
Effect of Vertebrate Grazing on Plant and Insect Community Structure

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Abstract: We compared species diversity of plants and insects among grazed and ungrazed areas of Ponderosa pine-grassland communities in Arizona. Plant species richness was higher in two of three grassland communities that were grazed by native elk and deer and domestic cattle than in ungrazed areas inside a series of three large (approximately 40-ha) grazing exclosures. Similarly, plant species richness was higher in grazed areas relative to ungrazed areas at one of two series of smaller (approximately 25-ha) and short-term exclosure sites. Evenness of plant distribution, however, was greater inside ungrazed long-term exclosures but was reduced inside ungrazed short-term exclosures relative to grazed areas. Relative abundances of forbs, grasses, trees, and shrubs, and native and introduced plants did not differ between the long- and short-term grazing exclosures and their grazed counterparts. Relative abundances of some plant species changed when grazers were excluded, however. In contrast, insect species richness was not different between grazed and ungrazed habitats, although insect abundance increased 4- to 10-fold in ungrazed vegetation. Our results suggest that vertebrate grazing may increase plant richness, even in nutrient-poor, semi-arid grasslands, but may decrease insect abundances.

Efecto del Pastoreo de Vertebrados en la Estructura Comunitaria de Plantas e Insectos

Resumen: Comparamos la diversidad de especies de plantas e insectos entre áreas pastoreadas y no pastoreadas en comunidades de pino-pastizal en Arizona. La riqueza de especies de plantas fue mayor en dos de tres comunidades de pastizales que fueron ramoneadas por alces y venados nativos y ganado vacuno, en comparación con áreas sin ramoneo dentro de una serie de tres encierros grandes para pastoreo (~40 ha). Similarmente, la riqueza de especies de plantas fue mayor en áreas ramoneadas en relación con áreas no ramoneadas en una de dos series de encierros pequeños (~25m²) y de corta duración. Sin embargo la distribución homogénea de plantas fue mayor dentro de encierros de largo plazo sin ramoneo, pero fue reducida en encierros de corto plazo sin ramoneo en relación con áreas ramoneadas. La abundancia relativa de hierbas, pastos, árboles y arbustos y plantas nativas e introducidas no difirió entre encierros para pastoreo de corto y largo plazo y su contraparte ramoneada. Sin embargo, las abundancias relativas de algunas especies de plantas cambiaron cuando los ramoneadores fueron introducidos. En contraste, la riqueza de especies de insectos no fue diferente entre hábitats ramoneados y no ramoneados, aunque la abundancia de insectos aumentó 4-10 veces en la vegetación sin ramonear. Nuestros resultados sugieren que el ramoneo por vertebrados puede incrementar la riqueza de las plantas, aun en pastizales pobres en nutrientes y semiáridos, pero puede disminuir las abundancias de insectos.

Introduction

Natural disturbances may increase species diversity by reducing competition from dominant species, thus al-

lowing rarer species to persist (Petraitis et al. 1989; Caswell & Cohen 1993), or by creating patches of habitat at different stages of regeneration, enabling early- and late-successional species to coexist (Connell 1978; Huston 1979, 1994; Ricklefs 1993). For example, the overt suppression of large-scale natural disturbances, such as periodic fire and flooding, may diminish diversity (D'An-

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tonio & Vitousek 1992; Leach & Givnish 1996; Wootton et al. 1996). Alternatively, catastrophic disturbances may extirpate local populations and thus reduce species diversity (Connell 1978; Huston 1979, 1994). One hypothesis, therefore, suggests that intermediate disturbances support higher species diversity than do rare or more frequent events or those disturbances occurring at higher or lower levels of intensity (Harper 1969; Paine & Vadas 1969; Connell 1978; Huston 1979, 1994; Aronson & Precht 1995).

Herbivory, especially grazing by vertebrates, has been considered one such disturbance that may increase plant diversity by reducing competitive dominants and allowing rarer species to coexist (McNaughton 1983, 1985; Huntly 1991; Ricklefs 1993; Howe 1994; Crawley 1997; Olf & Ritchie 1998) or by ameliorating the effects of other diversity-reducing disturbances such as fire (Collins et al. 1998). Recent evidence suggests, however, that vertebrate herbivory does not always increase plant diversity and occasionally may decrease it (Olf & Ritchie 1998). For example, grazing by livestock may increase or decrease plant species richness (Olf & Ritchie 1998), and thus the effect of livestock grazing on plant diversity remains an unresolved and controversial conservation issue (National Research Council 1994). Some resolution may be provided by recent models suggesting that variability in the effects of large herbivores on plant diversity depends on spatial scale and environmental gradients of soil nutrients and moisture (Huston 1994; Olf & Ritchie 1998).

