
Influence of a Large Herbivore Reintroduction on Plant Invasions and Community Composition in a California Grassland

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Abstract: *Despite many successful reintroductions of large mammalian herbivores throughout the world, remarkably little attention has focused on how these actions affect native and exotic vegetation at reintroduction sites. One such herbivore is tule elk (*Cervus elaphus nannodes*), which was on the brink of extinction in the mid 1800s, but now has numerous stable populations due to intensive reintroduction efforts. Here, we summarize results from a 5-year enclosure experiment that explored the effects of tule elk on a coastal grassland in northern California. Elk significantly altered the species composition of this community; the response of annual species (dominated heavily by exotic taxa) was dramatically different from perennial species. Elk herbivory increased the abundance and aboveground biomass of native and exotic annuals, whereas it either had no effect on or caused significant decreases in perennials. Elk also decreased the cover of native shrubs, suggesting that these herbivores play an important role in maintaining open grasslands. In addition, elk significantly reduced the abundance and biomass of a highly invasive exotic grass, *Holcus lanatus*, which is a major problem in mesic perennial grasslands. Our results demonstrate that the successful reintroduction of a charismatic and long-extirpated mammal had extremely complex effects on the plant community, giving rise to both desirable and undesirable outcomes from a management perspective. We suspect that these kinds of opposing effects are not unique to tule elk and that land managers will frequently encounter them when dealing with reintroduced mammals.*

Keywords: coastal grasslands, herbivory, plant functional groups, plant invasions, reintroduced mammals, shrub encroachment, tule elk

Influencia de la Reintroducción de un Herbívoro Mayor sobre Invasiones de Plantas y la Composición de la Comunidad en un Pastizal de California

Resumen: *A pesar de muchas reintroducciones exitosas de grandes mamíferos herbívoros en todo el mundo, notablemente se ha puesto poca atención en como estas acciones afectan a la vegetación nativa y exótica en los sitios de reintroducción. Uno de tales herbívoros es el alce (*Cervus elaphus nannodes*), que estaba a punto de extinguirse a mediados del siglo XIX, pero que ahora tiene numerosas poblaciones estables debido a esfuerzos intensivos de reintroducción. Aquí, resumimos los resultados de un experimento de exclusión de 5 años que exploró los efectos de alces sobre un pastizal costero en el norte de California. Los alces alteraron significativamente la composición de especies de esta comunidad; la respuesta de especies anuales (dominadas ampliamente por taxa exóticos) fue dramáticamente diferente a la de especies perennes. La herbivoría de alces incrementó la abundancia y biomasa de anuales nativas y exóticas, mientras que no tuvo efecto o no causó disminuciones significativas en las perennes. Los alces también disminuyeron la cobertura arbustos nativos, lo que sugiere que estos herbívoros juegan un papel importante en el mantenimiento de los pastizales abiertos. Adicionalmente, los alces significativamente redujeron la abundancia y biomasa de un pasto exótico*

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Paper submitted February 2, 2006; revised manuscript accepted July 18, 2006.

altamente invasivo, Holcus lanatus, que es un problema mayor en los pastizales mésicos perennes. Nuestros resultados demuestran que la reintroducción exitosa de un mamífero carismático tuvo efectos extremadamente complejos sobre la comunidad de plantas, dando lugar a consecuencias tanto deseables como indeseables desde una perspectiva de manejo. Sospechamos que estos tipos de efectos opuestos no son exclusivos de alces y que los gestores los enfrentarían frecuentemente cuando traten con mamíferos reintroducidos.

Palabras Clave: alce, grupos funcionales de plantas, herbivoría, invasión de arbustos, invasiones de plantas, mamíferos reintroducidos, pastizales costeros

Introduction

For thousand of years the abundance and distribution of large mammalian herbivores have been modified greatly by human activity (Martin & Klein 1984), and these effects increased substantially with European colonization of North America and other regions of the world (Naiman 1988; Knapp et al. 1999). During the past century programs were initiated to reintroduce extirpated mammals into parts of their historical range (Nielsen & Brown 1988), and many of these taxa have increased in numbers due to such conservation efforts (Noss 2001).

Extensive research has been conducted on herbivore populations to better understand how they respond to reintroduction (Nielsen & Brown 1988; Griffith et al. 1989; Noss 2001), but remarkably little is known about the effects of these long-absent taxa on recipient ecosystems (i.e., ecosystems into which species have been reintroduced). This is surprising, given that the results of many studies show that large mammalian herbivores can have substantial impacts on the composition and structure of plant communities (e.g., Crawley 1983; Huntly 1991; Knapp et al. 1999). How communities respond to the reintroduction of previously extirpated herbivores will be determined to some extent by the unfortunate reality that recipient ecosystems have been modified in many ways other than the loss of a dominant herbivore. For example, herbivore populations are commonly reintroduced into ecosystems that have been invaded heavily by exotic plant species (e.g., Vitousek et al. 1996; Mack et al. 2000; Mooney & Hobbs 2000). Native herbivores may negatively influence exotic plants by reducing their biomass, fecundity, and/or abundance in communities or they may avoid exotic plants and feed on only native hosts, thereby promoting the success of exotics by reducing the dominance of native species and freeing up resources that invaders can exploit (e.g., Davis et al. 2000; Maron & Vila 2001; Levine et al. 2004). Thus, it will be critical to understand if and how reintroduced herbivores affect the success of plant invaders and the structure and composition of communities.

The effects of reintroduced herbivores on plant communities will be determined in part by the life history characteristics and geographic origins of resident species present in the community. Plants from different

functional groups may vary greatly in their response to herbivory, as might native and exotic taxa within the same functional group. In addition, these herbivores may keep grasslands open by slowing or even preventing the encroachment of woody species. Furthermore, native shrubs in grasslands may alter the effects of herbivores on herbaceous plants in the system. For these reasons it will be critical to conduct studies that take a community approach and assess how reintroduced herbivores influence native and exotic taxa with different suites of life history characteristics.

