Multi-scale responses of vegetation to removal of horse grazing from Great Basin (USA) mountain ranges

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Abstract Although free-roaming equids occur on all of the world's continents except Antarctica, very few studies (and none in the Great Basin, USA) have either investigated their grazing effects on vegetation at more than one spatial scale or compared characteristics of areas from which grazing has been removed to those of currently grazed areas. We compared characteristics of vegetation at 19 sites in nine mountain ranges of the western Great Basin; sites were either grazed by feral horses (*Equus caballus*) or had had horses removed for the last 10–14 years. We selected horse-occupied and horse-removed sites with similar aspect, slope, fire history,

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grazing pressure by cattle (minimal to none), and dominant vegetation (*Artemisia tridentata*). During 1997 and 1998, line-intercept transects randomly located within sites revealed that horse-removed sites exhibited 1.1–1.9 times greater shrub cover, 1.2–1.5 times greater total plant cover, 2–12 species greater plant species richness, and 1.9–2.9 times greater cover and 1.1–2.4 times greater frequency of native grasses than did horse-occupied sites. In contrast, sites with horses tended to have more grazing-resistant forbs and exotic plants. Direction and magnitude of landscape-scale results were corroborated by smaller-scale comparisons within horse-occupied sites of horse-trail transects and (randomly located) transects that characterized overall site conditions. Information-theoretic analyses that incorporated various subsets of abiotic variables suggested that presence of horses was generally a strong determinant of those vegetation-related variables that differed significantly between treatments, especially frequency and cover of grasses, but also species richness and shrub cover and frequency. In contrast, abiotic variables such as precipitation, site elevation, and soil erodibility best predicted characteristics such as forb cover, shrub frequency, and continuity of the shrub canopy. We found species richness of plants monotonically decreased across sites as grazing disturbance increased, suggesting that either the bell-shaped diversity-disturbance curve of the intermediate-disturbance hypothesis does not apply in this system or that most sites are already all on the

greater-disturbance slope of the curve. In our study, numerous vegetation properties of less-grazed areas and sites differed notably from horse-grazed sites at local and landscape scales during a wetter and an average-precipitation year.

Introduction

After horses had been absent from North America for some 13,000 calendar years (Grayson 2006), domestic horses *Equus caballus* L. were brought to the southwestern United States by Spanish conquistadors near the end of the 16th century (Wagner 1983). Since their introduction, horses have played a controversial role in ecosystems of western North America (Beever 2003). Free-roaming horses of the Great Basin, USA represent a unique opportunity to investigate plant-herbivore dynamics in a unique management scenario. Whereas the legislation governing their management prevents their capture, branding, harassment, or harvest (unlike species of native ungulates, which are all hunted), it also declares horses "an integral part of the natural system of public lands" and requires a minimal-management mandate (unlike domestic animals, which are fenced and intensively managed).

This research opportunity is especially compelling in Great Basin shrublands, which have less coevolutionary history of abundant grazers than do savannahs, grasslands, or steppes (Grayson 2006). This leads one to predict that vegetation in the Basin may typically respond less favorably to herbivory than will vegetation in grasslands (Mack and Thompson 1982; Milchunas et al. 1988). A review by Milchunas et al. (1998) found that vegetation was one of the ecosystem components least affected by grazing in North American shortgrass steppe. A global analysis by Milchunas and Lauenroth (1993) of grazing-effects studies found that although years of protection from grazing was not important for vegetation in either grasslands or grasslands-plus-shrublands models, the factor was important in the shrublands model. However, although the vast majority of North America's free-roaming equids occur in shrublands (Anonymous 1997), studies of horse-vegetation relationships have occurred largely in grasslands (Detling 1998; Fahnestock and Detling 1999; Peterson 1999) and highly mesic areas (Turner 1987; Rogers 1991; Levin et al. 2002).

Free-roaming horses do not use landscapes homogeneously but instead move both seasonally (e.g., to higher sites in summer) and daily (e.g., to and from water), organized in bands (comprised usually of a stud and one to several mares with their offspring) and groups of one to several bachelor males. Due to differences in habitat use, mode of digestion, diet, evolutionary history, and morphology, it is inappropriate to assume that effects of grazing by feral horses are similar in nature or in magnitude to effects of grazing observed for other introduced or native species (Beever 2003). Furthermore, although numerous studies on grazing ecology of domestic horses have been published (Hafez et al. 1969; Reiner and Urness 1982), extrapolating these results to free-roaming (feral) populations may be problematic, particularly with respect to behavior (see Beever 2003, p. 892, for fuller discussion of this topic). Thus, there are relatively few studies investigating interactions of free-roaming horses and vegetation in semiarid systems of western North America that can be used to address horses' role in these systems, and fewer studies still that were conducted at broad spatial scales.

In the western United States, the domestic cow *Bos taurus* is the most widely distributed nonnative mammalian herbivore (Wagner 1983; Fleischner 1994), and has correspondingly received the greatest amount of synecological research attention. Despite the extensive research that has examined effects of livestock on vegetation and other taxa, research on how feral horses influence their surroundings is just beginning to emerge (e.g., Kissell 1996; Crane et al. 1997; Fahnestock 1998; Fahnestock and Detling 1999; Peterson 1999). Horses are also a common herbivore on the Great Basin landscape—horse management areas occupy fully 29% of Nevada's area (Anonymous 1997) and portions of 10 US states—though horses' potential role in vegetation alteration at landscape scales has rarely been investigated. Because *E. caballus* has occupied the western United States for almost four centuries (Wagner 1983), it is not clear whether plants of the upper and

lower sagebrush zones have evolved mechanisms to respond to horse grazing under field conditions.

Most of the above studies sought greater experimental control by limiting investigation to fewer sites within a relatively small geographic area. In contrast, our comparison of treatments across broad spatial scales encompassed large amounts of environmental variability; therefore, we used a set of response variables that are less influenced by local conditions, and that are applicable across all sites (Beever et al. 2003). For example, instead of comparing percent cover of individual species across sites, variables investigated herein instead included frequency and percent cover of each life-form, overall plant species richness, and cover of *Bromus tectorum* L. and *Artemisia tridentata* Nutt., two of the few species present at all sites.

Beever et al. (2003) sought to determine relationships among all sites (both horse-occupied and horse-removed) in multivariate ordination space, using data sets of plant frequency and cover (all species), cover of only those plant species monitored by managers (i.e., key forage species for horses), abiotic site attributes, and a diverse suite of disturbance-sensitive variables. The two types of sites appeared very similar in TWINSPAN and correspondence (reciprocal-averaging) analyses of data sets of abiotic site properties, cover of monitored plant species, and (to some degree) frequency of all plant species. However, sites were much more clearly discriminated using these multivariate analyses on disturbance-sensitive aspects of soils, ant mounds, plants, small mammals, and reptiles. Results from sampling of these other ecosystem components are detailed elsewhere (Beever and Brussard 2004; Beever and Herrick 2006) and are discussed here only to assist in the interpretation of vegetation findings.

In contrast, we had three objectives in the research reported here. First, we compared across a broad spatial domain (landscape scale) the cover, diversity, and structure of vegetation at sites grazed by feral horses to sites from which horses had been removed for 10–14 years, investigating each aspect of vegetation separately, as opposed to the whole-community multivariate analyses in Beever et al. (2003). For the cover analyses, we were particularly interested in cover of each plant life-form (grasses, forbs, shrubs), and of cheatgrass (the most ubiquitous non-native plant in the Great Basin) and sagebrush (upon which many species in the ecoregion obligately depend). Second, we compared those broad-scale results with plant responses to different grazing intensities within horse-grazed sites (local scale). Finally, using information-theoretic analyses we sought to ascertain which observed vegetation-related differences were explained by the presence of horses when the contributions of other abiotic factors that may have confounded comparisons were accounted for.

Methods

Study AREA

Located between the Sierra Nevada and the Wasatch Mountains of the western USA, the Great Basin has been used as a model system to test predictions of ecological theory because of its unique combination of physiography and climate (e.g., Johnson 1975; Wilcox et al. 1986). Because the Great Basin currently has the highest percentage of its area as public land of any ecoregion in the contiguous United States, it represents an important reservoir for biological diversity (Newmark 1995). However, the sagebrush-steppe, shrublands, and grasslands that dominate the Intermountain western United States are considered by some to be critically endangered ecosystems (Noss et al. 1995). By these authors' assessment, the sagebrush-steppe ecosystem of the Great Basin has been degraded across 98% of its original extent since European settlement, due primarily to livestock grazing.