If herbivory by vertebrates alters plant diversity and availability of resources, then concomitant changes in diversity and abundances of other herbivores, such as invertebrates, are also expected (Siemann et al. 1998). Because most insect herbivores are specialized to feed on only one or a few plant species (e.g., Strong et al. 1984), increases in plant diversity also should increase phytophagous insect diversity, but decreases in the quantity of resources may have opposing effects on abundances and, hence, diversity. Many studies have examined the effect of grazing on terrestrial plant communities, but few have examined how vertebrate grazing in these habitats may indirectly influence phytophagous insect diversity by altering plant abundances and diversity.

We examined the effect of native ungulate and introduced cattle grazing as a disturbance of plant and insect community structure in ponderosa pine-grasslands on the Mogollon Rim in Arizona. We compared plant and insect abundance and diversity in long- and short-term grazing exclosures to immediately adjacent areas that were grazed consistently and intensively by domestic cattle and native elk and deer. We also determined plant species composition and abundances relative to growth forms (i.e., forbs vs. grasses vs. shrubs and trees), life histories (i.e., annual, biennial, perennial), and native and non-native species in grazed and ungrazed treatments.

Methods

Sampling

In the summer of 1996, we sampled plant and insect richness and abundance at three open meadows in separate drainages that were flanked by stands of Ponderosa pine on the Mogollon Rim (elevation, 2200 m). At each site (Houston Draw, Merritt Draw, and Buck Springs) an electrified (solar-powered), 13 foot high (4 m) exclosure fence had prevented grazing by cattle, elk, and deer for the previous 8–9 years in large areas (approximately 40 ha). The fence is maintained annually by the U.S. Forest Service (S. Calish, personal communication). Vegetation inside and outside the exclosures shows marked differences in biomass, at least since we began studying these plots in 1994. Vegetation inside the exclosures is dense and approximately 1 m high, whereas vegetation outside the exclosures is consistently cropped by cattle, elk, or deer to <10 cm high.

We examined short-term (1 year) suppression of grazing on plant diversity at two additional, nearby sites at Clint's Well, where we constructed 10 small (5 × 5 m) exclosures with three strands of barbed wire in 1995. The small exclosures minimally prevented grazing by cattle but also probably by elk and deer because these grazers avoid jumping into small exclosures to feed (W. Miller, personal communication). We inspected and maintained the integrity of the small exclosures monthly, and none showed evidence of intrusion by cattle or native ungulates. The short-term exclosures occupied an area partially covered by pine canopy and, unlike the long-term sites, were on hillsides at least 1 km from any drainages.

Cattle are rotated onto both the long- and short-term exclosure sites each summer for periods ranging from 4 to 30 days, depending on the quality and quantity of forage. Generally, the number of cattle and duration of foraging is adjusted each summer such that about 70% of the standing, aboveground biomass is consumed (S. Calish, C. Finch, personal communication). Elk and deer, on the other hand, may forage year-round, except when prevented from doing so by snow cover. We could not ascertain the relative contribution of cattle, elk, and deer (deer are primarily browsers but also graze) to cumulative grazing at the long- and short-term sites. But deer and especially elk, however, are common at the study sites, and our question of interest is how vertebrate grazing in general affects plant and insect diversity.

In June and July of 1996, plants and insects were sampled along two parallel transects, one inside (ungrazed) and outside one (grazed) of each long-term exclosure. Parallel transects representing grazed and ungrazed treatments were positioned approximately 5 m apart (approximately 2.5 m from respective sides of the exclosure fence) to minimize differences in soils, nutrients,

and microclimates. We sampled species richness and abundance of plants in a total of 30 grazed and 30 ungrazed 1-m² quadrats (10 quadrats outside and 10 inside the exclosures at each of the three long-term sites) that were placed at 10-m intervals along the transects. We sampled insects in July 1996 by sweep-netting the vegetation over equal distances of the transect lines in grazed and ungrazed areas. Sweep netting is effective only for sampling part of the insect community (e.g., ground-dwelling insects are mostly excluded) but is commonly used to effectively sample insects associated with above-ground plant biomass (Southwood 1978). Insects were identified to at least the family level and thereafter were designated as morphotypes based upon morphological features.