Grasslands throughout California have undergone an extraordinary transformation over the past 200 years. Once dominated by native perennial bunchgrasses, they are now composed primarily of annual grasses from Eurasia (Heady 1988; Heady et al. 1988; 1992). Accompanying these changes has been a precipitous decline in mammalian herbivores and an increase in domesticated grazers (Wagner 1989). Like many large herbivores, populations of tule elk (*Cervus elaphus nannodes*) in California suffered rapid decline soon after the arrival of European settlers, going from an estimated 500,000 animals in 1769 to fewer than 10 individuals 70 years later (Phillips 1976; Toweill & Thomas 2002). By 1986 numbers had increased to over 2000 individuals distributed among 22 populations throughout California, largely due to successful reintroduction programs (McCullough et al. 1996). Tule elk thus provide an ideal opportunity to study the influence of herbivore reintroductions on a highly altered recipient grassland.

Here, we used a 5-year exclosure experiment to address four questions concerning the influence of reintroduced tule elk on a coastal grassland in northern California: (1) Does herbivory by reintroduced tule elk influence the abundance, species richness, and aboveground biomass of different plant functional groups in grassland communities that vary in shrub abundance? (2) Do native and exotic plant taxa vary in their responses to elk reintroduction? (3) Do tule elk deter the encroachment of shrubs into this grassland system? and (4) Can a dominant exotic grass escape herbivory by associating with a native shrub? We predicted that the reintroduction of tule elk would reduce the prevalence of shrubs in the grassland, decrease the prevalence of perennial grasses and forbs, and promote the success of annual species, which are

dominated heavily by exotic taxa. Our results should provide insight into the effects of a reintroduced native herbivore on the composition of an invaded grassland community and provide land managers with critical information needed for the effective and sustainable management of California grasslands.

Study System

The Tomales Point Elk Reserve is a 1030-ha wilderness area located within Point Reyes National Seashore, approximately 32 km north of San Francisco in Marin County, California. The climate is Mediterranean and typical of California's central coast, with moderate, rainy winters and cool, foggy summers with little rain.

Tule elk have been a dominant feature of all habitat types on Tomales Point since their reintroduction in 1980. Approximately 400 cattle were removed from Tomales Point in 1979, after more than 100 years of grazing (Lathrop & Gogan 1985). Within a year of the cattle removal, eight female and two male tule elk were reintroduced to the point from a population in the San Luis Island Wildlife Refuge near Los Banos, in central California (Lathrop & Gogan 1985). The elk population increased to 93 individuals by 1988 and to approximately 500 individuals by 2003 (N. Gates, personal communication). The diet of tule elk at Tomales Point consists primarily of herbaceous forbs and grasses, but they also consume shrub foliage during the winter months when there is less herbaceous material available (Gogan & Barrett 1995).

The vegetation of Tomales Point consists primarily of a mosaic of shrub-dominated coastal scrub and grassland, interrupted by steep canyons and swales containing dense riparian shrubs (Lathrop & Gogan 1985). We focused on the grassland component of Tomales Point, which consists of a diverse assemblage of both native and introduced herbaceous plant species intermixed with native shrubs. Three distinct grassland types occurred within the 300-ha study area: *Baccharis*-dominated grassland, *Lupinus*-dominated grassland, and open grassland. *Baccharis* grasslands were characterized by herbaceous-dominated patches intermixed with dense stands of the native woody shrub, *Baccharis pilularis* DC (coyote bush). *Lupinus* grasslands were located in predominantly open areas interspersed with a native nitrogen-fixing shrub, *Lupinus arboreus* Sims. And the open grasslands were dominated by herbaceous species and nearly devoid of dominant woody shrubs. All three of these vegetation types have a high proportion of herbaceous species overlap.

Herbaceous plant species at Tomales Point can be grouped into one of five functional groups based on life history and phylogenetic characteristics: annual mono-

cots, annual dicots, perennial monocots, perennial dicots, and nonangiosperms (ferns and their allies). Annual and perennial monocots at this site were almost exclusively grasses and included native perennials, such as *Bromus carinatus* Hook. & Arn., *Hordeum brachyantherum* Nevski, and *Danthonia californica* Bolander, and exotic perennials, such as *Lolium perenne* L. and *Holcus lanatus* L. Several species of exotic annual grasses (*Vulpia bromoides* [L.] S.F. Gray, *Aira caryophyllea* L., *Bromus hordeaceus* L., and *Cynosurus echinatus* L.) were also abundant, but we never encountered native annual grasses. Native perennial dicots (e.g., *Achillea millefolium* L. and *Eschscholzia californica* Cham.) and exotic perennial dicots (e.g., *Hypochaeris radicata* L. and *Plantago lanceolata* L.) were all abundant throughout the study area. *Pteridium aquilinum* (L.) Kuhn var. *pubescens* L. Underw. was the only nonangiosperm vascular plant observed in the study area.

Holcus lanatus (velvet grass) is an exotic perennial grass that has invaded many coastal grasslands throughout California. In our site, *Holcus* was abundant in the *Baccharis* grasslands, where it grew underneath shrub canopies and in shrub-free areas (B.E.J., personal observation). This exotic grass occurred less commonly in the open and *Lupinus* grassland types.

Methods

Experimental Design

In 1998 the U.S. National Park Service established an enclosure experiment within a 300-ha study area on Tomales Point to assess the effects of removing reintroduced tule elk on the plant community. Twenty-four 36 × 36 m plots were distributed equally among three grassland habitat types (*Baccharis* grassland, *Lupinus* grassland, and open grassland). Within each of the three vegetation types, there were four pairs of plots, with plots within pairs randomly assigned fencing to exclude elk or left unfenced to serve as controls. The fencing that surrounded each enclosure plot was 2.5-m tall and effectively excluded elk. Smaller herbivores that occur on Tomales Point, such as hares (*Lepus californicus*) and pocket gophers (*Thomomys bottae*), were not affected by the fencing (B.E.J., personal observation). Black-tailed deer (*Odocoileus hemionus columbianus*) were present in small numbers at the site and were able to enter the enclosures, although probably in reduced numbers. We restricted all vegetation sampling to the central 30 × 30 m area of each plot. This provided a 3-m-wide buffer around the perimeter of each plot and reduced possible edge effects caused by fencing.