Selection of study sites

Seven criteria were used to try to achieve ecological similarity between horse-occupied sites and sites from which both resident and immigrant horses had been removed for 10–14 years. Sites were only selected that were: (1) on east-facing (90 ± 45°) aspects; (2) of low (<40%) slope; (3) at elevations loosely corresponding to high-elevation (2,000–2,300 m) and low-elevation (1,350–1,700 m) sagebrush zones in the western Great Basin (Nevada); (4) dominated by sagebrush (*A. tridentata*); (5) within 1 km of a dirt road; (6) relatively unused by cattle in the past two decades, as observed by local land managers (U.S. Bureau of Land Management;

hereafter, BLM) and confirmed with fecal counts (see below); and (7) without evidence of recent (<15 year) fire within or adjacent to the site. These seven criteria were chosen because they are some of the strongest influences on levels of and variability within the response variables (Bonham 1989; Archer and Smeins 1991).

With these criteria, 10 horse-removed and nine horse-occupied sites were selected; each group was stratified nearly evenly into high- and low-elevation sagebrush sites (Table 1; see map in Beever and Brussard 2004). For the horse-occupied sites, we chose (with assistance from that agency's horse specialists) areas where horses had been found at least once during BLM aerial censuses of the past 3–8 years. Consequently, we investigated the ecosystem consequences of horse use of montane sagebrush habitats (relative to areas of horse removal), rather than comparing the average condition of all areas within horse-occupied and horse-removed management areas. Although our horse-occupied sites had all received some use, our adherence to our seven site-selection criteria listed above dictated that these sites did not receive anomalously high use by horses; in every HMA, we found one to several sites that were more heavily grazed. All sites were many kilometers from the nearest paved road and were located on secondary dirt roads infrequently traveled; consequently, ubiquitous presence of horse hoofprints and dungpiles on dirt roads suggested that criterion 5) above did not influence intensity of horse use at our sites. Sites were distributed across a vast area (3.03 million ha) of the western Great Basin.

At the finest spatial scale (e.g., within a basin, canyon, toeslope, or hillside), we located sites within homogeneous areas of vegetation distant from streams, because use by horses and other ungulates can be anomalously high near water sources in semiarid ecosystems (Crane et al. 1997; Beever and Brussard 2000). In practice, the most difficult criterion to satisfy was absence of cattle grazing. In addition to using BLM allotment data, we assessed density of ungulate defecations in the vicinity of each site, to find areas that appeared to have received significantly less use by cattle than by horses, following the approach described in Beever and Brussard (2004). Prior to the initiation of the study (i.e., during 1992–1995), horse densities for the management areas in which our sites were located

ranged from 0.005 to 0.015 horses/ha (Anonymous 1997).

Field sampling

Although sampling of other ecosystem components occurred during late May through early September each year, we sought to minimize any potential confounding effect of phenology on our vegetation response variables by concentrating vegetation sampling into much narrower temporal windows–7 July through 13 September in 1997 and 19 June through 29 August 1998. A 10×10 sampling-station grid with 15 m spacing provided the $135 \, \text{m} \times 135 \, \text{m}$ dimensions of the 1.82 ha area within which all sampling occurred. This area constituted the entire site for all metrics except site species richness (see below). The area was situated within the larger homogeneous block of vegetation in a manner that ensured that the seven aforementioned site-selection criteria were met, including minimizing the inclusion of areas heavily used by cattle.

In order to characterize structure, cover, diversity, and composition of vegetation, we used four 50 m line-intercept transects (Bonham 1989) per site. The starting point for each of four transects was placed at a randomly selected sampling station within each quadrant of the grid at each site, and the transect was placed along sampling-station rows. Its direction along the row was chosen to maximize the length that occurred within the quadrant and ensure that no more than 5 m of the transect went outside the grid (these 'overshoot' portions constituted only 0.56% of the total length of transects). In 1998, we allowed no overlap (re-sampling) of the previous year's lines (restricted random sampling; Goodall 1952). We recorded the species and length of intercept of each plant (including perennials and annuals) under the 50 m line. Species-accumulation curves suggested that four dispersed transects were sufficient to characterize the spatial heterogeneity and species diversity consistently at montane sagebrush sites.

Sampling for landscape-scale analyses

For measures of percent cover, dead annual forbs and grasses were not included. Given that phenology of many Great Basin grass and forb species could change

Table 1 Physiographic and habitat characteristics of 19 study sites in the Great Basin of western North America, sampled 1997–1998. Data for horse densities from Anonymous (1997)

	Mountain range	Horse density in HMA (horses/ha)	Site name	Elevation (m)	Site latitude (°N)	Site longitude (°W)	Average slope (%)[a]	Position on slope	Exposure[b]	Mean soil hardness (kg/cm²)
High-elevation, horse-excluded	Pah Rah Range	~0	Virginia Peak	2134	39.76	119.45	25	Upper	0	0.072
	Sonoma Range	~0	Lake valley hillside	2164	40.82	117.58	40	Middle	1	0.750
	Sonoma Range	~0	Cabin	2118	40.79	117.56	25	Lower	0	0.920
	Humboldt Range	~0	Pflum Creek Mine	2000	40.53	117.15	20	Middle	0	0.193
High-elevation, horse-occupied	Dogskin Mountain	0.00605	Dry Valley Creek saddle	2060	39.92	119.83	20	Upper	1	0.453
	Dogskin Mountain	0.00605	Dry Valley Creek peak	2200	39.91	119.82	30	Upper	1	1.414
	Seven Troughs Range	0.00197	Side road with junipers	2225	40.56	118.78	20	Upper	1	1.999
	Seven Troughs Range	0.00197	High saddle	2286	40.55	118.78	25	Middle	1	1.767
Low-elevation, horse-excluded	Pah Rah Range	~0	Bigmouth Canyon	1500	39.78	119.42	15	Lower	0	0.132
	Truckee Range	~0	Jeep trail	1540	39.98	119.16	5	Lower	1	0.138
	Truckee Range	~0	Sage Hen Creek	1500	39.96	119.11	10	Lower	0	0.173
	Humboldt Range	~0	Low side valley	1433	40.55	118.11	25	Middle	0	N/A[c]
	Virginia Range	~0	Fernley view	1400	39.55	119.27	5	Lower	1	0.062
	Virginia Range	~0	Homogeneous valley	1500	39.53	119.29	5	Middle	0	0.019
Low-elevation, horse-occupied	Dogskin Mountain	0.00605	Winnemucca Valley spur	1646	39.93	119.79	25	Middle	0	0.930
	Clan Alpine Mountains	0.00315	Dixie Valley vista	1340	39.83	117.71	10	Middle	0	2.913
	Clan Alpine Mountains	0.00315	Shoshone Pass	1700	39.74	117.63	15	Middle	1	1.667
	Virginia Mountains	0.00492	Juniper saddle	1646	40.13	119.79	20	Middle	1	2.462
	Virginia Mountains	0.00492	Juniper Basin	1554	40.14	119.80	25	Middle	0	1.173

[a] Obtained using a handheld clinometer, averaged across the entire sampling area

[b] Subjective classification of exposure, after Wentworth (1976). 0 = site somewhat protected by adjacent slopes, 1 = site on open slope, unsheltered by adjacent slopes

[c] This site could not be sampled for soil-surface hardness using our standardized criteria

during our sampling periods, we performed an unpaired *t*-test on the Julian date of vegetation sampling across all sites to compare the timing of sampling at horse-occupied versus -removed sites. Julian date of sampling did not differ significantly between treatments in either year, although horse-occupied sites were sampled slightly earlier than horse-removed sites in 1997 (mean = day 213 vs. 232). Earlier sampling at horse-occupied sites in 1997 should have translated into finding relatively more grass and forb cover at occupied (vs. removed) sites, given that senescence of plants was advancing at our sites during sampling periods. We generally visited sites in 1998 in reverse order of the sampling order used in 1997.

We recorded the number of individuals from each vegetation class (grass, forb, and shrub) intersected on each 50 m transect as an estimate of frequency, and averaged counts across the four transects within each site. The exotic grass *B. tectorum* (cheatgrass) was always senescent when we sampled vegetation (and thus not included in live grass cover); therefore, cheatgrass counts represent the number of stems (tillers) with heads that intersected the transect. To investigate richness at a broader scale than transects, cumulative lists of plants at each site ("site species richness") were created by adding all species from transects and other plants encountered in and immediately adjacent to (within 10 m of) the sampling-station grid (see Beever 1999 for plant species lists). We combined data from 1997 and 1998 to get an 'interannual' measure of species richness. Species were identified using Cronquist et al. (1972), and we used taxonomic affiliation and life forms of Hickman (1993) for our analyses.