At short-term grazing exclosure sites, we determined plant species richness and abundances within exclosures and in equal-sized (approximately 25 m²) and contiguous areas outside the exclosures in July 1996. All individual plants inside and outside the exclosures were censused.

Statistical Analysis

We compared plant and insect species richness in grazed and ungrazed communities using EcoSim® (Gotelli & Entsminger 1997). EcoSim® statistically compares species richness between two communities and accounts for differences in the number of individuals sampled by rarefaction (Sanders 1968). In brief, rarefaction uses randomization and probability theory to derive expressions for the expected mean and variance of species richness for a sample comprised of a given number of individuals (Hurlbert 1971; Heck et al. 1975; Simberloff 1979; Gotelli & Entsminger 1997). In practice, EcoSim iteratively draws a specified number of individuals (typically, the number of individuals sampled in the smaller of two communities is drawn from the larger community) randomly to generate a mean and variance of species richness (Gotelli & Entsminger 1997). In other words, the larger community in terms of sampled individuals is rarefied down to the smaller community. With many iterations (we used 1000), a 95% confidence interval for species richness is generated, and if the observed species richness of the smaller community falls outside this interval, the hypothesis that communities differ in species richness can be rejected at $\alpha = 0.05$.

For the following reasons, we used rarefaction of species richness via EcoSim instead of commonly used diversity indices, such as the Shannon-Weiner index. Diversity indices confound species richness and evenness in a single measure that cannot be easily interpreted statistically or biologically (Hurlbert 1971; Peet 1974; Krebs 1989; Gotelli & Entsminger 1997). Second, in comparing two communities most diversity indices do

not account for differences in sample size (Ludwig & Reynolds 1988; Krebs 1989).

We also compared evenness, or how individuals are distributed among species, of the grazed and ungrazed communities using Hurlbert's probability of intraspecific encounter (PIE). We used PIE, which is the probability that two randomly sampled individuals from the community are two different species (Hurlbert 1971), because this measure of evenness is unbiased by sample size and number of species in a sample, unlike most other evenness indices (Peet 1974; Ludwig & Reynolds 1988). As in the procedure described above, we used rarefaction (1000 iterations) to statistically test differences in plant and insect evenness in grazed and ungrazed communities. In addition, we determined relative abundances of plant and insect species for grazed and ungrazed communities by calculating the percentage of individuals of each species present in each sample.

To compare the relative abundances of forbs, grasses, and trees or shrubs inside and outside the exclosures, we used G tests (with Williams's correction) of independence (Sokal & Rohlf 1995) with 2 df (2×3 table for each comparison).

Results

Plant Community Structure

Plant species richness was greater in grazed areas than in ungrazed areas at two of three long-term sites (Table 1). Richness also tended to be greater in the grazed area of the other long-term site, although not significantly so. Similarly, grazing was associated with higher plant richness at one of two short-term exclosure sites (Table 1).

Evenness, or the relative distribution of individuals among species, was greater in two of three ungrazed long-term communities than in the grazed communities (Table 1). Evenness, however, was lower in both of the ungrazed short-term sites than in the grazed areas (Table 1).

At the long-term sites (Table 2), the relative abundances of forbs, grasses, or trees and shrubs did not differ among grazed and ungrazed areas (Houston Draw, $G = 0.32$, $p > 0.80$, 2 df; Buck Springs, $G = 3.6$, $p > 0.10$, 2 df; Merritt Draw, $G = 3.4$, $p > 0.10$). But the relative abundances of forbs, grasses, or trees and shrubs differed between the grazed and ungrazed areas at one of the short-term sites (N-1, $G = 10.6$, $p < 0.01$, 2 df) but not the other (B-3, $G = 2.1$, $p > 0.30$, 2 df). At the N-1 site, the relative abundance of grasses decreased and that of shrubs and trees increased outside the exclosures in grazed areas.