Plant Community Composition

In May and June 2002 we harvested all aboveground plant biomass from three randomly chosen 25 × 25 cm quadrats in each plot. We restricted harvests to areas in plots that had <5% shrub cover and sorted aboveground living biomass into annual and perennial plant groups. We also collected accumulated dead biomass (thatch) from the quadrats that were in the *Baccharis* and open plots. We dried living and dead biomass at 60° C for a minimum of 48 hours, and weighed the material immediately after removal from the oven. In the spring of 2003 we quantified abundance of all plant species in the 24 plots within six randomly placed 50 × 50 cm quadrats by counting the number of individuals for each species. In addition, we determined the identity of all plant species that occurred in each plot to obtain whole-plot species richness. We grouped plant species according to their geographic origin (i.e., native or exotic) and then placed them into eight functional groups based on life history characteristics: native and exotic annual dicots, exotic annual monocots, native and exotic perennial dicots, native and exotic perennial monocots, and ferns (native annual monocots were absent from the site). We encountered few ferns during sampling, so this group was not analyzed. Plant nomenclature for all sampling and analysis followed Hickman (1993).

Cover and Density of Shrubs

In July and August 2003 we estimated the aerial cover of shrubs in each of the 24 plots with standard line-intercept methods (Bonham 1989). We established five parallel 30-m transects in all plots at 5-m intervals and measured the extent of shrub cover encountered directly below or above the transect to the nearest centimeter. We determined proportion of shrub cover by dividing total length of shrub coverage along each transect by 30 m.

In June 2003 we determined the abundance of *Lupinus arboreus* juveniles and mature shrubs within the central 30 × 30 m area of each *Lupinus* grassland plot. We classified plants as juveniles if they lacked flowers and fruits and had not yet produced any woody material. Because we rarely encountered *Lupinus* shrubs in the open and *Baccharis* grasslands, we did not sample plots from these areas.

Interactions among Elk, *Holcus*, and *Baccharis*

To evaluate the impact of tule elk and a native shrub species on a dominant invasive grass, we quantified the aboveground biomass and abundance of *Holcus lanatus* in areas within plots dominated by *Baccharis* shrubs and in shrub-free areas. We restricted sampling to the eight *Baccharis* plots because *Holcus* and *Baccharis* rarely occurred in the *Lupinus* and open grasslands. In June 2002 we randomly placed three 25 × 25 cm quadrats in shrub-

free areas of each plot and three quadrats in areas with >75% aerial cover of living *Baccharis* foliage. In each quadrat we harvested all aboveground living biomass and separated out all living *Holcus* plant material from samples. We then dried the *Holcus* at 60° C for a minimum of 48 hours and weighed the samples immediately after removal from the oven. In June 2003 we determined the abundance of *Holcus* in each of these same *Baccharis* plots, sampling six 50 × 50 cm quadrats in shrub-free areas and six quadrats in sites with >75% aerial cover of living *Baccharis* foliage.

Statistical Analyses

We performed all statistical analyses with SAS 8.2 (SAS Institute, Cary, North Carolina) and PC-ORD 4.2 (MjM Software, Gleneden Beach, Oregon). We used nonmetric multidimensional scaling (NMS or nMDS) analysis to reduce the dimensionality of the data set and visualize community-level treatment effects. We also used multiresponse-blocked permutation procedure (MRBP), a nonparametric randomization version of a blocked multivariate analysis of variance (MANOVA), to statistically assess treatment effects on community structure. We did not include very rare species (taxa occurring in fewer than three plots) in the analyses to reduce the number of null values in the data matrix. We used Sørensen (Bray-Curtis) distance measure in the NMS analysis and Euclidean distance in the MRBP analysis. For the MRBP analysis, we used elk treatment (present or absent) and plot pair (1-12) as our grouping factors.

To determine the influence of elk on different plant functional groups in the three grassland types, we analyzed our data using multifactor MANOVAs, with elk treatment (elk present or absent), grassland type (*Baccharis*, *Lupinus*, open grasslands), and plot pair (1-12) nested within vegetation type as the grouping factors ($n = 24$ plots). We treated plot pair as a random factor and used Wilks' lambda values throughout. Response variables for the two MANOVAs were plant species richness and abundance for the following seven groups: exotic annual monocots, exotic annual dicots, exotic perennial dicots, exotic perennial monocots, native annual dicots, native perennial monocots, and native annual dicots. We performed a third MANOVA with the same model, with annual and perennial biomass as the two response variables. Prior to the analysis, we averaged data from all quadrats within each plot and log-transformed abundance and living biomass data to correct for heterogeneous variances. Data for whole-plot species richness met the assumptions of normality and equal variances and were left untransformed.

For all MANOVAs with significant elk treatment effects or any interaction terms that included elk treatment, we proceeded with "protected" analysis of variances (ANOVAs) on the individual response variables. As

discussed at length by Scheiner (2001), this approach is an effective method for dealing with potential correlations among multiple dependent variables and is used commonly with community data (e.g., Harrison et al. 2001; Alvarez & Cushman 2002; Cushman et al. 2004; Tierney & Cushman 2006). To determine whether elk influence the amount of dead biomass (thatch), we used an ANOVA with the above model and thatch biomass as the response variable. We log transformed thatch data to correct for heterogeneous variances.

To determine the effect of elk on the shrub cover, we analyzed data using a three-way ANOVA, with elk treatment (elk present or absent), grassland type (*Baccharis*, *Lupinus*, open grasslands), and plot pair (1–12) nested within vegetation type as the grouping factors ($n = 24$ plots). The response variable for this analysis was percentage of total shrub cover in each plot. We transformed proportion data to the arc-sine square root prior to analysis. To determine whether elk influenced the abundance of mature *Lupinus* shrubs, we used a two-way ANOVA with elk treatment (present or absent) and plot pair (1–4) as the grouping factors and mature *Lupinus* abundance as the response variable.