Digging of four soil pits per site and subsequent textural analysis via the hydrometer method (BYU Soil Analysis Lab, Provo, UT) revealed that horse-occupied and -removed sites were similar in their texture (coarse-fragment, clay, silt, and sand fractions), soil color, degree of calcic soils, and depth to bedrock. Complete details on field methods used to sample soils and other indices appear in Beever et al. (2003). Because soil properties exhibited significant variability within the 1.82 ha area at each site, we estimated values of several other soil variables at sites using an average weighted to reflect the percentage of area of the soil-map unit that each soil series occupied, as indicated by NRCS soil surveys. These analyses showed that sites also did not

differ systematically in their permeability, consistence, structure, or plasticity (Beever et al. 2003). Furthermore, horse-occupied and -removed sites were indistinguishable in multivariate ordinations of all uncorrelated abiotic variables in both 1997 and 1998 (Beever et al. 2003). PRISM-estimated precipitation at our sites was 1.04 times higher than the 30 years (1961–1990) average in 1997, and 1.20 times higher in 1998.

Horse-trail transects (local scale)

To provide smaller-scale, more-controlled comparisons within horse-occupied sites, we created one to two 50 m transects along the most-evident horse trails within the 135 m × 135 m area by placing a tape 25–30 cm away from and parallel to the center of the trail. Measuring vegetation along the center of the trail would be tautological, because the existence of a linear path of (largely) bare earth in these semiarid ecosystems is the most reliable way to identify animal trails. Instead, we measured vegetation out of the path of direct trampling, yet within the lateral domain in which the herbivory and rubbing of horses might still occur. We measured the same variables in these 'horse-trail' transects as we did in regular transects to examine effects of heterogeneity of horse grazing within small areas. Because we desired to maintain similarity between horse-trail and randomly selected transects, we limited investigations to trails within and immediately adjacent to (i.e., within 10 m of) the grid. For horse-trail transects, a coin flip determined if the transect was placed on the uphill or downhill side of the trail. We completed two horse-trail transects in 1997: one at a high-elevation site and one at a low-elevation site. During 1998, we sampled either two trails or two distant (≥35 m apart) sections of the same trail within the sampling grid at each of five sites. Within each site, we compared these horse-trail transects to the transects that were designed to characterize vegetation across the entire horse-occupied site; hereafter, we refer to this latter type simply as "randomly located transects."

Fecal counts

Standardized counts of fecal piles from cattle, horses, and other ungulates revealed that horses were the

dominant non-native grazer at our sites in recent years, as the ratio of horse defecations/cattle defecations, averaged across years, at all horse-occupied sites exhibited a geometric mean of 10.4:1 (Beever et al. 2003). Furthermore, fecal counts suggested that intensity of herbivory by cattle or by other ungulates (primarily mule deer, *Odocoileus hemionus*, and pronghorn antelope, *Antilocapra americana*) did not differ between horse-grazed and horse-removed sites (Beever et al. 2003).

Analytical methods

To characterize plant composition at each site from our line-intercept transects, we calculated Simpson's and log-series diversity indices with frequency values, following Magurran (1988). To characterize vegetation structure at each site, we defined shrub-continuity (i.e., the opposite of canopy-dissectedness) indices as the average of the four largest intercept lengths of shrubs from the pool of line-intercept transects ($n = 4$) at the site. We used two such indices (for all species combined and for sagebrush only) to test whether, within elevational strata (high- or low-elevation sites), the trampling, herbivory, or rubbing (physical damage) associated with grazing would cause horse-occupied sites to have smaller maximum sizes of shrubs.

Tests of the intermediate-disturbance hypothesis (landscape scale)

The intermediate-disturbance hypothesis (Connell 1978) predicts that species richness should exhibit a bell-shaped curve over a gradient of disturbance frequency, balancing the inhibition by dominant competitors (in the absence of disturbance) with physiological and energetic costs of very frequent disturbance. To test whether sites exhibited a unimodal relationship between plant diversity and disturbance frequency/intensity (as predicted by Connell 1978), we compared the fit (using adjusted r^2 values) of linear and quadratic regressions of site species richness (using 1997, 1998, and cumulative lists) against number of either horse or horse + cattle defecations.

Comparing horse-occupied and horse-removed areas (landscape scale): analytical techniques

Because we performed tests on numerous permutations of diversity indices, we evaluated significance of these tests using sequential Bonferroni corrections (Sokal and Rohlf 1995). For comparisons of each response variable of vegetation, we performed a two-way analysis of variance (ANOVA) using horse presence and elevation as binary categorical variables, reflective of our 2×2 factorial research design. Probabilities in Table 2 refer to main effects of horses across all sites when stratified by elevation. For probabilities of effects of elevation on plant response variables, see Beever (1999). If the horse presence × elevation interaction was significant, we tested for a main effect of horses within each elevational stratum. We used Bartlett's test of homogeneity of variances to identify significant heteroscedasticity or severely non-normal distributions (Sokal and Rohlf 1995).

When needed, arcsine (for all percentage variables) or logarithmic transformations (for some diversity indices, and for cheatgrass frequency in 1998) were used to achieve homoscedasticity, normality, and additivity of treatment effects (Sokal and Rohlf 1995). For logarithmic transformations with 0 values, we added 1 to the value of all sites before transforming the data for count variables, and 0.1 to all sites for variables with lower values (i.e., diversity indices) (Sokal and Rohlf 1995). In the absence of significant interaction and non-significant effect of horse presence when stratified by elevation, we used post hoc Bonferroni–Dunn comparisons to identify cases in which horse presence exerted a significant main effect ($N = 2$; Table 2). Unless otherwise noted, we used $\alpha = 0.05$ to determine significance for all statistical tests. Statistical comparisons and correlations were performed using StatView v4.02 and v5.0 (SAS 1998), and evaluation of numerous alternative mixed-effects models in an information-theoretic framework were performed in WinBUGS (for species richness only; Spiegelhalter et al. 2003) or S + (Pinheiro and Bates 2000).

Horse-trail transects (local scale)

Variation in shrub cover was statistically analyzed with a paired-sample *t*-test (i.e., horse-trail vs.

Table 2 Means ± 1 SE for each plant response variable at sites in the western Great Basin, USA, during 1997 and 1998 for each treatment–elevation category

Elevation	1997						1998					
	High		Low				High		Low			
Horse presence	Removed	Occupied	Removed	Occupied	F	Probability[a]	Removed	Occupied	Removed	Occupied	F	Probability[a]
Percent cover grasses (%)	5.8 ± 1.2	2.0 ± 0.3	3.2 ± 1.3	1.7 ± 0.9	5.65	0.034[d]	12.6 ± 1.7	4.5 ± 1.2	6.7 ± 2.2	3.6 ± 1.2	8.41	0.011[d]
Abundance of grasses (*/transect)	28.3 ± 2.9	13.7 ± 3.4	11.3 ± 4.3	5.6 ± 2.5	9.60	0.009[d]	52.3 ± 6.0	21.8 ± 5.4	15.1 ± 4.6	13.3 ± 4.2	10.1	0.006[c, d]
Percent cover forbs (%)	4.1 ± 1.7	12.9 ± 3.2	2.2 ± 1.1	1.5 ± 0.3	5.07	0.042[c, d]	14.3 ± 2.7	22.7 ± 4.4	2.6 ± 1.5	1.4 ± 0.3	1.26	0.28[d]
Abundance of forbs (*/transect)	19.4 ± 4.2	35.9 ± 8.5	7.2 ± 3.5	9.9 ± 2.6	3.73	0.075[d]	90.0 ± 13.7	73.8 ± 11.0	11.5 ± 5.0	16.8 ± 3.6	0.44	0.52[d]
Percent cover shrubs (%)	51.1 ± 0.9	32.7 ± 5.4	26.3 ± 3.8	24.9 ± 3.7	6.23	0.027[d]	53.1 ± 4.0	27.8 ± 2.9	28.9 ± 2.8	23.3 ± 2.3	24.0	0.0002[c, d]
Abundance of shrubs (*/transect)	47.9 ± 5.0	44.8 ± 3.3	24.6 ± 3.9	26.5 ± 2.7	0.03	0.87[d]	48.4 ± 6.1	42.6 ± 2.7	28.0 ± 2.5	27.2 ± 2.6	0.27	0.61[d]
Total percent cover (Grasses + Forbs + Shrubs) (%)	61.1 ± 2.2	47.5 ± 4.6	31.7 ± 4.4	28.1 ± 4.3	4.17	0.062[d]*	80.0 ± 5.1	55.0 ± 6.3	38.2 ± 4.9	28.2 ± 2.8	12.8	0.003[d]
Total percent cover (G + F + S + Trees) (%)	61.1 ± 2.2	47.5 ± 4.6	32.9 ± 5.0	28.1 ± 4.3	4.67	0.051[d]*	82.5 ± 5.1	55.0 ± 6.3	38.4 ± 4.8	28.2 ± 2.8	15.0	0.001[d]
Cheatgrass abundance (stems / 50-m transect)	34.1 ± 22.8	54.9 ± 27.2	289.3 ± 76.5	197.4 ± 61.1	0.43	0.52	39.3 ± 14.2	103.4 ± 55.8	266.9 ± 46.0	419.5 ± 126.8	1.06	0.32[b]
Transect species richness	12.1 ± 0.9	10.9 ± 0.9	7.3 ± 0.6	7.0 ± 0.4	1.22	0.29[d]	22.8 ± 2.1	18.5 ± 0.8	10.5 ± 1.0	10.5 ± 0.4	3.62	0.077[d]
Site species richness	20.8 ± 1.3	18.0 ± 1.2	14.8 ± 0.8	12.4 ± 1.0	5.50	0.036[d]	39.0 ± 4.1	27.0 ± 1.7	22.3 ± 2.0	18.6 ± 1.7	10.3	0.006[d]
Interannual site species richness (both years)							43.0 ± 5.1	31.0 ± 2.9	25.8 ± 1.7	22.4 ± 1.9	6.13	0.028[d]