There were no consistent differences between grazed and ungrazed areas in relative abundances of introduced plant species, which may be of particular interest to conservation biologists (Tables 2 & 3). For example,

Table 1. Differences between grazed and ungrazed communities in plant species richness, Hurlbert's PIE.^a

Site	Species richness		p ^c	Hurlbert's PIE		p ^c	Abundances	
	grazed	ungrazed		grazed	ungrazed		grazed	ungrazed
Long term								
Houston	33	30	ns	0.83	0.92	<0.05	883	694
Buck Springs Draw	27 ^b	20	<0.05	0.77	0.83	<0.05	1453	1207
Merritt Draw	25 ^b	23	<0.05	0.88	0.89	ns	393	463
Short term								
B-3	21	24	ns	0.72	0.66	<0.05	448	813
N-1	31 ^b	31	<0.05	0.86	0.79	<0.05	729	1150

^aProbability of intraspecific encounter, a measure of evenness.

^bIndicates species richness greater than at ungrazed sites at $p < 0.05$ based upon rarefaction; they are greater than expected.

^cns, not significantly different at $\alpha = 0.05$.

Cerastium vulgatum, a naturalized weed from Europe (Table 2), and *Tragopogon dubius*, European goats-beard (Table 3), were found in only one of the grazed areas, but *Brassica tournefortii*, an introduced weed, was found in only one of the ungrazed short-term sites (Table 3). Other non-native plants, *Potentilla anserina* (Argentine silverweed) and *Taraxacum officinale* (dandelion), were in greater relative abundances overall in ungrazed and grazed areas of long-term plots, respectively, but were also found in both grazed and ungrazed areas of short-term and long-term sites (Tables 2 & 3). The relative abundance of one of the dominant plant species at the three long-term sites, *Achillea lanulosa* (yarrow or milfoil), increased consistently in grazed areas (Table 2).

Insect Community Structure

Insect species richness was not different between grazed and ungrazed plant communities (Table 4). Because relatively few individuals were sampled, however, confidence intervals were wide, and thus rejection of the null hypothesis of no difference in richness was improbable. Evenness of insect species was generally high in all of the grazed and ungrazed long-term areas, with no differences in grazed and ungrazed areas (Table 4). The abundances of insects, as measured by total number of individuals collected in standardized net sweeps, was 4–10 times greater inside long-term grazing exclosures than in grazed areas (Table 4). Several insect species occurred only in ungrazed areas, but conclusions regarding individual species are tenuous because generally we collected low numbers of individuals per species.

Discussion

Plant Diversity and Relative Abundances

The general increase in plant species richness in grazed grasslands relative to ungrazed areas inside the exclosures suggests that ungulate grazers alter species rich-

ness by reducing dominant and competitive plants, thus allowing other, less competitive plants to persist. Changes in plant species richness may be positively related to the duration and intensity of disturbance (e.g., Collins 1987; Huston 1994), at least up to some point (Connell 1978; Huston 1979, 1994), and may also depend on timing of grazing, successional stage, and the effects of dominant species on rare species (Armesto & Pickett 1985). Similar results for the short-term sites suggest that the effects of grazing may occur relatively quickly (within one or two growing seasons) and in plant communities with different species compositions and relative abundances (Tables 2 & 3).

Large herbivores may generally maintain diversity by altering plant competitive hierarchies (McNaughton 1983; Collins 1987; Facelli 1988; Gibson 1988; Chanton & Facelli 1991) and by increasing the amount of light in the canopy. At the long-term sites, excluding large grazers consistently decreased relative abundances of the dominant western yarrow (*Achillea lanulosa*) and generally increased evenness (Tables 1 & 2). Western yarrow is a low-growing, unpalatable forage plant for both cattle and native ungulates and often increases in areas that are severely overgrazed (U.S. Department of Agriculture 1988). Increases in the relative abundance of western yarrow in grazed areas suggest that grazing reduces competition by more palatable or taller species.

Differences in direction of evenness with exclusion of grazers in long- and short-term plots may be related to differences in starting plant communities in those plots or may suggest temporal changes in plant dominance hierarchies after exclusion of vertebrates. Short-term exclusion of grazers was associated with decreased evenness (Table 1), suggesting relatively rapid increases in the dominance and rarity of some plant species. For at least one of the short-term exclosures, N-1, exclusion of grazers was associated with an increase in grasses at the expense of shrubs and trees. Increases in the relative abundance of grasses stems mainly from increases in the already dominant *Festuca arizonica* (Arizona fescue, Table 3). Arizona fescue is a common and important forage

Table 2. Plant species composition and relative abundances at long-term grazing exclusion sites.