To determine whether the effects of elk herbivory on *Holcus* varied between *Baccharis* and shrub-free areas, we analyzed data on the biomass and abundance of this exotic grass using a three-way ANOVA, with elk treatment (present or absent), shrub (present or absent) and plot pair (1–4) as the grouping factors ($n = 16$) and plot (1–8) nested within pair. Prior to analysis, we averaged data from all quadrats within each plot and shrub level and data on *Holcus* biomass were log transformed to correct for heterogeneous variances. We analyzed data on juvenile abundance of *Lupinus* per plot with a one-way analysis of covariance (ANCOVA), with elk treatment (present or absent) as the grouping factor and abundance of mature shrubs per plot as the covariate.

Results

Plant Community Composition

The NMS analysis indicated that the composition of plant assemblages where elk were present differed from where they were excluded (Fig. 1). The MRBP analysis indicated significant differences between fenced and control plots ($A = 0.35$, $p = 0.0004$). In addition, a MANOVA indicated that tule elk significantly altered plant species richness of the seven plant groups considered collectively (Fig. 2; $F_{7,3} = 19.26$, $p = 0.017$). Subsequent protected ANOVAs showed that this result was due to significant differences in three of the seven plant groups and a trend in a fourth group. The presence of elk caused an 18% increase in richness of exotic annual monocots, a 47% increase in richness of native annual dicots, a 42% increase in richness

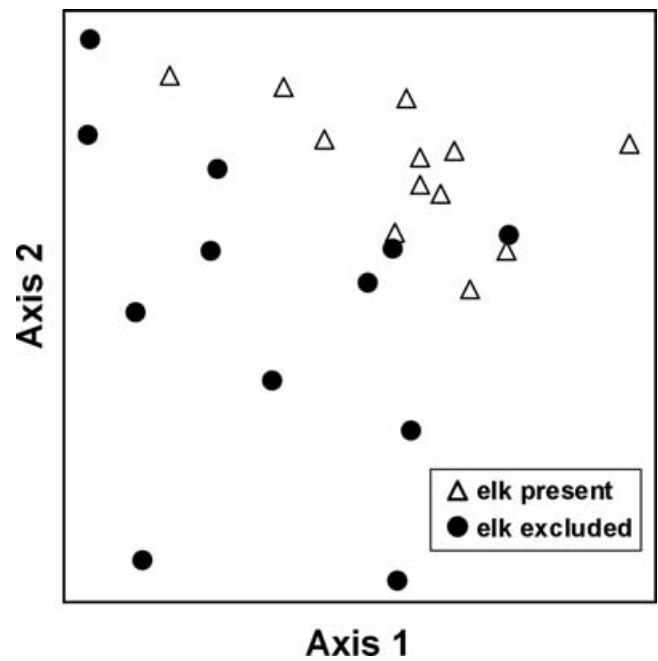


Figure 1. Results of nonparametric multidimensional scaling analyses of data on plant species abundance from plots where elk were present (open symbols) and where elk were excluded (closed symbols).

of native perennial monocots, and a 23% decrease in the species richness of native perennial dicots compared with exclosure plots (Fig. 2 & Table 1). In contrast to these four groups, elk had no significant effect on the richness of exotic annual dicots, exotic perennial monocots, or exotic perennial dicots (Fig. 2 & Table 1). Nevertheless, species richness varied significantly among grassland types for exotic annual dicots, native annual dicots, exotic perennial monocots, native perennial monocots, exotic perennial dicots, and native perennial dicots (Fig. 2 & Table 1). For all plant groups the response of species richness to elk manipulations was similar among grassland types, as indicated by the absence of significant treatment \times vegetation type interaction terms ($p > 0.10$ in all cases).

A second MANOVA revealed that elk had a significant influence on the abundances of the seven plant groups considered collectively (Fig. 3; $F_{7,3} = 10.78$, $p = 0.038$). Protected ANOVAs on individual groups indicated that this result was due primarily to elk causing a 315% increase in the abundance of exotic annual monocots, a 78% increase in the abundance of exotic annual dicots, and a 245% increase in native annual dicots (Fig. 3 & Table 1). In contrast, elk had no effect on the abundance of exotic perennial monocots, native perennial monocots, exotic perennial dicots, or native perennial dicots (Fig. 3 & Table 1). Plant abundance varied significantly among grassland types for native annual dicots, exotic perennial monocots, and native perennial monocots (Fig. 3 & Table 1). For all plant groups, again the effects of elk were

