

Effects of feral horses in Great Basin landscapes on soils and ants: Direct and indirect mechanisms

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Abstract

We compared soil-surface penetration resistance and abundance of ant mounds at 12 western Great Basin sites (composed of 19 plots) either grazed by feral horses (*Equus caballus*) or having had horses removed for the last 10–14 years. Across this broad spatial domain (3.03 million ha), we minimized confounding due to abiotic factors by selecting horse-occupied and horse-removed sites with similar aspect, slope, fire history, grazing pressure by cattle (minimal to none), and dominant vegetation (*Artemisia tridentata*). During both 1997 and 1998, we found 2.2–8.4 times greater abundance of ant mounds and 3.0–15.4 times lower penetration resistance in soil surfaces at horse-removed sites. In 1998, thatched *Formica* ant mounds, which existed predominately at high elevations, were 3.3 times more abundant at horse-removed sites, although abundance varied widely among sites within treatments. Several types of analyses suggested that horses rather than environmental variability were the primary source of treatment differences we observed in ecosystem components. Tests of several predictions suggest that alterations occurred through not only direct effects, but also indirect effects and potentially feedback loops. Free-roaming horses as well as domestic grazers should be considered in conservation planning and land management in the Great Basin, an ecoregion that represents both an outstanding conservation opportunity and challenge. Published by Elsevier Ltd.

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1. Introduction

Grazing animals may affect ecosystem properties and processes directly (e.g., by foliage consumption or soil-surface trampling), indirectly (e.g., alteration of ant communities due to herbivore-induced reduction of plant cover), or through a feedback loop. Although the ecological literature is replete with reports of direct effects of a particular land use or type of disturbance on one or more response variables, less commonly is there explicit quantitative consideration of the indirect effects and feedbacks that may modify or modulate the disturbance's influence.

We measured penetration resistance of soil surfaces and density of ant mounds in areas with and without feral horses (*Equus caballus*) in order to test the overarching hypothesis that the presence of horses fundamentally changes key soil properties, and to increase our understanding of the potential importance of soil–plant–animal feedbacks in this ecosystem. Free-roaming horses in western North America move widely both daily (e.g., to and from water sources) and seasonally (e.g., to higher elevations in hottest months), and use some portions of the landscape more intensively than others at both local (e.g., wallows, communal defecation sites) and landscape scales (e.g., meadows, springs in otherwise arid regions). In addition to testing whether sites experiencing horse grazing differed in penetration resistance and ant-mound abundance from ecologically similar sites from which feral horses had been removed 10–14 years earlier, we used regression and correlational analyses to test whether relationships predicted by different mechanisms of change (e.g., direct and indirect effects) were operating. To our knowledge, this is the first investigation of ecological effects of feral horses on either soil properties or ants, and one of relatively few ecoregional-scale investigations of the ecological consequences of grazing by large ungulates in North America.

1.1. Direct effects

Horses have been shown to have direct effects on vegetation characteristics in semi-arid ecosystems (Reiner and Urness, 1982; Fahnestock and Detling, 1999; Gerhardt and Detling, 2000), and cattle in semi-arid ecosystems can directly affect soil properties, including bulk density, through trampling (Weltz et al., 1989; review in Lull, 1959). We predicted that horses would have similar effects on soil compaction, namely: (a) horse-occupied sites would exhibit higher mean penetration resistance than would horse-removed sites; and (b) resistance would increase across plots with increasing numbers of horse defecations, a surrogate of recent grazing intensity.

Large-bodied, broad-hoofed animals may reduce density of ant mounds directly by trampling. We predicted that: (a) some recently trampled mounds would be encountered during our field surveys; and (b) the number of defecations at plots should be negatively correlated with density of ant mounds.

1.2. Indirect effects

In intertidal marsh communities, free-roaming horses have been shown to exert a variety of indirect effects on diversity and abundance of crabs, birds, and fishes, through their effects on the dominant vegetation (Levin et al., 2002). In semi-arid communities, most indirect effects of ungulates are associated with removal of plant biomass or with

the combination of biomass removal and direct effects of trampling on soil structure (Thurow, 1991). Preferential removal of one or more plant species can contribute to shifts in plant community composition (Hobbs, 1996; Augustine and McNaughton, 1998). Due to the very different physical and chemical effects of different plant species on soils and the fact that a species shift is generally more persistent than the removal of plant biomass, changes in species composition in response to grazing can have dramatic impacts on infiltration (Thurow, 1991). Herbivore-induced reduction in vegetative cover at semi-arid sites can affect soils through at least three mechanisms: (a) reduction of soil organic-matter inputs; (b) reduction in shading of soils, and consequent increase in soil-surface temperatures; and (c) reduction of precipitation interception by above-ground plants, resulting in greater erosion. We predicted that, if horses were affecting penetration resistance through their effects on vegetative cover, total cover at plots would inversely predict resistance after recent grazing intensity (# horse defecations) and soil texture (%clay) were accounted for (i.e., as ‘forced’ variables in a stepwise regression).