Species	Plant characteristics*	Relative abundance (%)					
		Houston Draw		Buck Springs		Merritt Draw	
		grazed	ungrazed	grazed	ungrazed	grazed	ungrazed
Forbs							
<i>Acillea lanulosa</i>	PNF	35.4	14.8	30.0	14.8	26.0	18.4
<i>Agoseris aurantiaca</i>	PNF	0.91	0.14	0.14	1.08	0	2.16
<i>Antennaria parvifolia</i>	PNF	7.47	0	36.6	34.4	2.30	6.05
<i>Arenaria lanuginosa</i>	PNF	0.11	0	0	0	0	0
<i>Cerastium vulgatum</i>	PIF	0	0	0	0	0.25	0
<i>Comandra pallida</i>	PNF	0.11	0	0	0	0	0
<i>Desmodium grabami</i>	PNF	0	0.14	0	0	0.51	0
<i>Draba asprella</i>	PNF	1.36	0	0	0	0.51	3.67
<i>Dulgaldia boopesii</i>	PNF	1.81	12.1	0.14	0	1.78	3.67
<i>Erigeron formosissimus</i>	PNF	1.93	0	1.10	0	0	0
<i>Erigonum racemosum</i>	PNF	2.83	0	0.69	0	0	0
<i>Erysimum wheeleri</i>	BNF	0	0	0	0	0	0.22
<i>Fragaria bracteata</i>	PNF	1.36	6.48	1.51	0.08	6.36	0
<i>Fragaria ovalis</i>	PNF	0	0	0	0	2.54	0.432
<i>Geranium caespitosum</i>	PNF	1.70	2.59	0.14	0	4.58	1.08
<i>Geum macrophyllum</i>	PNF	0	0	0.07	0	0	0
<i>Houstonia rubra</i>	PNF	0	1.01	0	1.66	0	0
<i>Hymenoxys cooperi</i>	BNF	0	0	1.93	0	0.25	0.65
<i>Isis missouriensis</i>	PNF	0	0.57	0	0	0	0
<i>Lepidium montanum</i>	PNF	0	0.29	0.07	0	0	0
<i>Lupinus</i> spp.	A/PNF	0.79	3.46	0	0	0.51	2.38
<i>Phacelia heterophylla</i>	BNF	0	0	0.07	0	0	0
<i>Potentilla anserina</i>	PIF	0.57	4.32	2.13	9.11	0	0
<i>Potentilla arguta</i>	PNF	0	2.45	0	0	0	0
<i>Pseudocymopterus montanus</i>	PNF	1.35	1.73	2.13	0	0	0
<i>Pteridium aquilinum</i>	PNF	0.79	0.29	0	0	1.27	0.432
<i>Senecio neomexicanus</i>	PNF	0	0.43	0.07	0	0	1.51
<i>Senecio wootonii</i>	PNF	0	0	0.07	0	0	0
<i>Smilacina stellata</i>	PNF	0	3.75	0	0	0	0
<i>Swertia radiata</i>	PNF	1.81	6.34	0	0	1.78	0.22
<i>Taraxacum officinale</i>	PIF	2.27	0.87	2.41	4.14	5.85	2.59
<i>Thermopsis pinetorum</i>	PNF	4.98	8.79	0	0.08	0	0
<i>Tblaspi montanum</i>	PNF	0.57	0	0	0	0	0
<i>Vicia americana</i>	PNF	6.34	3.60	1.79	2.57	9.16	16.2
<i>Viguiera multiflora</i>	PNF	0.11	0.14	0	2.15	0	0
Unknown forb sp. 1		0.23	0.72	0	0	0	0
Unknown forb sp. 2		0.23	0	0	0	0	0
Unknown forb sp. 3		0	0	0	0.41	0	0
Unknown forb sp. 4		0	0	0	0.33	0	0
Unknown forb sp. 5		0.79	0	0	0.66	0	0
Unknown forb sp. 6		0.11	0	0	0	0	0
Unknown forb sp. 7		0.11	0	0	0	0.51	0
Unknown forb sp. 8		0	1.15	0	0	0	0
Unknown forb sp. 9		0	0	0	0	0	3.89
Unknown forb sp. 10		0	0	0	0	0.76	0
Total forbs (%)		76.0	76.2	81.0	71.5	64.7	63.5
Grasses							
<i>Andropogon scoparius</i>	PNG	1.70	1.44	1.45	4.97	0.51	0.86
<i>Festuca arizonica</i>	PNG	1.36	3.46	3.10	2.49	2.80	2.38
<i>Hilaria belangeria</i>	PNG	0.68	0.14	2.00	4.06	0.25	0.86
<i>Poa pratensis</i>	PNG	1.93	4.90	1.03	7.29	10.9	7.56
<i>Aristida longiseta</i>	PNG	17.0	12.4	8.12	7.13	12.0	19.7
Total grasses (%)		22.7	22.3	15.7	25.9	26.5	31.4
Shrubs and trees							
<i>Lotus wrightii</i>	PNS	0	0	0.07	0	0	0
<i>Penstemon liniaroides</i>	PNS	1.13	1.15	2.13	2.49	4.83	1.73
<i>Pinus ponderosa</i>	PNT	0	0	0	0.08	0	0
<i>Quercus gambelli</i>	PNT	0.11	0.29	0.14	0	0.51	0
<i>Rosa fendleri</i>	PNS	0	0	0.90	0	3.31	3.46
Total shrubs/trees (%)		1.24	1.44	3.23	2.57	8.65	5.19