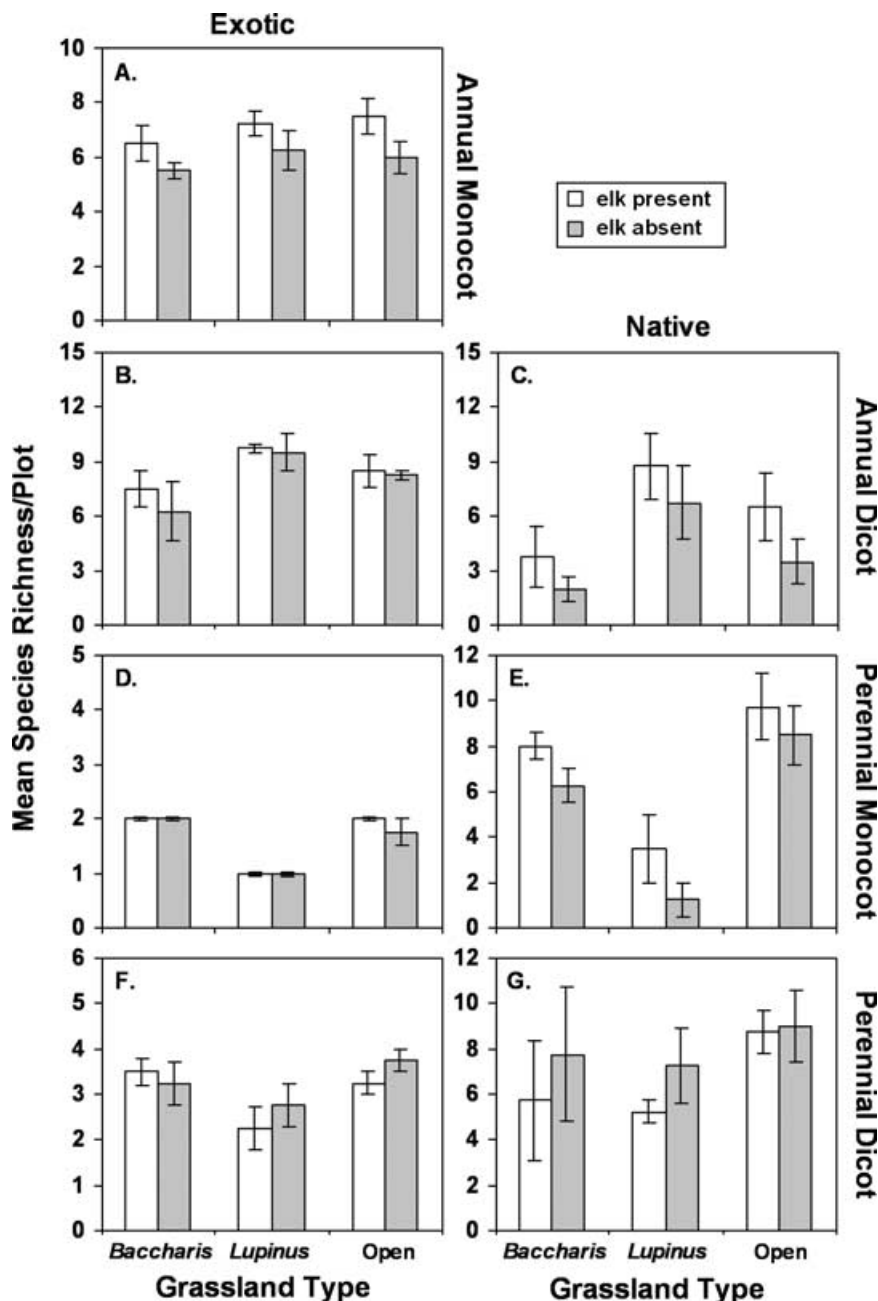


Figure 2. Plant species richness (mean \pm 1 SE) of seven herbaceous plant groups as a function of grassland type (Baccharis, Lupinus, and open) and the presence or absence of tule elk: (a) annual monocots, (b, c) annual dicots, (d, e) perennial monocots, and (f, g) perennial dicots.

consistent across grassland types, as indicated by insignificant treatment \times grassland type interaction terms ($p > 0.10$).

In a third multiway MANOVA tule elk significantly influenced the aboveground dry biomass of annual and perennial plant species considered collectively (Fig. 4; $F_{2,8} = 5.81$, $p = 0.028$). Subsequent protected ANOVAs revealed that elk increased annual biomass by 34% ($F_{1,9} = 7.13$, $p = 0.026$) but decreased perennial biomass by 50% ($F_{1,9} = 11.67$, $p = 0.008$) (Fig. 4). Annual and perennial biomass did not differ significantly among grassland types (Figs. 4a-b; $F_{2,9} = 1.94$, $p = 0.199$ and $F_{2,9} = 0.77$, $p = 0.491$, respectively). For both annuals and perennials, the effects of elk were consistent across grassland types, as

indicated by the lack of significant treatment \times grassland type interaction terms ($p > 0.10$). In addition, there was a nearly 200-fold increase in thatch where elk were excluded (Fig. 4c; $F_{1,7} = 47.65$, $p = 0.002$), and the influence of elk was greater in *Baccharis* plots than in open plots, as indicated by a significant treatment \times grassland type interaction ($F_{1,6} = 19.42$, $p = 0.005$).

Cover and Density of Shrubs

Total shrub cover varied significantly among grassland types (Fig. 5a; $F_{2,6} = 24.36$, $p = 0.0002$). Cover was much greater in *Baccharis* grasslands than in *Lupinus* and open grasslands. In addition, elk caused a decrease in total

Table 1. Results from seven multiway analysis of variances for an enclosure experiment evaluating the effects of tule elk on the plant species richness and abundance for seven herbaceous functional groups across three different grassland types in northern California.*

Variable and source	df	Abundance		Species richness	
		F	p	F	p
Exotic annual monocot					
grassland type	2,9	1.83	0.215	3.00	0.100
elk treatment	1,9	35.35	0.0002	16.33	0.003
pair (grassland type)	9,9	2.45	0.099	4.44	0.018
G × ET	2,9	0.09	0.915	0.33	0.725
Exotic annual dicot					
grassland type	2,9	3.97	0.058	5.90	0.023
elk treatment	1,9	4.18	0.071	0.79	0.396
pair (grassland type)	9,9	0.44	0.878	1.91	0.175
G × ET	2,9	0.19	0.833	0.26	0.777
Native annual dicot					
grassland type	2,9	29.05	0.0001	3.12	0.094
elk treatment	1,9	5.20	0.049	5.47	0.044
pair (grassland type)	9,9	3.50	0.038	2.41	0.103
G × ET	2,9	1.47	0.281	0.13	0.878
Exotic perennial monocot					
grassland type	2,9	6.49	0.018	57.00	<0.0001
elk treatment	1,9	0.05	0.833	1.00	0.343
pair (grassland type)	9,9	2.98	0.060	1.00	0.500
G × ET	2,9	0.44	0.659	1.00	0.405
Native perennial monocot					
grassland type	2,9	45.55	<0.0001	40.97	<0.0001
elk treatment	1,9	0.57	0.469	7.83	0.021
pair (grassland type)	9,9	5.04	0.012	3.37	0.043
G × ET	2,9	1.18	0.352	0.21	0.812
Exotic perennial dicot					
grassland type	2,9	15.55	0.001	15.55	0.001
elk treatment	1,9	2.45	0.152	2.45	0.152
pair (grassland type)	9,9	6.82	0.004	6.82	0.004
G × ET	2,9	2.45	0.141	2.45	0.141
Native perennial dicot					
grassland type	2,9	4.76	0.039	4.76	0.039
elk treatment	1,9	3.69	0.087	3.69	0.087
pair (grassland type)	9,9	8.05	0.002	8.05	0.002
G × ET	2,9	0.63	0.557	0.63	0.557

*Abundance data were log transformed to correct for heterogeneous variances. Key: G, grassland type; ET, elk treatment.

shrub cover ($F_{1,9} = 3.78$, $p = 0.084$). Although this effect was greatest in the open grassland, we did not detect a significant treatment × grassland type interaction term ($F_{2,9} = 0.89$, $p = 0.445$). Elk significantly increased the abundance of juvenile *Lupinus arboreus* (Fig. 5b; $F_{1,4} = 10.55$, $p = 0.031$), which was not explained by differences in the number of mature *Lupinus* plants (mature × juvenile *Lupinus* interaction; $F_{1,4} = 0.27$, $p = 0.629$). Nevertheless, elk did not affect the abundance of mature *Lupinus* shrubs ($F_{1,3} = 0.0711$, $p = 0.807$).