Table 2 continued

Elevation	1997						1998					
	High		Low				High		Low			
Horse presence	Removed	Occupied	Removed	Occupied	F	Probability[a]	Removed	Occupied	Removed	Occupied	F	Probability[a]
Simpson's index (cheatgrass excluded)	6.3 ± 0.1	7.5 ± 0.9	5.4 ± 1.6	4.7 ± 0.6	NT	NT	14.9 ± 2.2	27.2 ± 13.8	272.1 ± 92.1	134.7 ± 44.6	0.25	0.63[b]
Simpson's index (cheatgrass included)	6.0 ± 0.9	6.3 ± 1.4	1.4 ± 0.1	2.4 ± 0.6	1.03	0.33[b]	9.8 ± 0.8	6.2 ± 1.9	1.5 ± 0.1	1.7 ± 0.3	NT	NT
Log-series index (cheatgrass included)	3.9 ± 0.3	4.0 ± 0.4	3.0 ± 0.9	2.3 ± 0.3	0.25	0.63	4.8 ± 1.1	2.2 ± 1.6	3.4 ± 1.5	0.4 ± 0.1	11.4	0.004[b]
Log-series index (cheatgrass excluded)	3.9 ± 0.4	3.9 ± 0.5	2.3 ± 0.3	2.0 ± 0.2	0.14	0.71	8.2 ± 1.1	5.7 ± 0.5	4.4 ± 0.6	3.5 ± 0.4	6.53	0.022[d]
% cover sagebrush shrubs (%)	34.4 ± 4.2	16.6 ± 4.6	23.4 ± 6.0	19.9 ± 3.5	1.69	0.22[d]	32.0 ± 3.8	14.8 ± 2.7	20.3 ± 4.3	18.5 ± 2.7	5.11	0.039[d]
Sagebrush abundance (stems / 50-m transect)	25.9 ± 1.6	17.1 ± 2.6	19.8 ± 4.0	19.0 ± 3.0	2.83	0.12[d]	25.1 ± 2.5	16.9 ± 2.7	17.4 ± 2.9	20.7 ± 3.3	0.67	0.43[d]
Average of 4 longest shrub tape lengths (m)	1.7 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	13.20	0.003[d]	1.5 ± 0.0	1.0 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	28.0	<0.0001[dc]

[a] Probability refers to P-value of the test of the effect of presence of horses on each response variable at 19 sites, as measured by two-way ANOVAs with elevation as a binary cofactor. In the few instances in which the (horse presence × elevation) interaction was significant, horse effects were assessed within each elevational stratum

[b] Log 10-transformed data

[c] Significant interaction; presence of horses only significant among high-elevation sites

[d] (Absolute) difference between horse-occupied and horse-excluded values for variable was greatest at high-elevation sites

*Bonferroni-Dunn post hoc tests showed effect of horse presence was significant ($P < 0.050$) as a main effect

randomly located transects). For the other comparisons, we investigated direction and magnitude of differences in vegetation between the two types of transects as a second scale of investigation of horse influences.

Interannual variability (landscape scale)

To determine interannual variability in our response variables (and ultimately, the sensitivity of our results to climatic and other interannual fluctuations), we compared values of selected variables at each site between 1997 and 1998 using paired *t*-tests. In addition, we used correlation coefficients to determine relationships between values of different years and employed Fisher's *R*-to-*z* transformation to test whether the correlation differed significantly from 0. Furthermore, we included 'year' as a fixed and a random effect in information-theoretic analyses.

Testing for confounding of apparent (landscape-scale) horse effects by abiotic factors

To assess whether our results were confounded either by a site's position on a slope (upper, middle, or lower) or level of exposure (exposed or sheltered; both variables follow descriptions of Wentworth 1976), we performed two-way ANOVAs of each response variable against position and exposure. Results of these ANOVAs suggested that these factors were not significant determinants of any response variable that differed significantly ($P < 0.05$; Table 2) between horse-occupied and removed sites. Beever and Brussard (2004) provide further commentary on the topic.

To ensure that spatial interspersion of horse-occupied and horse-removed sites was effective in achieving ecological equivalency between the two groups, we tested for the occurrence of pre-existing differences (independent of horses) by comparing abiotic properties of horse-occupied and -removed sites (Table 5). We used two-way ANOVAs and unpaired *t*-tests to test for differences at either high or low elevations in the following conditions at sites: exact (±15 m) elevation; mean slope gradient (%); precipitation during 1997, 1998, and the average during 1961–1990, each estimated (Hungerford et al.

1989) using information from the nearest weather station and a correction factor from PRISM model data (Daly et al. 1994); and mean annual temperature, frost-free days, soil productivity, available water capacity, and erosion factors K and T (from published and unpublished soil surveys). PRISM data have become a data source of choice in the Intermountain West for estimating by interpolation the conditions at sites not near weather stations, in the absence of long-term climatic data at the remote field site. Erosion factor K is an index of susceptibility of soils to erosion by rainfall, and erosion factor T estimates the maximum rate of soil erosion tolerated to permit sustained crop productivity. Because we had no a priori predictions about directionality of differences and because the question was essentially the same across abiotic variables, we employed sequential Bonferroni corrections for multiple tests to maintain experimentwise α values at 0.05 (Sokal and Rohlf 1995).

Finally, we used mixed-effects models in an information-theoretic framework to determine whether presence of horses significantly predicted vegetative response in the face of dominant abiotic variables (Tables 3 and 4). Because we were particularly interested in the residual effect that the addition of horse presence would have on analyses of response variables, we paired our candidate models into different collections of environmental covariates; in each pair, one model included horse presence, and the other model did not include the factor. Mixed-effects models are comprised of fixed effects, which are parameters associated with an entire population, and random effects, which are individual experimental units drawn at random from a population. The generic form of a mixed-effect model is:

$y_{ij} = \beta + \beta_1 X_j + b_i + \varepsilon_{ij}$, where β is the grand intercept, β_j is the slope for the *j*th covariate (X_j), the random effects (i.e., site or year) are expressed as b_i and are assumed independent for different *i*, and ε_{ij} are the within-group independent errors.

This mix of fixed and random effects allowed us to control for sampling variability resulting from the grouping of data by site and year and thus, in turn, provide unbiased parameter estimates for the environmental characteristics we were interested in (Pinheiro and Bates 2000). By associating random effects to observations sharing the same level of a

Table 3 Variable weights of explanatory variables used in information-theoretic analyses, for each of ten response variables

Response variables	Fixed effects										Random effects	
	Presence of horses	Precipitation[a] (cm)	Elevation (m)	Julian date of sampling	Frost-free days/year	Available water cap.	Exposure[b]	Erosion Factor K	Site	Year[c]	Site	Year[c]
Percent cover grasses (%)	0.783	0.022	0.008	~0	0.109	~0			~0	1.000	1.000	~0
Frequency of grasses (#/transect)	1.000	0.560	~0	~0	1.000	~0			~0	~0	~0	1.000
Percent cover forbs (%)	0.162	0.954	0.014	~0	~0	~0			~0	0.381	1.000	~0
Frequency of forbs (#/transect)	0.284	0.800	1.000	~0	0.102	0.021			0.471	1.000	~0	~0
Percent cover shrubs (%)	0.461	~0	~0		0.298	0.013			~0	0.015	1.000	~0
Frequency of shrubs (#/transect)	1.000	0.120	1.000	~0	~0	~0			1.000	~0	1.000	~0
Total percent cover (all life-forms) (%)	0.555	0.033	0.554	~0	0.257	0.008			0.138	0.978	1.000	~0
% cover sagebrush shrubs (%)	0.436	~0	~0		0.007	0.004			~0	~0	0.989	0.011
Frequency of sagebrush	0.860	~0	~0		0.234	0.424	0.477		~0	~0	1.000	~0
Average of 4 longest shrub tape lengths (m)	0.157	~0	~0		0.011			0.740	~0	0.388	1.000	~0
Site species richness	0.964	0.988	0.949[d]	0.693	0.330	0.633			~0	~0	1.000	1.000

If a given explanatory variable was not used in analyses for a particular response variable, that cell is blank; in contrast, if the variable was used but simply did not appear in any of the highest-ranking models, we denote that variable weight as "~0"

[a] Precipitation received at site in previous 12 mos, estimated using PRISM data as described in text

[b] A site on an open, unsheltered slope was coded as 1; a site somewhat protected was coded as 2

[c] 1997 was coded as 0, 1998 as 1

[d] In addition to this linear effect of elevation, species richness also was well modeled by a quadratic term of elevation (variable weight = 0.949)

Table 4 Model-averaged estimates of coefficients for effects of various predictor variables on each of 10 response variables

| Response variable | Link | Explanatory variables | | | | | | | | | | Random effects | | Top-ranked model | | |
| | | Fixed effects | | | | | | | | | | | | | | |
		Presence of horses	Precipitation[a] (cm)	Elevation (m)	Julian date of sampling	Frost-free days/year	Available water cap.	Exposure	Erosion Factor K	Site	Year[b]	SD (Site)	SD (Year)[b]	r²	ω	residual σ
Percent cover grasses (%)	Log	−0.650	0.021	0.001	~0	−0.020	~0			~0	0.972	0.869	~0	0.64	0.66	0.56
Frequency of grasses (#/transect)	normal	−5.628	0.530	~0	~0	−0.532	~0			~0	~0	~0	6.495	0.65	0.56	9.42
Percent cover forbs (%)	Log	0.073	0.083	0.00005	~0	~0	~0			~0	0.098	0.979	~0	0.92	0.61	0.001
Frequency of forbs (#/transect)	normal	24.571	0.269	3.676	~0	−1.367	0.0022			0.198	23.351	~0	~0	0.66	0.32	19.45
Percent cover shrubs (%)	normal	−0.139	~0	~0	~0	−0.004	0.0004			~0	−0.0005	0.308	~0	0.95	0.34	0.12
Frequency of shrubs (#/transect)	normal	−8.589	−0.008	0.035		~0	~0			0.476	~0	5.908	~0	0.96	0.84	3.17
Total percent cover (all life-forms) (%)	normal	−0.196	0.0004	0.0006	~0	−0.004	0.000001			−0.006	0.150	0.248	~0	0.96	0.48	0.19
Percent cover sagebrush shrubs (%)	Log	−0.043	~0	~0		−0.00002	−0.000005			~0	~0	0.081	0.0009	0.94	0.54	0.09
Frequency of sagebrush	normal	−3.162	~0	~0		−0.03400	−0.209000			~0	~0	5.456	~0	0.96	0.43	3.17
Average of 4 longest shrub tape lengths (m)	normal	−0.138	~0	~0		−0.0003		0.542	1.548	~0	−0.129	0.339	~0	0.93	0.25	0.57
Site species richness	Log	−0.301	0.004	0.242[d]	−0.056	−0.004	−0.034			~0	~0	0.075	5.617	0.90	0.27	0.06

If a given explanatory variable was not used in analyses for a particular response variable, that cell is blank; in contrast, if the variable was used but simply did not appear in any of the highest-ranking models, we denote that coefficient as "~0". Three digits after the decimal are given, except for coefficients of very small magnitude. The rightmost three columns pertain only to the top-ranked model for each response variable

[a] Estimated precipitation received at site in previous 12 mos, estimated using PRISM data as described in text

[b] A site on an open, unsheltered slope was coded as 1; a site somewhat protected was coded as 2

[c] 1997 was coded as 0, 1998 as 1

[d] In addition to this linear effect of elevation, species richness also was well modeled by a quadratic term of elevation (model-averaged coefficient = −0.120)

classification factor (i.e., site or year), the mixed-effects models accommodated the covariance structure caused by the grouping of data. For a number of models we evaluated whether intra-class correlation structures might more credibly describe the variance structure than the assumption that they were independent.

A priori-identified abiotic fixed effects used in competing models included elevation, elevation^2, precipitation received at the site during the previous 12 months (see Beever et al. 2003 for detail on how this was estimated), number of frost-free days per year, Erosion Factor K, available water capacity, and Julian date of sampling. In addition to evaluating the effect of site and year as random effects, for a number of models we evaluated them as fixed effects as well. We evaluated the effect of elevation as a binary variable (low- vs. high-elevation sites, following our experimental design) compared to as a continuous variable. Because all models in which elevation was treated as a continuous variable performed better than the corresponding model with elevation treated as binary, we restricted our inferences and presentation of model results to those using the continuous form of the variable. Including the quadratic term for elevation allowed us to evaluate potential nonlinearities (specifically, a peaked distribution, as has often been found for species richness and other vegetative characteristics) in the effect of elevation on vegetative response. However, because the quadratic contributed little to explained variance but had the effect of adding parameters, excluding it always led to models with lowered Akaike's information criterion (AIC_c); the factor was removed from the final suite of models except for species richness.

To accommodate the distributional assumptions of the response data, we employed three approaches: linear (identity link on a normal distribution), log-linear (log link on a normal distribution), and Poisson (log link on a Poisson distribution) regression (Table 4). For all models, we fit null models without random effects, models with random effects but no fixed-effect covariates, models with fixed-effect covariates but no random effects, and the global model with all fixed and random effects. In cases in which the fit of both site and year as random effects was not possible, we proceeded to fit models of fixed effects for the random effect that resulted in a lower information criterion.

We fit and predicted models of site species richness with WinBUGS 1.4.1 (Spiegelhalter et al. 2003), a statistical package for conducting Bayesian inference with Markov chain Monte Carlo analyses. Parameters were assigned diffuse or non-informative priors and hyperpriors. For each model, we ran the Markov chain until convergence occurred (500 iterations) and for an additional 14,000 iterations past convergence. We used the Gelman–Rubin diagnostic to evaluate model fit between three replicate chains (Spiegelhalter et al. 2003), comparing within-chain and between-chain variability. We guarded against multicollinearity in the environmental variables by inspecting the multi-chain iteration histories and the Gelman–Rubin diagnostic plots of the slope parameters. Fixed effects for these models were standardized by subtracting the mean and dividing by the standard deviation to aid model convergence.

We fit all other models with S + (Pinheiro and Bates 2000, including the CorrelatedData library). To avoid underestimation of the variance parameters, restricted maximum likelihood was used. Because the average of four longest shrub tape lengths and average of four longest sagebrush tape lengths were highly correlated ($r = 0.89$), we modeled only the relationship between environmental characteristics and the average of four longest shrub tape lengths.

We employed an information-theoretic perspective to our modeling by comparing the deviance information criterion (DIC) (for site species richness) and Akaike's information criterion for small sample sizes (AIC_c; for all other variables) among models. DIC is an information criterion analogous to AIC that evaluates models in a Bayesian framework (Spiegelhalter et al. 2002); for each information metric, the most parsimonious model possesses the smallest information criterion value. We calculated model weights, variable weights, averaged parameter estimates, and model-evidence ratios according to Burnham and Anderson (2002).

Results

Tests of the intermediate-disturbance hypothesis (landscape scale)

In all six tests of the relationship between plant-species richness (three alternative measures) and

disturbance (two measures), the linear regression achieved better fit of the data (i.e., higher adjusted-r^2 values) than did the quadratic, and the regression coefficient was negative in each case. In other words, variability in species richness was best described by a monotonically decreasing trend as disturbance intensity increased.

Landscape-scale comparisons of horse-occupied versus horse-removed sites

All plant response variables (except for frequency of shrubs and forbs, cover of forbs, and cheatgrass-related variables; see Table 2 for list) had higher values at horse-removed sites than at horse-occupied sites in both elevational strata (see coefficients in 'presence of horses' column in Table 4), and the magnitude of difference was greatest among high-elevation sites (Table 2). Our explanatory variables were successful in accounting for most (64–96%; average = 85.1%; Table 4) of the variability in all response variables modeled in information-theoretic analyses except cheatgrass frequency.

During 1997 and 1998, horse-removed sites averaged 2.94 and 2.81 times greater grass cover than horse-occupied sites at high elevations, and 1.89 times greater cover at low elevations ($P \leq 0.03$; Table 2). Similarly, in both years we encountered a lower frequency of grass intercepts per transect at horse-occupied sites, ranging from 14.6 to 30.4 fewer plants/transect at high elevations and 1.8–5.7 fewer plants/transect at low-elevation sites ($P \leq 0.006$; Table 2). Information-theoretic analyses indicated that frequency and cover of grasses were two of the variables most strongly affected by the presence of horses (variable weight = 1.000 and 0.783, respectively), in spite of marked interannual variability in both response variables (Table 3).

Horse-removed sites also averaged 1.56 and 1.91 times greater total shrub cover than horse-occupied sites at high elevations in 1997 and 1998, and 1.06 and 1.24 times greater shrub cover at low elevations ($P < 0.03$; Table 2). Accordingly, no explanatory variable other than a random effect of site had a higher variable weight than did presence of horses, in information-theoretic analyses (Table 3). Although frequency (i.e., stem density) of shrubs did not differ meaningfully between horse-occupied and horse-

removed sites in either year, information-theoretic analyses suggested that when influences of other variables were accounted for, shrub density varied with presence of horses and elevation, as well as among sites (Table 3).

Not surprisingly in light of the above differences in grass and shrub cover, total plant cover was significantly higher at horse-removed sites in both years, and averaged 1.29–1.50 times greater cover among high-elevation sites and 1.17–1.36 times higher among low-elevation sites ($P \leq 0.05$; Table 2). As was true for grass cover and shrub cover, total plant cover had only one fixed-effect variable that appeared more influential than presence of horses—in this case, the effect of interannual variability (i.e., 'year'; Table 3).

When all shrub species were pooled within sites, maximum lengths of shrub intercepts at horse-removed sites averaged 0.17–0.24 m longer than lengths at horse-occupied sites at low-elevation and 0.56–0.57 m longer at high elevations ($P \leq 0.003$; Table 2). Similarly, mean length of the four longest sagebrush intercepts averaged 0.07–0.10 m longer at low elevations and 0.54–0.63 m longer at high elevations ($P \leq 0.03$; Beever 1999). Although variable weight of the presence of horses was lower than for 'year' and two abiotic characteristics of sites, the 95% confidence interval on the parameter estimate of the horse-presence model-averaged coefficient (–0.272, –0.072) did not overlap zero, suggesting that the effect of horse presence was consistently negative on maximum shrub lengths, across all models. This non-overlap of zero by the parameter estimate for presence of horses contrasted with all three variables with greater variable weight than horse presence (erosion factor K, exposure, year).

Horse-removed sites had significantly higher richness of plant species than did horse-occupied sites in both years and cumulatively, averaging 3—12 more species per site at high elevations, and 2—4 more species at low elevations ($P < 0.04$; Table 2). As was the case for maximum length of shrub interceptions, the 95% confidence interval on the horse-presence coefficient (–0.482, –0.117) did not overlap zero; elevation was the only other fixed effect for which this was true for species richness.

Although there was no difference in the frequency (i.e., stem count) of sagebrush shrubs in either year, percent cover of sagebrush was significantly (1.1–

2.2 times) higher at horse-removed than at horse-occupied sites during 1998 but not during 1997 (1.1–2.1 times higher, but more variable among sites within treatments; Table 2). Information-theoretic analyses confirmed that presence of horses (variable weight = 0.436) was a strong determinant of sagebrush cover when influences of abiotic variables were included in competing models; a random effect of site was the only other explanatory variable with a weight >0.011 (Table 3).

In addition, although the trend was not significant in 1998, sites with horses had 1.44–3.13 times greater forb cover than did horse-removed sites in 1997, due largely to greater abundance of unpalatable *Lupinus* and grazing-tolerant *Wyethia* forbs at high elevations (*P* = 0.04; Table 2). Abundance of forbs did not differ meaningfully between treatments in either year (Table 2). Information-theoretic analyses indicated that cover and frequency of forbs were the only response variables of those analyzed for which the coefficient of the presence of horses was positive (Table 4); that is, presence of horses appeared to increase, rather than decrease, them, after the influence of abiotic covariates were accounted for. Nonetheless, among the ten response variables in Table 3, variable weights for presence of horses suggested that the partial effect of horse presence was more marginal on forb cover and frequency, compared to other response variables.

Frequency of the non-native annual cheatgrass (*B. tectorum*) was usually higher at horse-occupied sites. These sites possessed an average of 1.61–2.63 times more intersecting cheatgrass stems at high elevations across years than did horse-removed sites, and 1.57 times more intersecting stems at low elevations in 1998 (Table 2). Cheatgrass stem intercepts were 1.47 times more frequent at low-elevation sites without horses in 1997 (Table 2), due in part to an exceedingly high value of cheatgrass stem counts at the most recently (but ≥15 years ago) burned site, which was a horse-removed site (12th site, Table 1). Information-theoretic analyses, which used a log-linear mixed-effects model fitted by restricted maximum likelihood, suggested that two models (each with $r^2 \approx 0.88$) were relatively superior to others. In the first (which had $\omega = 0.65$), inference suggested that the frequency of *B. tectorum* stems varied by site and year but little at all relative to the other environmental covariates. The competing model

($\omega = 0.35$) suggested that stem frequency varied only by site and patterns in annual precipitation. However, residuals from both models were heteroscedastic, indicative of a problem with model fit. Therefore, inference from these models should be used with caution. Although trends of greater cheatgrass cover at horse-occupied sites were not significant at $\alpha = 0.05$ because of relatively high coefficients of variability for horse-occupied sites (especially at lower elevations), this is the first investigation of this relationship, the outcome of which has important implications for management of Great Basin resources.

Simpson's and log-series diversity indices did not differ meaningfully between treatments in either year (Table 2). For a number of conceptual and analytical reasons, these indices were not modeled with information-theoretic analyses.

Horse-trail transects (local scale)

Comparisons within sites between the randomly located vegetation transects (which sought to characterize vegetation within the entire site) and transects located adjacent to horse trails, although naturally limited in sample size, largely showed the same trends (with respect to direction and magnitude of effect) observed in comparisons between horse-occupied and horse-removed sites, especially at high-elevation sites. In 1998, randomly located transects had from 21 to 218% greater percent cover of grasses than horse-trail transects at three of the five sites. At the other two (lowest-elevation) sites, one had equivalent cover between the two types of transects, and one had lower grass cover in the randomly located transects. Percent cover of forbs along horse trails was either equivalent to or greater than forb cover in randomly located transects at all five sites in 1998. Percent cover of shrubs differed strongly between transect types, and was 9–146% (mean = 61%) greater in randomly located transects at all five sites (paired $t = 3.0$, d.f. = 4, $P = 0.04$). Species richness of shrubs was greater in randomly located transects at three of the five sampled sites, equal at another site, and slightly lower at the fifth site. However, mean difference between the transect types ranged from only 0.25 to 0.75 species per transect. At four of the five sites, total species richness was higher

in the randomly located transects, ranging from 6 to 29% greater species richness, and was 9% lower at the fifth site.

Results of horse-trail sampling in 1997, the year in which we sampled trails less extensively, mirrored the direction and magnitude of results from 1998 sampling. Percent cover of grasses was notably higher in randomly located transects than in horse-trail transects—2.3 times higher at high elevation, and 9.5 times higher at low elevation. Forb cover along a horse trail was 37% higher than for randomly located transects at high elevation, but was marginally lower than the average for randomly located transects at low elevation. Species richness of shrubs was 56% higher in randomly located transects than along a horse trail at high elevation, and twice as high at low elevation. As compared to the horse-trail transect, total species richness was 23% higher in randomly selected transects at high elevation, but about equal (6.5 vs. 7 species) at low elevation.

Interannual variability (landscape scale)

Five of eight plant variables exhibited significant differences in means between years ($P < 0.05$), yet all variables except cheatgrass frequency ($r = 0.68$, $P = 0.002$) were very highly correlated between years ($r > 0.75$, $P \leq 0.0004$; 6 variables had $r \geq 0.825$). Whereas cover of grasses and forbs were, respectively 9.7% and 8.2% higher in (the wetter) 1998 than in 1997, shrub cover averaged <1% less in 1998 ($P > 0.55$; all percentages are absolute differences) and the sagebrush continuity index also differed little between years ($P > 0.15$). In information-theoretic analyses, modeling year as a fixed effect suggested strong interannual contribution to variability in forb frequency, grass cover and total plant cover, and to a lesser degree, forb cover and connectedness of the shrub canopy. Counts for all fecal types generally exhibited strong correlation between years ($P < 0.03$), and were generally not statistically different between years. Finally, mean sampling date of sites occurred approximately 28 days earlier in 1998 ($t_{16} = -3.12$, $P = 0.007$). However, contrary to our predictions, sampling date had a non-zero variable weight in information-theoretic analyses for only two of 10 response variables, neither one of which was herbaceous—

species richness (the variable that had greatest likelihood of being overfitted) and shrub cover (variable weight = 0.100).

Confounding effects of abiotic variables (landscape scale)

When we corrected alpha levels using sequential Bonferroni corrections, none of the ten abiotic variables differed significantly between horse-removed and horse-occupied sites, either across all sites or among high- or low-elevation sites only (Table 5). Among high-elevation sites only, horse-occupied sites averaged an estimated 27 more frost-free days per year than did horse-removed sites, even though they occurred at slightly higher (89 m) elevations (Table 5). Horse-occupied sites tended to receive slightly more precipitation than did horse-removed sites using NRCS estimations, 1997 PRISM estimates, 1998 PRISM estimates, and especially on average during 1961–1990, but no comparison was significantly different (Table 5). Furthermore, even if these two trends were *biologically* important although not statistically significant, they are counterintuitive to our finding of lower plant cover and diversity at horse-occupied sites (Table 2); greater precipitation or longer growing seasons (at high-elevation sites) would have been expected to dampen (rather than magnify) the magnitude of horse-grazing effects.

Discussion

Feral grazers may alter vegetation in semi-arid ecosystems via (1) soil compaction (and subsequent increased runoff), (2) selective plant consumption, (3) trampling and rubbing, (4) removal of terminal meristems, and (5) redistribution of nitrogen and other nutrients (Kauffman and Krueger 1984; Archer and Smeins 1991; Butler 1995; Belsky and Blumenthal 1997). Of these five mechanisms, strong negative correlations between plant cover and *both* fecal counts and penetration resistance of soils (e.g., $r < -0.7$ for both relationships, among low-elevation sites in 1998) suggest that all of the first three mechanisms are acting to some degree. Penetration resistance was the variable most strongly different between horse-removed and horse-occupied sites

Table 5 Comparison of 10 abiotic variables between horse-occupied and horse-removed sites in the Great Basin of western North America. Data sources are listed in the text

Abiotic site attribute	F-value	P-value*	Mean difference with respect to horses [(removed)–(occupied)]
Mean slope gradient (%)	0.43	0.52	–3.61
Arcsin (% cover bedrock)[a]	0.20	0.66	–1.56
Available water capacity (in/in)	2.21	0.16	1.11
Erosion factor K	0.07	0.80	0.006
Erosion factor T	0.01	0.92	–0.18
Non-horse disturbance[b]	0.80	0.39	0.40
Frost-free days/year, high-elevation sites[c]	$Z = -2.31$	0.02	–27.5
Frost-free days/year, low-elevation sites[d]	$t = 0.08$	0.93	0.67
Frost-free days/year, all sites combined[e]			–10.2
Production (lb/ac), high-elevation sites	1.37	0.29	201.0
Production (lb/ac), low-elevation sites	2.83	0.13	–178.0
Production (lb/ac), all sites combined[e]			–11.69
Precipitation (cm/year), 1997 PRISM	0.91	0.36	–3.50
Precipitation (cm/year), 1998 PRISM	0.58	0.46	–5.60
Precipitation (cm/year), 1961–1990 PRISM	6.56	0.02	–7.45
Precipitation (cm/year): NRCS estimates	0.32	0.58	0.00
Elevation, all sites combined	4.40	0.06	–121.9

[a] Values taken from 1998 sampling at 19 sites, $N = 4$ transects per site

[b] Subjective classification of disturbance by humans and livestock during 1997–1998, after Wentworth (1976). 1, apparently undisturbed; 2, slight disturbance; 3, moderate; 4, heavy; 5, severe. Due to small N within categories, data were analyzed as if continuous

[c] Mann-Whitney test

[d] Unpaired t-test

[e] Significant (horse presence × elevation) interaction. Presence of horses not tested as a main effect

*Except for cases of significant treatment–elevation interaction, two-way ANOVAs of horse presence and elevation were used to analyze variables. Due to the large number of variables analyzed, critical levels of alpha were adjusted using sequential Bonferroni corrections

(Beever and Herrick 2006), and the fact that other authors have attributed catastrophic shifts in vegetation of grazed systems to altered soil properties (e.g., Van de Koppel et al. 1997) may have relevance here. Previous research has shown that the degree to which grazing affects soil compaction (measured as bulk density or a surrogate, infiltration rates) depends upon soil texture (with finer soils more vulnerable to compaction; Van Haveren 1983), grazing system (Wood and Blackburn 1984), and stocking rate (Van Haveren 1983). Fewer studies have addressed, however, how long such compaction will persist under various freeze-thaw cycles.

In addition to soil changes, observed losses to the granivorous rodent guild and mound-building ants (both of which can assist in seed dispersal and germination) may be other potential drivers of vegetation alteration (Andersen 1991; Beever and Brussard 2004; Beever and Herrick 2006). In contrast to our results in support of the first three mechanisms, our finding of largest shrub lengths at horse-removed sites suggests that a wider, more bushy growth form due to meristematic removal is either not occurring in shrub species at our sites, or its effect is overshadowed by the first three mechanisms.

Numerous exclosure studies have suggested that vegetation retrogression in arid and semi-arid systems of North America may be protracted and unpredictable (McLean and Tisdale 1972; Rice and Westoby 1978; West et al. 1984), in part because successional trends do not necessarily follow previously conventional paradigms of linear return to some equilibrium

climax state (Laycock 1991). Our results, however, demonstrated many significant differences in vegetation between sites from which horses have been removed for 10–14 years and sites currently occupied by horses (Table 2). As a result of our numerous site-selection criteria (e.g., low slope gradient, east-facing aspect, no recent fires), horse-occupied sites in this study do not represent extreme cases of horse use (see Beever and Brussard 2000, 2004), a commonly used experimental approach criticized by Brown and McDonald (1995). If transition thresholds (Laycock 1991) are not crossed, current grazing can influence foliar cover without directly affecting species frequency, whereas changes in density often reflect longer-term impacts on the plant community. We chose to record and analyze foliar rather than basal plant cover because in the Great Basin and surrounding ecoregions (e.g., Mojave Desert communities), a 50-m line with no width intercepts herbaceous plant bases so infrequently that basal cover is often a highly variable and inconsistent indicator of grazing intensity (E.A. Beever and D.A. Pyke, unpublished data; E.A. Beever, unpublished data).

Tests of the intermediate-disturbance hypothesis (landscape scale)

Our finding of monotonically decreasing species richness across sites as grazing disturbance (indexed by fecal counts) increased suggests that either the bell-shaped curve of the intermediate-disturbance hypothesis does not apply in this system or that contemporary influences or the long-term past grazing history of these sites has resulted in generally all of them being located on the more disturbed side of the bell-shaped curve.

Landscape-scale influences of horses on vegetation

Because horses primarily consume graminoids (Hanley and Hanley 1982; McInnis and Vavra 1987), our findings of lower frequency and percent cover of grasses at horse-occupied sites (Table 2) as well as strong variable weight for presence of horses in information-theoretic analyses of these two response variables (Table 3) is not surprising. Our

finding of greater species richness (2–4 species/site at low-elevation sites, and 3–12 species/site at high-elevation sites) at horse-removed compared to horse-occupied sites agrees with previous work that found decreased richness of plants under greater livestock grazing (Rusch and Oesterheld 1997; Ludwig et al. 1999). In contrast, grazing can lead to increased species richness when grazers suppress the ability of competitive dominants to exclude other species or when grazing creates gaps that allow density increases in existing species or colonizations by other species (Milchunas et al. 1988; Archer and Smeins 1991). Especially at high-elevation sites, we observed (as did Ruthven 2007) slightly greater forb cover at horse—occupied sites—not surprising, given that two of the most abundant forb species at the horse-occupied sites are unpalatable or toxic to large herbivores (Hickman 1993). Decreases in grass cover may also have contributed to greater forb cover at horse-occupied sites, via competitive release.

While care must be taken to ensure that other factors such as soil type, precipitation, and others are accounted for when making comparisons of maximum shrub length, we believe that shrub-continuity variables are of value in assessing the degree to which a landscape has been structurally modified by a large herbivore. Although horse diets have been shown to contain minor amounts of shrubs (e.g., McInnis and Vavra 1987), our finding of greater shrub dissectedness and 1.1–1.9 times lower shrub cover in the presence of horses may be instead due to trampling and rubbing. Loss of connectivity in the shrub canopy may increase rates of insolation, evapotranspiration, and soil loss at small spatial scales and may lessen habitat value of a site for animal species that obligately use shrubs for shade, food, or escape cover (Hoffmeister 1986; Butler 1995; Belsky and Blumenthal 1997).

Our finding of decreased shrub cover agrees with results of Brady et al. (1989), who observed increased shrub species richness and cover 16 years after removal of livestock, as well as with the majority of studies in western North America reviewed by Jones (2000). In contrast, however, other authors have documented increases in sagebrush and other shrubs in the presence of herbivory (Dobkin et al. 1998; many authors cited in Archer and Smeins 1991). The relative dominance of shrubs in grazed landscapes will depend upon the

comparative strength of the processes of shrub trampling by horses and release of shrubs from competition with sympatric grazed plant species, as well as on the longer-term history of livestock use.

The fact that plant-related variables at horse-occupied sites were most different from horse-removed sites at high elevations may be due to a number of factors. First, most of the vegetation-class variables responded significantly to elevation, with high-elevation sites exhibiting higher absolute levels. In other words, high-elevation sites had more vegetation to alter, as compared to low-elevation sites. Furthermore, a global analysis revealed that effects of grazing by large herbivores increased with increasing primary productivity of the site (Milchunas and Lauenroth 1993). Finally, feral horses generally graze at higher elevations during late spring, summer, and early fall, the periods when most plant growth occurs.

As a result of the influences mentioned above that large mammalian herbivores exert on landscapes, these animals can modify ecosystems by altering spatial heterogeneity, modulating successional processes, influencing size/density relationships within species, and controlling the switching of ecosystems between alternative states (Hobbs 1996). As with other large herbivores (Milchunas et al. 1988), the effects that horses impose upon a given ecosystem depend upon many factors, including the plant-animal coevolutionary history, soil development, climate, recent weather, frequency and seasonality of the grazing, effects of other sympatric species, animal density, and longer-term grazing history of the site. Particularly in semiarid ecosystems, degradation of vegetation occurs most commonly under excessive livestock grazing pressure, spring grazing, or long-term continuous grazing, although some authors have found grazing to have no significant effect on these ecosystems (see Milchunas et al. 1988).

Ecosystem components in semiarid regions such as the Great Basin are predicted to respond less favorably to herbivory than are components in systems (such as grasslands) having a long, continuous coevolutionary history of grazing pressure (Mack and Thompson 1982; Milchunas and Lauenroth 1993). *E. caballus* has inhabited North America for only the past ~400 years, after an absence of all equids from the Great Basin for some 13,000 calendar years (Grayson 2006). Thus, horses may be considered ecologically as part of a novel disturbance regime in the Great Basin rather than as a native species.

Perhaps because vegetation is sampled easily and is influenced directly by horses, research to this point on grazing ecology of feral horses (Turner 1987; Rogers 1991; Detling 1998; Fahnestock 1998; Fahnestock and Detling 1999) or domestic horses in seminatural conditions (Reiner and Urness 1982) has focused almost exclusively on interactions of horses with vegetation. In contrast, research on interactions of free-roaming horses with other ecosystem components in arid or semiarid regions is just beginning to emerge (Peterson 1999; Beever and Brussard 2004; Beever and Herrick 2006). As a result of the non-uniform patterns of habitat use by horses (as for other ungulates; see Hobbs 1996), the magnitude of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily.

Horse-trail transects (local scale)

Stronger statistical inference could be gained in future studies by sampling more transects along horse trails. However, the 1998 sampling represented the upper bound for sample size for 1.82 ha sites, as it was difficult to find more sampling locations (trails) in a small 135 m × 135 m grid without placing horse-trail transects immediately adjacent to each other. Differences between horse-trail and randomly located transects at each horse-occupied site (e.g., grass, shrub, and forb cover, species richness) occurred in the same direction and magnitude as differences between horse-occupied and horse-removed sites. Thus, we were able to document differences in vegetation apparently caused by horses at both local and landscape scales. We advocate that future research into characterization of animal-trail effects seek to elucidate how far impacts extend (i.e., how rapidly effects subside as one moves) laterally from the trail center.

Although natural animal trails have been noted anecdotally numerous times in ecological literature, they have rarely received quantitative treatment (Butler 1995). Antelope in arid grassy dunes that spent much time under shade trees were found to trample soil locally but also enrich it with their fecal pellets (Dean and Milton 1991). Even though animal-

generated trails have been noted for bison (*Bos bison* L.) in the Great Plains grasslands, mountain goats (*Oreamnos americanus* de Blainville) in the Rocky Mountains, caribou (*Rangifer tarandus* L.) in arctic tundra, and elephants (*Loxodonta africana* Blumenbach) in tropical grasslands (e.g., Eaton 1917; Clayton 1975; Butler 1995), this work is the first to our knowledge to quantitatively compare transects along trails to randomly-chosen transects within the same site yet more distant from trails. In the absence of available manipulative experiments, horse-trail transects allow investigation of heterogeneity of use within horse-grazed areas and provide another level of evidence to suggest that horses (rather than other factors) are altering communities at our sites.

Interannual variability (landscape scale)

Much of the interannual variation we observed in herbaceous-plant variables may be attributed to earlier sampling in 1998 (mean = 28 days earlier). The robustness of our results across years in spite of significant interannual variation suggests that climatic variations did not eclipse effects imposed by horses on semiarid ecosystems, contrary to findings from research on feral horses in two grassland national parks (Detling 1998).

Conclusions and management implications

Investigating response of various aspects of vegetation to a large-bodied herbivore across regional scales requires separation of clinal and abiotic influences on vegetation from herbivore-induced alterations to the plant community. Although this broader spatial scale does not allow for the same degree of experimental control as is found in smaller-scale studies, managers benefit from the knowledge that the domain of inference for such larger studies represents a significant fraction of land under their jurisdiction, rather than merely several to a few hundred ha in one valley or range, for example. Furthermore, because horses in the US are currently managed to be 'free-roaming' under a minimal-management mandate, experimental manipulation of horse density is often exceedingly difficult to implement. In the absence of a true experiment, we instead employed several methods

such as interspersion of sites from different treatments, comparison of abiotic site attributes between treatments, and multi-scale investigations of effects of herbivory through use of horse-trail transects, and evaluation of numerous competing models that asserted importance of different subsets of abiotic factors to address alternative hypotheses about causes of vegetation differences. Collectively, our results suggest that effects of free-roaming horses constitute a non-trivial contribution to landscape condition, at least in semiarid regions such as the Great Basin at the local and landscape scales we investigated.

As this study illustrates, much remains to be learned about small- and broad-scale response of Great Basin vegetation to varying densities of or removal of free-roaming horses; how fire, invasions of cheatgrass and other non-native plants, and other sympatric grazers alter horse-vegetation relationships; and how horse effects are quantitatively distributed across the landscape. Given the everincreasing importance of cheatgrass in landscape dynamics of the Great Basin, our finding of higher frequency of cheatgrass at horse-occupied sites (as Whinam et al. 1994 and Weaver and Adams 1996 have found in Australia for other non-native plants, due to horses' transport of seeds via their excreta or externally via their coat) arguably demands highest future research priority for broad-scale investigations. With a better understanding of horses' ecology and the response of components of semiarid ecosystems to this non-native yet charismatic herbivore, future management can be adapted to prescribe grazing intensities and mosaics that accommodate many species occupying western public lands.

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