*First letter: A, annual; B, biennial; P, perennial. Second letter: N, native; I, introduced. Third letter: F, forb; G, grass; T, tree.

Table 3. Plant species composition and relative abundances at short-term grazing exclosure sites.

Species	Plant characteristics*	Relative abundance (%)			
		B-3 site		N-1 site	
		grazed	ungrazed	grazed	ungrazed
Forbs					
<i>Achillea lanulosa</i>	PNF	0	0	3.29	0
<i>Antennaria parvifolia</i>	PNF	7.59	12.2	7.41	4.70
<i>Aster commutatus</i>	PNF	2.90	0.98	0	0
<i>Brassica tournefortii</i>	AIF	0	0	0	0.09
<i>Castilleja</i> spp.	PNF	0	0	0.27	0.17
<i>Corydalis aurea</i>	PNF	0	0	1.10	1.13
<i>Draba asprella</i>	PNF	0	0	0	3.48
<i>Draba aurea</i>	PNF	0	0	0.41	0
<i>Dugaldia boopesii</i>	PNF	0	0	0.14	0
<i>Erigeron formosissimus</i>	PNF	0.22	0.49	0.14	1.04
<i>E. oreophilus</i>	PNF	0	0	0	0.09
<i>Geranium caespitosum</i>	PNF	0.89	1.35	0	0
<i>Heterotheca villosa</i>	ANF	0	0	0.55	1.48
<i>Houstonia rubra</i>	PNF	0	0	2.06	0.17
<i>Hymenoxys cooperi</i>	BNF	0.67	0.98	6.45	4.26
<i>Leucelene ericoides</i>	PNF	0.45	0.25	3.29	10.7
<i>Lotus corniculatus</i>	PIF	0	0	0.82	0.09
<i>Mentzelia pumila</i>	BNF	0	0.12	0	0
<i>Oxytropis lambertii</i>	PNF	0	0	0.14	0.17
<i>Pedicularis centranthera</i>	PNF	7.81	6.15	0	0
<i>Petalostemum occidentale</i>	PNF	0	0	0	0.09
<i>Potentilla anserina</i>	PIF	1.34	0.25	1.23	0
<i>Pseudocymopterus montanus</i>	PNF	0.67	0.25	0	0.09
<i>Senecio neomexicanus</i>	PNF	1.12	0.74	1.37	0.09
<i>Taraxacum officinale</i>	PIF	0	0	0.14	0.09
<i>Tragopogon dubius</i>	PIF	0	0	0.14	0
<i>Vicia americana</i>	PNF	0	0	0.69	0
<i>Viguiera multiflora</i>	PNF	1.12	0.49	0.41	2.47
Unknown forb sp. 3		0	0.744	0	0
Unknown forb sp. 11		0.89	0	0	0
Unknown forb sp. 12		1.34	0.37	0	0
Unknown forb sp. 13		0	0	0.27	0.52
Unknown forb sp. 14		0	0	0.69	0.26
Unknown forb sp. 15		0	0	0	0.09
Total forbs (%)		27.0	25.4	31.0	31.3
Grasses					
<i>Festuca arizonica</i>	PNG	50.2	56.3	30.2	38.9
<i>Hilaria belangeria</i>	PNG	0.89	0.98	13.9	9.74
<i>Poa pratensis</i>	PNG	0	0.12	2.19	0
<i>Sitanion bystrix</i>	PNG	12.5	6.15	12.3	16.6
<i>Aristida longiseta</i>	PNG	0	0	0	1.30
Unknown grass spp.		0	0	0.27	0
Total grasses (%)		63.6	63.6	58.9	66.5
Shrubs and trees					
<i>Bouvardia glaberrima</i>	PNS	0	0	0.96	0.52
<i>Cerocarpus</i>	PNS	3.35	1.85	0	0.87
<i>Cornus stolonifera</i>	PNS	0	0	1.51	0.35
<i>Lotus wrightii</i>	PNS	0.45	0.49	1.37	0.26
<i>Penstemon linariodes</i>	PNS	3.13	3.32	6.04	0.96
<i>Phlox woodhousei</i>	PNS	2.01	3.81	0	0
<i>Pinus ponderosa</i>	PNT	0	0	0.41	0.17
<i>Quercus gambelii</i>	PNT	0.45	1.60	0	0
<i>Senecio douglasii</i>	PNS	0	0.37	0	0
Total shrubs/trees (%)		9.38	11.4	10.3	3.13