Interactions among Elk, *Holcus*, and Shrubs

The influence of elk on the abundance of the exotic grass, *Holcus lanatus*, varied significantly with the local neighborhood inhabited by this invader. Specifically, we detected a significant interaction between herbivore treatment and local neighborhood (i.e., whether *Holcus* occurred underneath the canopy of the native shrub, *Bac-*

charis pilularis, or whether it occurred in shrub-free areas). Elk had a negative effect on the abundance of *Holcus* in the open grassland, but had no impact when the grass grew in association with *Baccharis* (Fig. 6a, $F_{1,6} = 6.15$, $p = 0.048$). There was a similar significant shrub × elk interaction term for aboveground dry biomass of *Holcus* (Fig. 6b, $F_{1,6} = 22.23$, $p = 0.003$).

Discussion

In our 5-year enclosure experiment we examined the effects of a reintroduced herbivore on the composition of a grassland community in coastal California. Annual and perennial plant groups responded to elk herbivory in distinct ways, but plant taxa within the same functional group generally responded similarly to herbivory, regardless of whether they were native or exotic. In particular,

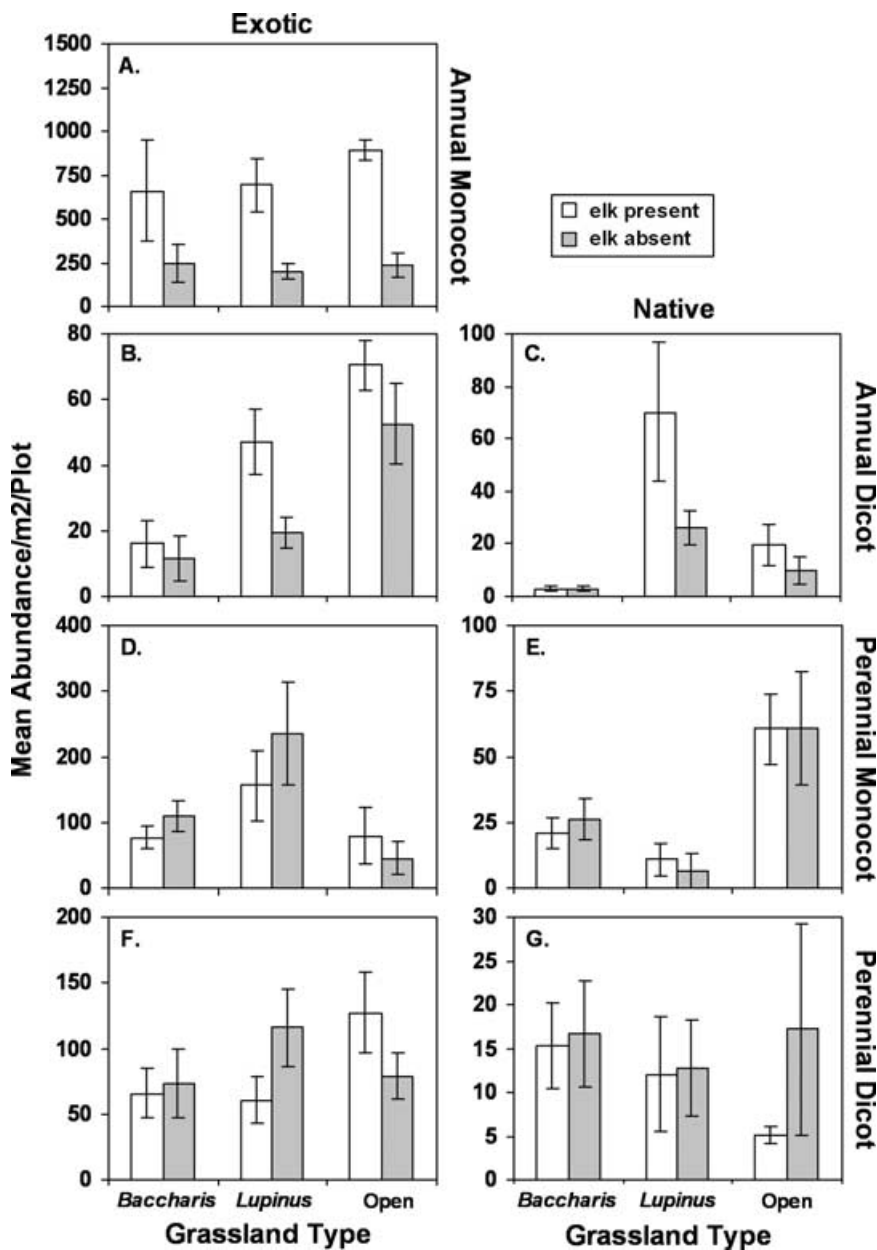


Figure 3. Abundance (mean \pm 1 SE) of seven herbaceous plant groups as a function of grassland type (Baccharis, Lupinus, and open) and the presence or absence of tule elk: (a) annual monocots, (b, c) annual dicots, (d, e) perennial monocots, and (f, g) perennial dicots.

elk increased the abundance and biomass of both native and exotic annuals, decreased the biomass of native and exotic perennials, and had only minimal effects on perennial abundance (Figs. 3 & 4). Although elk herbivory enhanced native annual species, this came at the expense of increased abundance of exotic annuals.