Ants play pivotal roles in semi-arid ecosystems, acting as seed consumers, seed dispersers, soil manipulators, generalized herbivores, and most commonly, scavengers (Rosenberg et al., 1986; Petal, 1991; Andersen and Sparling, 1997; MacMahon et al., 2000). In addition to the potential direct effect of ungulates on ant mounds mentioned above, herbivores may thus reduce ant-mound densities indirectly by removing vegetation, which is used by ants in Great Basin ecosystems for both nesting material and nutrition. In addition to trampling and consumption of plant biomass, grazing animals can also affect the ratios and spatial distribution of nutrients available to plants through their patterns of urination and defecation. We predicted that either shrub cover or total cover at plots would predict ant-mound abundance after recent grazing intensity (# horse defecations) was accounted for (i.e., as a ‘forced’ variable in a stepwise regression). Additionally, we predicted that an index of continuity of the shrub canopy would correlate positively with abundance of ant mounds.

1.3. Objectives

Feral horses are a common herbivore on the Great Basin landscape, yet their potential role in landscape alteration has rarely been investigated. Management areas for feral horses occupy 29% of the land area of Nevada (Anonymous, 1997), the state central to the Great Basin, plus portions of all states that comprise the Basin. The objective of this study was to enhance our understanding of the direct and indirect effects of feral horses on ecosystem structure and function. Other reports (Gerhardt and Detling, 2000; Beaver et al., 2003) have described vegetation differences associated with feral horses. In this study, we specifically sought to quantify differences in soil-surface penetration resistance and ant-mound density in horse-grazed and ungrazed areas, and to use a variety of analytical approaches together with a literature review to investigate how these differences may be directly and indirectly associated with feral horses. To ensure that the results of our study were not related to the idiosyncrasies of a particular site, we replicated our plots in ranges across an area of 3.03 million ha. Based on our analyses and the literature review, we developed a conceptual model (Fig. 1) to describe our current understanding of the relationship between feral horse impacts on these two properties, and more general ecosystem functions.

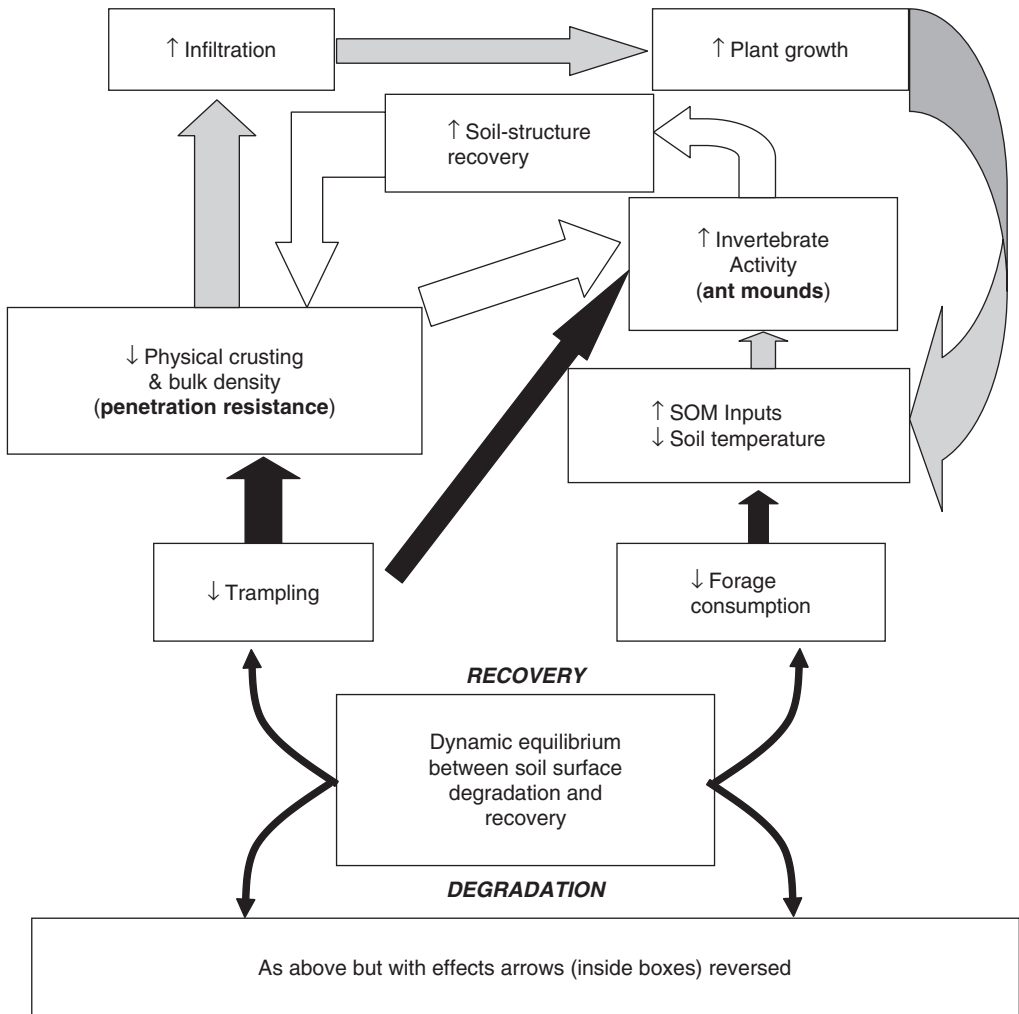


Fig. 1. Diagram illustrating connections between horse grazing (and trampling) and various ecosystem properties and processes, for pathways of both degradation and recovery. Black arrows represent direct effects of horses, gray arrows indicate indirect effects, and white arrows indicate potential feedback loops.