*First letter: A, annual; B, biennial; P, perennial. Second letter: N, native; I, introduced. Third letter: F, forb; G, grass; S, shrub; T, tree.

Table 4. Differences in species richness, Hurlbert's PIE^a and abundances of insects between grazed and ungrazed communities at long-term sites.^b

Site	Species richness		Hurlbert's PIE		Abundances	
	grazed	ungrazed	grazed	ungrazed	grazed	ungrazed
Houston Draw	9	22	0.91	0.74	13	62
Buck Springs	10	27	0.92	0.96	13	52
Merritt Draw	6	45	0.95	0.96	7	74

^aProbability of intraspecific encounter, a measure of evenness.

^bNone of the differences were significant at $\alpha = 0.05$.

grass in the southwestern United States but often decreases when overgrazed (U.S. Department of Agriculture 1988). At the long-term sites, evenness was generally higher in ungrazed areas, suggesting that, over time, dominant species become less so. There were fewer grasses at the long-term sites (Table 1), however, so differences in the direction of evenness may simply reflect variation among plant communities.

Olf and Ritchie's (1998) recent review proposes that the net effects of large grazers on plant diversity vary with spatial scale and environmental conditions, notably soil nutrients and moisture. They predicted that grazing by large herbivores should reduce plant diversity in dry, infertile habitats. Both the long- and short-term sites in this study are semiarid grasslands in Arizona, and both are characterized by low soil nutrients (Schulthess & Faeth 1998). The long-term sites generally have greater soil moisture because they are in low-lying drainage areas of perennial or semi-persistent streams. Nonetheless, our plant diversity results do not support the predictions of Olf and Ritchie (1998) at least at two spatial scales (25-m² and 40-ha exclosures).

Insect Diversity and Abundances

Insect diversity is usually positively related to plant biomass (Lawton 1983), plant structural diversity (Allan et al. 1975; Lawton 1983), and plant species diversity (Murdoch et al. 1972; Siemann et al. 1998) because most insect species (approximately 75%) are phytophagous (Lawton & Strong 1981). By altering plant communities, ungulate grazers may indirectly influence insect diversity. Greater insect species richness has occurred in habitats experiencing intermediate disturbances (Szentkiralyi & Kozar 1991), but we found no differences in insect species richness between grazed and ungrazed grassland at long-term exclosure sites. Because sweep sampling is effective for only a fraction of insect species (mainly those associated with aboveground vegetation) and because total numbers of insects were relatively low, any conclusions about the effects of grazing on insect diversity should be made cautiously. Insect abundances were 4–10 times higher in ungrazed areas than grazed areas. Insect abundance may have increased in ungrazed areas because of greater plant biomass and more complex

plant structural diversity (Southwood et al. 1979; Morris 1981), despite reduced plant diversity.

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