Several hypotheses may explain the opposing effects of elk on annuals and perennials at our coastal grassland site. First, because elk reduce the accumulation of dead plant biomass (Fig. 4c), they may create favorable microsites for the germination and establishment of annuals by freeing up space in an otherwise closed grassland habitat. Support for this hypothesis comes from the many studies that show thatch can adversely influence the germination, survival, and/or growth of colonizing annuals (e.g., Carson

& Peterson 1990; Facelli & Pickett 1991; Foster & Gross 1998).

Second, foraging elk may create favorable microsites for annuals in grasslands by trampling the dominant perennial vegetation with their hooves. Such disturbances favor annual taxa—especially exotics—that are adept at colonizing habitat openings (Hobbs & Hueneke 1992; Cushman et al. 2004). Perennials should be less responsive to both thatch reduction and trampling, given that members of this group (especially perennial grasses) exhibit lower recruitment and reduced colonization ability than annuals (Dyer et al. 1996; Hamilton et al. 1999; Seabloom et al. 2003; Tierney & Cushman 2006).

Third, elk may either feed preferentially on perennials or may simply have a greater effect on them because they

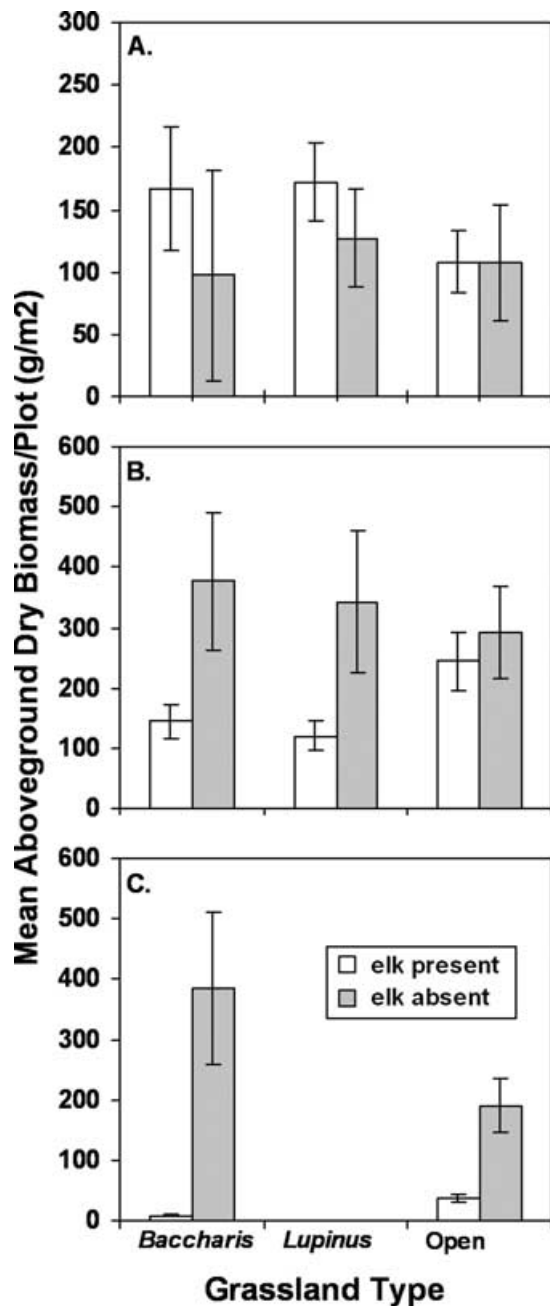


Figure 4. Aboveground dry biomass (mean \pm SE) of (a) living annuals, (b) living perennials, and (c) dead biomass (thatch) as a function of grassland type (Baccharis, Lupinus, and open) and the presence or absence of tule elk. The scale of (a) is half that of (b).

are the dominant functional group in this system (Fig. 4). The decreased dominance of perennials should lead to increased water and nutrient availability that annuals can capitalize on. Results from several studies support this hypothesis, showing that mammalian herbivores can reduce dominant species and allow less competitive plant groups to flourish (e.g., McNaughton 1983; Collins 1987; Hart-

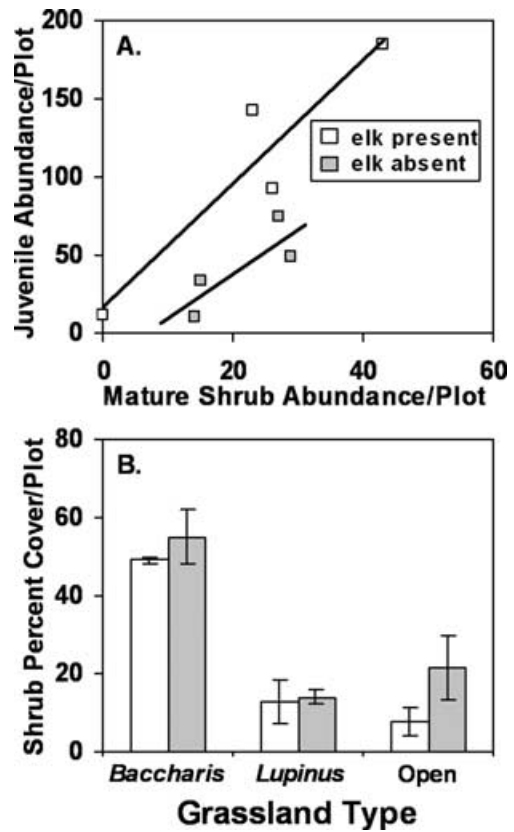


Figure 5. (a) Percent cover of shrubs (mean \pm 1 SE) as a function of grassland type (Baccharis, Lupinus, and open) and the presence or absence of tule elk and (b) the relationship between abundance of juvenile and established bush lupines (*Lupinus arboreus*) as a function of presence or absence of tule elk.

nett et al. 1996; Proulx & Mazumder 1998; Hayes & Holl 2003). For example, Collins (1987) demonstrated that cattle grazing increases the richness of tallgrass prairie annuals and that this increase is likely due to herbivores consuming a dominant grass species. We suspect that each of these factors—reduced accumulation of thatch, trampling of vegetation, differential impacts of herbivory, and altered competitive dynamics—were likely factors explaining the opposing responses of annuals and perennials to elk in our study.

From a management perspective, one of our most important findings is that elk herbivory greatly reduced the abundance and aboveground biomass of the highly invasive exotic perennial grass, *Holcus lanatus*. This species is a problematic invader in many mesic grasslands along the coast of California, and our work suggests that grazing may be an effective way to control its abundance and subsequent spread in open grasslands. Hayes and Holl (2003) also found that cattle grazing significantly reduced *Holcus* abundance at numerous sites in California.

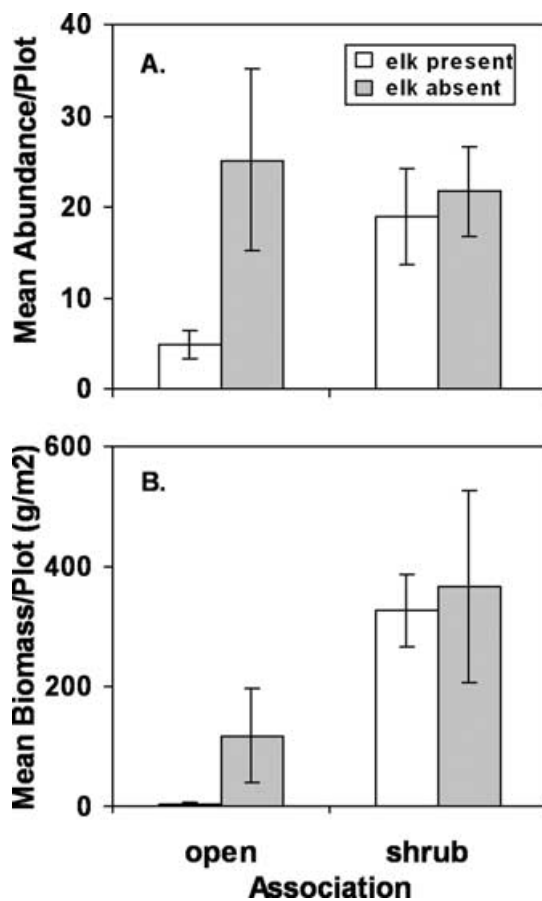


Figure 6. (a) Abundance and (b) aboveground dry biomass (mean \pm 1 SE) of velvet grass (*Holcus lanatus*) as a function of the presence of coyote bush shrubs (*Baccharis pilularis*) and the presence or absence of tule elk.

A caveat to our results is that negative effects of elk on *Holcus* disappeared when the invader grew underneath the canopy of the native shrub, *Baccharis pilularis* (Figs. 6a-b). This type of associational resistance to herbivory is most likely due to elk having greater difficulty accessing *Holcus* when it grows beneath the canopies of *Baccharis* shrubs than when it occurs in the open. Others have considered the possibility that plants can avoid herbivory by associating with neighboring plants that make them less susceptible to herbivory (e.g., Atsatt & O'Dowd 1976; Huntly 1991; Hamback et al. 2000; Milchunas & Noy-Meir 2002). For example, Rebollo et al. (2002) demonstrated that the cactus, *Opuntia polyacantha*, provides protection from cattle grazing to many plant species that grow in association with it and that seed production is greater beneath cacti than in adjacent open areas. Our work builds on these results and illustrates the complexities that can arise in human-altered landscapes, where extirpated but now reintroduced native herbivores can control the dominance of problematic exotic plants, and

that these invaders can in turn escape such control by associating with native shrubs.

Mesic grasslands in California are prone to shrub invasion (Hobbs & Mooney 1986; Callaway & Davis 1993), and our data show that elk decreased the cover of such taxa (Fig. 5b). These results are consistent with findings from other studies of elk in North America (Singer et al. 1998; Peinetti et al. 2001; Brookshire et al. 2002) and suggest that elk may play an important role in maintaining grasslands. The negative effect of elk on shrubs was stronger in the open grassland than in the *Baccharis*- and *Lupinus*-dominated grasslands. Over time we suspect that shrub cover will increase in the absence of elk but that such effects might be less pronounced in *Lupinus* and *Baccharis* grasslands because other environmental factors, such as water availability or variations in soil type, may be important regulators of shrub cover that override the effects of herbivores. An increase in shrub cover in any of the grassland types would result in a loss of plant richness in those areas because most herbaceous plant species on Tomales Point occur in open areas and not beneath shrubs (B.E.J., unpublished data).

Although elk had an overall negative effect on shrub cover, they had varying effects on *Lupinus arboreus* at different life stages (Fig. 5a). Elk increased the abundances of juvenile bush lupines, whereas they had no effect on the abundances of mature shrub. Elk may have promoted the initial establishment of lupines by disturbing the soil and/or by reducing the biomass of neighboring plant species (primarily grasses) that would otherwise compete with these juveniles for light, water, or soil nutrients. Once lupines reached maturity, they may have no longer competed with these neighboring taxa or other factors negated the initial increase in *Lupinus* juveniles caused by elk. For example, other herbivore species, such as invertebrates and mammals, reduce the growth and survival of juvenile bush lupines and may thus limit the abundance of mature plants (Maron 1998; Warner & Cushman 2002; McNeil & Cushman 2005).

Tule elk have been reintroduced in many parts of California that differ markedly in temperature, precipitation regimes, and community composition. This expansive distribution across a diversity of conditions makes it challenging to predict how broadly our results will apply to other locations. Although we suspect that elk will have profound effects on plant communities at all reintroduction sites, the magnitude and direction of these impacts may vary greatly. Hayes and Holl (2003) evaluated the effects of cattle grazing on multiple coastal grasslands in northern California and obtained results similar to ours for elk: grazing increased the species richness and cover of native annual forbs and decreased these parameters for native perennial forbs. Hayes and Holl hypothesized that cattle promote annuals by reducing the dominance of perennial grasses and dead biomass and thereby free up resources. Results from this study combined with our

own suggest that domesticated and native grazers may have similar impacts on coastal grasslands and that our results are applicable to other mesic grasslands along the Pacific coast.

In more arid grasslands large mammalian herbivory may exert radically different influences on grasslands (Olf & Ritchie 1998; