. (2001) suggest two general scenarios in which grazers reduce spatial heterogeneity in composition: (1) when grazing is spatially homogenous or otherwise not based on the distribution of vegetation and (2) when grazing decreases the contrast between patches through selectivity that follows the spatial template of the vegetation. Grazing in the low-rainfall Serengeti plains

is ubiquitous for much of the wet season, and while it may not be random, ungrazed vegetation is rare; reduced compositional similarity in our low-rainfall sites is probably best explained by scenario 1. In comparison, vegetation removal is more sporadic at northern sites, as resident herbivores are relatively rare and migrants graze these sites while migrating to dry-season foraging locations in Kenya. Herbivores at these northern sites may graze heavily on patches of palatable species and thus increase compositional similarity by promoting the dominance of herbivore-tolerant species, similar to Adler et al.'s (2001) scenario 2.

Herbivory, congener coexistence, and plant functional types

The negative effect of herbivore removal on plant species richness across sites reflected a lack of coexistence of congeners of the grass genera *Sporobolus* (seven species), *Eragrostis* (six species), *Digitaria* (three species), *Brachiaria* (two species), *Pennisetum* (two species), and *Panicum* (two species). To the best of our knowledge, this is the first study to recognize that native herbivores increase species richness in a natural ecosystem via this mechanism. Studies of congeneric species from the Mediterranean region corroborate the hypothesis that grass congeners often show clear ecological differentiation and differ in both competitive and colonization ability (Lavergne et al. 2004). Although not explicitly considered, previous studies suggest that grazing may promote congener coexistence in other grazing ecosystems, such as European subalpine grasslands (Schutz et al. 2003) and Indian savannas (Pandey and Singh 1991). On the other hand, congeners were more likely to coexist in lightly or ungrazed grasslands in South America (Bisigato and Bertiller 1997, Rusch and Oesterheld 1997). More research is needed to reveal what evolutionary, environmental, and dispersal forces affect congeneric species coexistence (Noy-Meir et al. 1989, Tofts and Silvertown 2002).

The observed effects of grazing on plant functional types was not typical for arid grazing lands in northern and southern Africa, South America, or the Mediterranean, where grazing often eliminates palatable functional types such as grasses and sedges in favor of unpalatable forbs and shrubs (Noy-Meir et al. 1989, Bisigato and Bertiller 1997, Rusch and Oesterheld 1997, Knapp et al. 2004). The promotion of grasses and sedges in grazed plots reveals the strongly coevolved association between the graminoids and the abundant ungulate herbivore fauna for which East African savannas are famous (McNaughton 1984, Milchunas et al. 1989).

Synthesis

Our results were not explained well by a theory of variation in palatability of dominant species across the environmental gradient we studied. Instead, responses of plant species richness and composition more closely match the predictions of heterogeneous food web

models (Leibold 1996, Leibold et al. 1997). These models predict a unimodal relationship between plant species richness and resource availability, a negative relationship between resource availability and compositional similarity between grazed and ungrazed plant communities, and greater coexistence between closely related species in the presence of herbivores. We found all three of these patterns in our results (Figs. 2 and 4) despite a lack of correlation between ungrazed biomass and rainfall or soil N or P, as the theory predicts. The interesting twist in the Serengeti is that plant dynamics may be governed by trade-offs between herbivory resistance and competitive ability for multiple resources instead of one, e.g., soil N, soil P, water, and light (McNaughton 1983, 1985). If productivity is limited by multiple resources, it may be poorly predicted by a single resource gradient, but traits that allow competitive coexistence for these multiple resources may still trade off with tolerance of herbivory and yield the patterns we found. For example, our sites varied much less in productivity than expected from variations in any single resource gradient, such as if productivity depended solely on rainfall.

The trade-off between coexistence on multiple resources and herbivory resistance may explain many of our unexpected and most important results, such as the importance of P in diversity–herbivory interactions and rainfall in composition–herbivory interactions, even in otherwise N-limited tropical grassland (Table 1; McNaughton et al. 1988). We also illustrate the potential for herbivores to yield large changes in plant composition without large changes in species richness. Our results suggest that gradients in nutrients, precipitation, and herbivory interact in ways that challenge current community dynamics models and ecologists' understanding of mechanisms that determine diversity in terrestrial ecosystems (House et al. 2003).

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APPENDIX A

A table showing site comparisons of soil available nitrogen, soil available phosphorus, soil N:P ratios, grazed standing biomass, ungrazed standing biomass, and grazing intensity (*Ecological Archives* E088-075-A1).

APPENDIX B

A table showing Pearson correlation coefficients and associated *P* values among site variables from Table 1 and Appendix A (*Ecological Archives* E088-075-A2).