2. Methods

2.1. Selection of study sites

Management areas administered by the Bureau of Land Management for free-roaming horses include 318 herd-management areas (hereafter, HMAs) and 41.7 million ha across 10 US states, although 109 HMAs totaling 27.5 million ha are not currently managed for horses (BLM, unpublished data). Horse herd sizes may increase >20% annually in the Great Basin; consequently, periodic horse removals (roundups) are implemented to limit ecosystem degradation due to overgrazing. Seven criteria were used to try to achieve

ecological similarity between horse-occupied plots and plots from which all resident and immigrant horses had been removed for 10–14 years. To minimize confounding factors, we selected only plots that were: (1) on east-facing slopes; (2) of low slope gradient; (3) at elevations loosely corresponding to high-elevation (2000–2300 m) and low-elevation (1350–1700 m) sagebrush zones in the western Great Basin; (4) dominated by sagebrush (*Artemisia tridentata*); (5) relatively unused by cattle in the past two decades; and (6) had no evidence of recent fire within or adjacent to the plot (Beaver and Brussard, 2004). With these criteria, 10 horse-removed and 9 horse-occupied plots were selected within nine mountain ranges (Appendices A and B and Fig. 2). Given that locations of horse removals were selected on socio-political (specifically, railroad-owned jurisdiction) rather than biological criteria, and that horse-removed and horse-occupied sites were relatively interspersed across the landscape, we did not expect a priori confounding differences in sites of the treatment groups (Beaver and Brussard, 2004).

In practice, the most difficult criterion to satisfy was finding plots not grazed by cattle. In addition to using BLM stocking-rate data, we performed fecal counts at all sites to find areas that had received significantly less recent use by cattle than by horses. At the finest spatial scale, we located plots so as to avoid obvious ecotones and plant-community shifts, which represented <5–10% of the sagebrush-dominated areas within our HMAs. Plots were also located at least 1.5 km from perennial streams, because use by both horses and cattle can be anomalously high near water sources in semi-arid ecosystems (Crane et al., 1997; see Beaver and Brussard (2004) for more details on site selection).

2.2. Field sampling

We sampled each of our response variables (mean penetration resistance, ant-mound abundance, and thatched-mound abundance at sites; see Beaver (1999) for vegetation response variables) from May through August in both 1997 and 1998. Each plot consisted of a 135 m × 135 m (1.82-ha)², defined by a 10 × 10 grid of sampling stations with 15 m between both columns and rows. We added the soil and ant components to our sampling protocol in the middle of the 1997 season; therefore, we have soil penetration resistance data for only eight sites and ant data for only 14 sites in 1997. In 1998, however, we sampled ant mounds at all 19 plots and penetration resistance at 18 plots (Table 1).

2.2.1. Soil sampling

We measured soil-surface penetration resistance using a handheld pocket penetrometer (Soiltest, Inc., Chicago, IL, USA) by depressing the 6.4-mm diameter tip 1 cm into the soil at a constant rate (Bradford et al., 1986; US Department of Agriculture, 1993). Values of penetration resistance exhibited great variability in preliminary sampling; therefore, we adopted a two-tiered sampling strategy that involved taking 250 soil subsample measurements at each plot. At every fourth sampling station (100/4 = 25 locations), 10 subsamples were taken in areas not under vegetative canopy but within a 1-m diameter circle at a randomly selected cardinal direction from the center point. The 1-m diameter circle was enlarged if the original circle did not contain areas of open soil. One low-elevation, horse-removed site could not be sampled because areas with exposed soil could not be found near most sampling stations. Values of penetration resistance ranged from 0 to an instrument-imposed maximum of 4.7 kg/cm². Sampling locations were offset by two sampling stations from 1997 locations for sampling in 1998. Precipitation and resulting soil

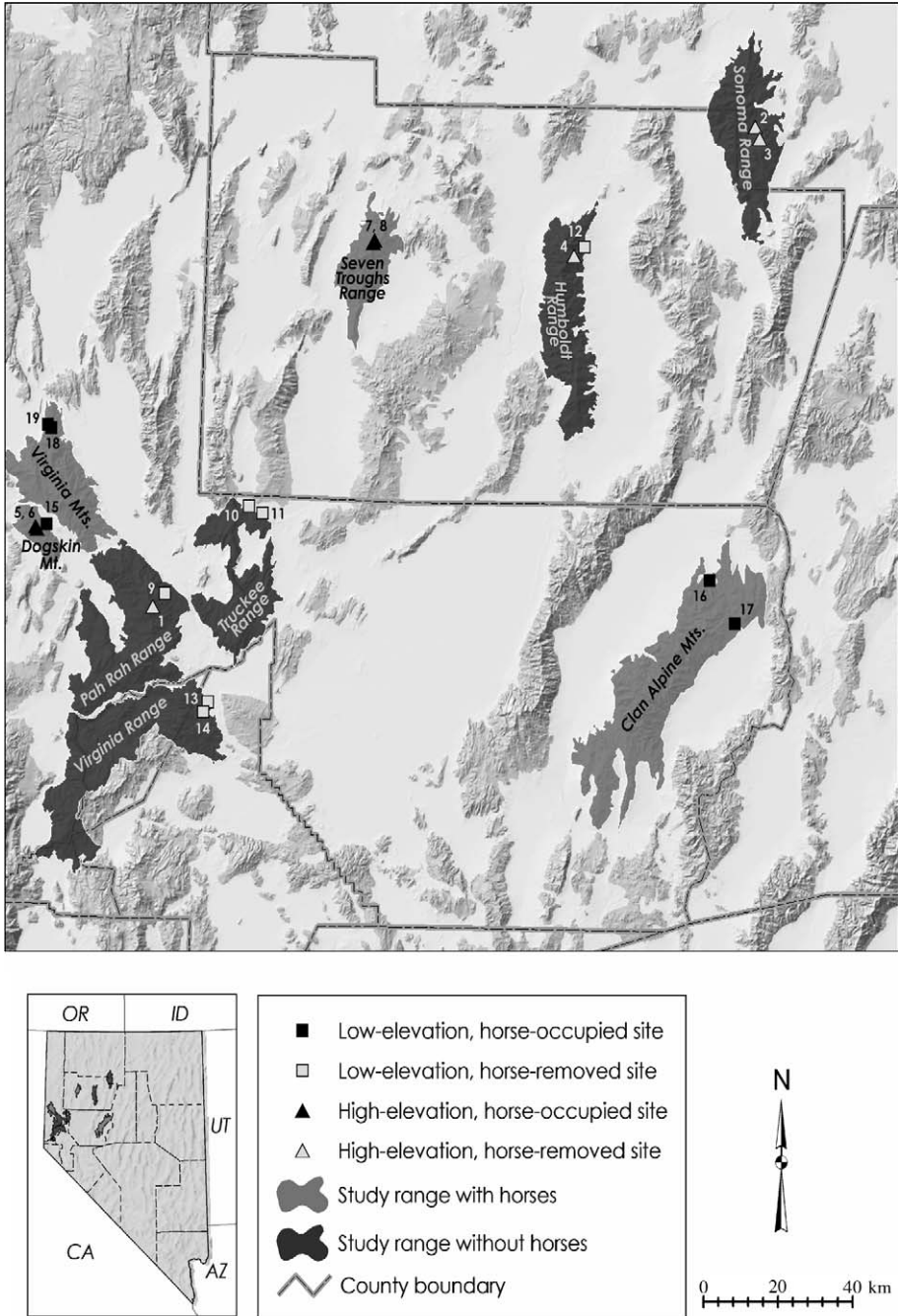


Fig. 2. Location of 19 study ‘sites’ (i.e., plots), stratified into high-elevation (2000–2286 m) and low-elevation (1340–1700 m) sagebrush zones in mountain ranges of the western Great Basin of North America. Site labels refer to “Site number” in Appendix A. Plots of the same treatment and elevational stratum within the same range were treated as subsamples for analyses.

Table 1
Means ± 1 SE for our response variables at 12 sites in the western Great Basin, USA, during 1997 and 1998 for each treatment-elevation category.

Elevation	1997						1998					
	High		Low		Probability		High		Low		Probability	
	Removed	Occupied	Removed	Occupied	Removed	Occupied	Removed	Occupied	Removed	Occupied	Removed	Occupied
Horse presence N: #sites (# plots)	3 (4)	2 (4)	3 (4)	3 (5)	3 (4)	3 (5)	3 (4)	2 (4)	4 (6)	3 (5)	3 (5)	3 (5)
<i>Soil-surface compaction (penetration resistance)</i>												
Mean soil harness (MPa)	0.2 ± 0.1	0.5	0.2 ± 0.1	0.9	0.026 ^a		0.4 ± 0.2	1.4 ± 0.5	0.1 ± 0.0	1.7 ± 0.4	0.0027 ^b	
<i>ANT mounds</i>												
Mean total # of ant mounds per site	8.7 ± 5.4	2.0	1.7 ± 0.9	0.2 ± 0.2	0.09 ^b		21.8 ± 13.3	7.8 ± 0.3	7.3 ± 1.9	3.2 ± 2.5	0.09	
Mean # thatched mounds per high site							18.8 ± 12.3	5.0 ± 0.9			0.25	

Probability refers to *p*-value of the test of the effect of presence of horses on response variables, as measured by two-way ANOVAs with elevation as a binary cofactor. Tests considered 'sites' as replicates, and averaged values from plots to obtain a site value.

^aDue to small *N* (total sites sampled = 8) and non-significant effect of elevation on resistance both years, this test reflects a one-way ANOVA.

^bLog₁₀—transformed data.

moisture can temporarily change the surface characteristics of soils as a result of cohesive and adhesive forces (USDA, 1993). Consequently, we sampled sites only when they had received no precipitation during the previous 48 h. Typical of the Great Basin during summer, high soil-surface evaporation at our sites ensured that the top 2 cm of the soil was effectively air-dry at the time of sampling. We chose to measure penetration resistance of soil surfaces rather than bulk density for one biological reason and one practical reason. Biologically, conditions on the soil surface will affect many more biotic and abiotic processes in Fig. 1 (e.g., seed germination, water capture vs. runoff) than will bulk density at far-belowground horizons. Logistically, we sought to use a sampling instrument that might feasibly be implemented by land managers in a time- and cost-effective manner, yet still provide robust information.

2.2.2. Ant mounds

We tallied above-ground ant mounds by counting mounds in a 4-m wide corridor (2 m on each side) located along the row-by-row path through the sample-station grid (1485 m length). Mounds fell into two categories: thatched mounds (produced by *Formica* ants, often at high elevations) and pebble mounds (usually constructed by *Pogonomyrmex* ants). Mounds were tallied by type in 1998 but not during 1997. Although we performed tests on mound *abundance* (occasionally transformed), given that all censuses occurred within a 4×1485 m area, abundance translates directly to mound *density*. To begin to assess composition of ant communities at plots, we collected individuals ($n \geq 7$) from two different mounds encountered during sampling at each site during 1998. If both types of mounds were present at a plot, we collected ants from a mound of each type. *Formica* ants were identified to species group and *Pogonomyrmex* ants to species using Wheeler and Wheeler (1986).

2.2.3. Fecal counts

Scanning the same area used to census ant mounds, we counted the number of fecal piles from cattle, horses, and other ungulates in the 4 m wide corridor along trap lines in the sampling-station grid (following Beever and Brussard, 2004). Communally used defecation sites (often termed ‘stud piles’), which can exceed 20 m^2 in extent, were each assigned a value of 7 defecations, reflecting the average ratio of fecal material in stud piles vs. individual defecations that we observed anecdotally across hundreds of stud piles. Horses appeared to be the dominant ungulate grazer at our sites in recent years, as the geometric mean of ratios of horse defecations/cattle defecations across years at all horse-occupied plots was 10.4:1 (Beever et al., 2003). Fecal counts further suggested that intensity of neither cattle grazing nor browsing by other ungulates (primarily *Odocoileus hemionus* and *Antilocapra americana*) differed between horse-occupied and -removed sites during 1997 or 1998 ($p > 0.20$; Beever et al., 2003).

2.3. Analyses

We used a conservative approach and considered plots within the same mountain range and elevational stratum as subsamples and averaged values from the two plots to produce a ‘site’ value. This approach is conservative for the following reasons: (1) replicate plots within the same range and elevational stratum were separated from each other by up to 12.3 km; (2) replicate plots in horse-occupied sites are overridingly used by different bands

of horses; (3) many of the replicate plots in horse-removed sites were de-stocked at different times; (4) reciprocal averaging analyses (also known as correspondence analyses) showed that same-range plots were less similar to each other than to plots in other ranges for 4 of 5 previously analysed datasets (Beaver et al., 2003), and (5) ant mound density at plots within the same range were consistently less similar to each other than to other plots in the same treatment-elevation category. We considered all plots as replicates when using number of defecations (rather than the binary horse-treatment variable) in regressions and correlations to understand the mechanisms underlying ecosystem alteration.

We calculated means for penetration resistance at each plot using the 25 subsample means, and used the overall site mean for testing of treatment effects. For analyses of treatment effects on response variables, we performed two-way ANOVAs using horse density and elevation as binary categorical variables (i.e., main effects); probabilities in Table 1 refer to the main effect of horse presence across all sites when stratified by elevation. We used Bartlett's test of homogeneity of variances to identify significant heteroscedasticity or severely non-normal distributions (Sokal and Rohlf, 1995). When needed, logarithmic transformations were used to achieve homoscedasticity, normality, and additivity of treatment effects (Sokal and Rohlf, 1995). Since the variables undergoing logarithmic transformations had some zero values, we added 1 to the value of all sites before transforming the ant-mound data (a count variable), and 0.1 to all sites before transforming the penetration-resistance data (Sokal and Rohlf, 1995). To determine inter-annual variability in our response variables, we compared values of selected variables at each plot between 1997 and 1998 using paired *t*-tests. We used correlation coefficients to determine whether the relative values of response variables across sites persisted between years (a desirable characteristic for indicators of disturbance) and employed Fisher's *R*-to-*z* transformation to test whether correlations were significantly different from zero. Statistical analyses were performed using StatView versions 4.02 and 5.0 (SAS Institute Inc., 1998). We performed fewer tests on 1997 data for penetration resistance, due to our lower sample size that year ($n = 8$ plots).

We compared numerous abiotic variables between horse-occupied and horse-removed sites, to test the assumption that any differences in ant and soil response variables were due to presence of horses rather than abiotic parameters. These variables included some that we measured at plots, and some generated by precipitation models (Daly et al., 1994) or published and unpublished soil surveys from Natural Resources Conservation Service (NRCS) (Appendix C). Using two-way ANOVAs, unpaired *t*-tests, and Mann–Whitney tests, we found that no variable was significantly different between horse-removed and horse-occupied sites in individual analyses, nor were the two types of sites distinguishable in multi-variate analyses of all uncorrelated physical site attributes (Beaver et al., 2003; Beaver and Brussard, 2004). Furthermore, by digging four soil pits per plot, we found that horse-removed and -occupied sites also did not differ systematically in their soil color, structure, consistence, or effervescence (Beaver et al., 2003). Perhaps most important to penetration resistance, we compared soil texture across sites, using the four pits/plot. Horse-removed and -occupied sites again did not differ significantly in any soil particle-size fraction, including clay or gravel ($p > 0.10$). Textural characterizations were performed using the hydrometer method (BYU Soil Analysis Lab, Provo, UT, USA) on four samples (depth 0–20 cm) per plot.

Finally, we used pre-planned stepwise regression analyses with forward selection (yet backward-looking to remove variables from the model whose *F*-value fell below 3.996) on

both abundance of ant mounds and penetration resistance. Variables used to explain penetration resistance, in the order they were entered initially into the analysis, included average %clay, available water capacity, USLE soil erodibility factor (K), and horse presence. For ant mounds, variables included precipitation, K , horse presence, elevation (in m), and mean slope gradient of sites. These stepwise models sought to confirm our ANOVA results and ensure that an abiotic variable (rather than the presence of horses) was not obviously driving variability in response variables that differed significantly between horse-occupied and -removed sites. We also performed simple- and multiple-linear regressions to investigate contributory mechanisms of change, following our predictions above.

3. Results

3.1. Direct effects

Penetration resistance of soil surfaces was significantly higher at sites with horses in both 1997 ($F_{1,4} = 11.9, p = 0.026$) and 1998 ($F_{1,7} = 20.4, p = 0.003$; Table 1). In 1998, horse-occupied sites exhibited 15.4 times higher penetration resistance than did horse-removed sites at low elevations and 3.8 times higher penetration resistance at high elevations. Evidence of a direct effect of horses on penetration resistance was best illustrated by a strong correlation in 1998 (the year of more extensive soil sampling) of average penetration resistance and total number of horse defecations ($r = 0.69, n = 18, p = 0.001$; Fig. 3a). This correlation was apparent both among high-elevation plots ($r = 0.71, n = 8, p = 0.05$) and among low-elevation plots ($r = 0.77, n = 10, p = 0.0065$). Corroborating the strength of the direct effect was the result of the stepwise regression in 1998 on penetration resistance. Among the four variables considered (see Section 2.3), presence of horses was the only variable to enter the model, regardless of whether plots or sites were treated as replicates (using number of horse defecations or categorical horse presence, respectively, to analyse horse effects). Data from 1997 provided a weaker test of the mechanism, as only seven sampled sites had all NRCS data available; however, %clay and the presence of horses were the strongest determinants of penetration resistance among those sites.

Across years and elevational strata, ant mounds occurred in greater abundance at horse-removed sites than at horse-occupied sites. Ant mounds occurred 2.2–4.0 times more densely at horse-removed than at horse-occupied sites at high elevation, and 3.6–8.4 times more densely at horse-removed sites at low elevation. Although there was high variability within the high-elevation horse-removed category, horse-removed sites tended to have a greater number of ant mounds in both 1997 and 1998 ($p = 0.09$; Table 1). Across both years, we observed few mounds that appeared to have been recently trampled by horses. In 1998 among high-elevation sites, whereas thatch mounds were 3.8 times more abundant at horse-removed than at horse-occupied sites, pebble mounds were nearly equivalent in their density at horse-removed (3.0 mounds/5940 m² strip transect) and horse-occupied sites (2.8 mounds/5940 m²). Total number of horse defecations at plots was poorly related inversely to abundance of ant mounds in both years, and defecations accounted for only 6–9% of the variation in mound abundance in both 1997 ($r = -0.23, n = 14, p = 0.42$) and 1998 ($r = -0.30, n = 18, p = 0.23$; Fig. 3b). Furthermore, no variable entered the stepwise model for abundance of ant mounds at sites in either year, although presence of horses was

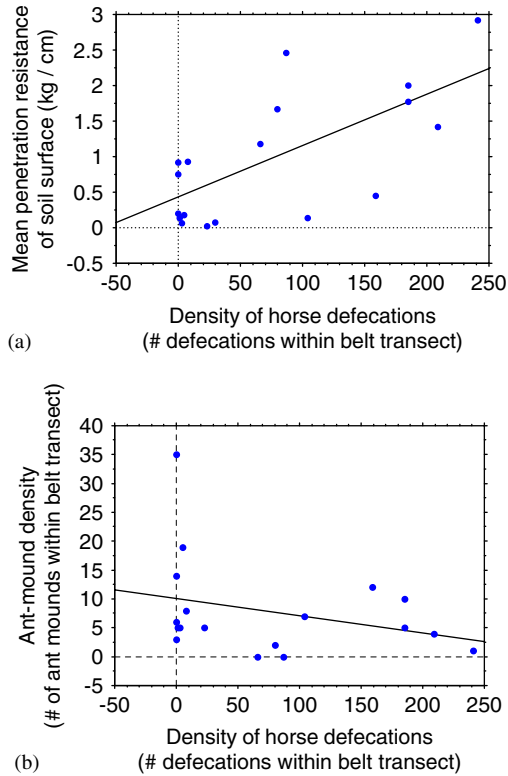


Fig. 3. (a) Mean penetration resistance at plots regressed linearly against the density of horse defecations observed within a standardized belt transect ($1485 \times 4 \text{ m} = 5940 \text{ m}^2$) at each plot, 1998 data. Regression equation: Y (in kg/cm^2) = $0.434 + 0.007 * (\# \text{defecations}) + \varepsilon$; $r^2 = 0.467$. (b) Mean number of ant mounds encountered within the ($1485 \times 4 \text{ m}$) 5940-m^2 belt transect at each plot, regressed linearly against the density of horse defecations observed within that plot's belt transect, 1998 data. Regression equation: Y (in # of mounds) = $0.434 + 0.007 * (\# \text{defecations}) + \varepsilon$; $r^2 = 0.092$.

the strongest predictor of abundance out of all predictor variables (ranked by partial correlation and corresponding F -value).

3.2. Indirect effects

When number of horse defecations and %clay were forced in a stepwise model for penetration resistance at plots in 1998, total cover at plots did not enter the stepwise regression ($r_{\text{partial}} = -0.137$; $F = 0.3$). Nonetheless, the two forced variables accounted for much of the variability in resistance, and the regression model (with only the two forced variables) strongly predicted resistance ($F = 10.7$; $p = 0.001$). In contrast, only 6–9% of the variability in mound abundance was accounted for by our stepwise models in 1997 and 1998 ($0.7 < F < 1.6$; $p > 0.20$), and neither cover of shrubs nor total cover of vegetation entered the model once recent horse-grazing intensity was accounted for. However, our index of the continuity of the shrub canopy—the average of the four longest shrub

interceptions across all four 50-m line-intercept transects at a plot—which was significantly lower at horse-occupied compared to horse-removed sites in both years (Beaver, in revision), was positively correlated with abundance of ant mounds across plots in both 1997 ($r = 0.57, n = 14, p = 0.03$) and 1998 ($r = 0.42, n = 18, p = 0.09$).

3.3. Inter-annual variability

Although the number of ant mounds at a plot was highly correlated between years ($p < 0.0001$), we encountered about 5.2 more mounds per plot during 1998 than in 1997 ($t_{12} = 3.34, p = 0.006$). 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 plots occurred approximately 28 days earlier in 1998 ($t_{16} = -3.12, p = 0.007$).

4. Discussion

E. caballus has inhabited North America for only the past 400 years, after an absence of all equids from the Great Basin for at least 13,200 years (Grayson, 1989). Thus, horses should be considered ecologically as part of a novel disturbance regime in the Great Basin (rather than as a native species), and their effects should be considered along with those of domestic livestock when planning for conservation of Great Basin landscapes (Beaver, 2003). As a result of the non-uniform patterns of habitat use by horses (as for other ungulates; see references in Hobbs, 1996), the magnitude of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily (Beaver, 2003). In our research, we observed notable differences in ant mounds and soil-surface penetration resistance between sites grazed by horses and sites from which horses had been removed for 10–14 years, when comparing sites at the landscape scale. Results of our analyses suggest that these apparent ecosystem alterations are likely due to a combination of direct and indirect effects (Fig. 1). Our analyses and a literature review also suggest the potential importance of feedback loops.

4.1. Direct effects

4.1.1. Soils

Of all ecosystem components measured at sites, penetration resistance was the variable that differed most strongly between horse-occupied and -removed sites. Although it is possible to have trampling without herbivory, it is not possible to have herbivory without concomitant soil trampling. Our predictions for two tests of direct effects of horses on penetration resistance were confirmed in both cases. First, soil surfaces at horse-occupied sites exhibited significantly higher penetration resistance than did those at horse-removed sites, in both 1997 and 1998 (Table 1). Second, resistance was clearly and positively related to number of horse defecations across sites in 1998 ($r = 0.69, p = 0.001$), when soil sampling was most extensive.

Soil compaction has been found to increase linearly with increasing livestock grazing intensity in fields of Kentucky bluegrass (Alderfer and Robinson, 1947; Bryant et al., 1972), in riparian zones (Orr, 1960; Kauffman and Krueger, 1984), and at areas with silty clay soil (Rauzi and Hanson, 1966). In Colorado grasslands, finer-textured soils are the

most likely to exhibit increases in soil compaction due to grazing (Van Haveren, 1983). Alderfer and Robinson (1947) found that grazing on clay and sandy loams resulted in compaction of only the top 5 cm of soil, but density of soil in this horizon increased from 1.09 g/cm³ on ungrazed sites to 1.51 g/cm³ on lightly grazed sites, and 1.54–1.91 g/cm³ on heavily grazed sites. This is consistent with our results, which showed significant compaction of the soil surface of our loamy soils (averages at sites ranged from 13.3% to 29.0% clay). In addition, increases in bulk density have been experimentally demonstrated for domestic cattle in New Mexico after as little as one month of grazing (Weltz et al., 1989). Significantly higher penetration resistance at horse-occupied sites raises concern, because alterations of the soil environment can affect a wide variety of ecosystem processes (Fig. 1; Thurow, 1991).

4.1.2. Ant mounds

We found greater abundance of ant mounds at horse-removed as compared to horse-occupied sites in both 1997 and 1998, with 2.2–4.0 times more mounds at high-elevation sites, and 3.6–8.4 times more mounds at low-elevation sites (Table 1). Greater abundance of ant mounds at horse-removed sites is particularly interesting, given that several factors would seem to suggest that numbers should be higher at horse-occupied sites, where: (a) the greater amount of open space should mean more substrate for mound-building activities, especially for *Pogonomyrmex* species; and (b) reduced vegetative cover should favor warmer microclimates, the latter of which would allow for longer activity periods (especially at high-elevation sites), both seasonally and diurnally (Crist and Williams, 1999). In spite of this coarse-level difference (i.e., horse-occupied vs. -removed sites) in mound abundance, there was less support ($p > 0.20$) for a linear relationship between horse-grazing intensity (as measured by defecation counts) and ant-mound abundance (compared to the horse intensity–soil relationship).

Several possible explanations could account for our inability to find recently trampled mounds at horse-occupied sites. First, horses may avoid pebble and thatch ant mounds in semi-arid mountain ranges, particularly the latter, given that *Formica* ants sting. Alternatively, horses may indeed trample mounds, but ants rebuild their mounds quickly enough that we rarely observed trampled mounds. Finally, horses may trample mounds, but such trampled mounds may be quickly abandoned, and without regular maintenance, are obliterated by wind, rain, or activity of other animals.

Although we did not comprehensively investigate species richness of ants at sites, our finding of greater species richness per site across pooled horse-removed versus horse-occupied sites (Appendix D) is consistent with findings of some previous research on ants. Suarez et al. (1998) found reduced species richness of native ants as habitat fragmentation increased, generally caused by the presence of the exotic Argentine ant (*Iridomyrmex humilis*). While other authors have also found decreased species richness of ants at sites disturbed by grazing animals (e.g., Majer, 1985; Majer and Beeston, 1996; Andersen and Sparling, 1997; Nash et al., 1998), a number of other studies found no negative effects of grazing (e.g., Heske and Campbell, 1991; Whitford et al., 1999).

Alternative explanations for our results (e.g., differences in historical or current livestock grazing between horse-removed and -occupied sites, confounding by site properties such as exposure and position on the slope) were reviewed by Beaver and Brussard (2004) in their research on small mammals and reptiles at these sites. In brief, analyses overwhelmingly

failed to support these alternative explanations as drivers of the differences in penetration resistance and ant-mound abundance we observed between horse-removed and -occupied plots.

4.2. Indirect effects and potential feedbacks

Research on soil-surface penetration resistance and ant mounds (as depicted by our conceptual model in Fig. 1) suggests that in semi-arid ecosystems, alteration of the vegetative canopy may be one of the stronger pathways by which grazers indirectly affect soil surfaces and ant mounds. Indeed, horse-occupied sites in this study had significantly lower abundance and cover of grasses, lower shrub cover, lower total vegetative cover, lower species richness at the site level, and a less continuous shrub canopy, compared to horse-removed sites (Beaver, 1999; Beaver, unpublished data). Greater vegetative cover can: provide more extensive shading for soils to retain greater soil moisture; reduce soil erosion by intercepting more incident precipitation and reducing surface wind velocities; and provide greater organic-matter inputs to soils, which in turn alter both chemistry and physical properties of soils (Fig. 1).

Furthermore, Van de Koppel et al. (1997) attributed catastrophic shifts in vegetation reported by several other authors to deterioration of soil conditions and reduction of standing biomass. In the two focal examples of van de Koppel et al. (1997), irreversible changes in the vegetative mosaic were attributed to increased herbivory. Other authors (e.g., Archer and Smeins, 1991; Belsky and Blumenthal, 1997) have similarly related herbivore-induced alterations in soil properties and vegetation, through various pathways. USDA (1993) reported that numerous plant species experience physical root restriction when penetration resistance is greater than 1.0 MPa. In our sampling in 1998, up to 23 (92%) of 25 sampling stations at horse-occupied sites had at least two subsamples with resistance above that threshold, and the value was exceeded at a minimum of 10 sampling stations. This is a minimum estimate of average resistance, because our instrument for sampling penetration resistance had a maximum value of 4.7 kg/cm².

Our results also support indirect effects on ant abundance associated with changes in vegetative cover and the potential existence of feedbacks as shown in Fig. 1. We found a positive (though weak) correlation between ant mound abundance and total vegetative cover across all sites in both 1997 and 1998. Stronger correlation between these two variables has been observed by other researchers, however (Sneva, 1979; Andersen, 1991; Andersen and Sparling, 1997). Furthermore, mound abundance correlated quite strongly with an index of shrub-canopy continuity in both 1997 ($r = 0.57, p = 0.03$) and 1998 ($r = 0.42, p = 0.09$), suggesting that small-scale *pattern* in vegetation cover may influence abundance more than simply the *quantity* of cover. The discrepancy between the strength of these last two types of correlations is consistent with findings of other investigators of ants. For example, Bestelmeyer and Wiens (1996) found that community diversity of ants in Argentina varied with respect to both season (wet vs. dry) and scale of analysis. After analyzing low-level aerial photographs of ant distributions, Crist and Wiens (1996) suggested that ant distributions are influenced both by fine-scale determinants such as neighborhood interactions and by broad-scale factors such as grazing, topography, and soils.

5. Conclusions

Previous research demonstrated that free-roaming horses can alter aspects of vegetation, granivorous small mammals, and reptiles in Great Basin mountain ranges (Beaver, 1999; Beaver and Brussard, 2004). This, in addition to the findings presented here that horse-occupied sites have more compacted soil surfaces and lower abundances of ant mounds, suggest that horses as well as domestic livestock need to be considered in conservation planning in semi-arid ecosystems. For example, given that horses use steeper and higher-elevation locations than do cattle, addition of horses to landscapes means that non-native herbivory and trampling occurs across a greater percentage of the physiographically heterogeneous Great Basin than if only domestic stock were present (Beaver, 2003). Several lines of evidence also suggest that efforts of conservation researchers and land managers alike would be more effective if both direct and indirect disturbance effects were considered. The relative importance of different types of effects needs to be further quantified with manipulative experiments.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at: [doi:10.1016/j.jaridenv.2005.11.006](https://doi.org/10.1016/j.jaridenv.2005.11.006).

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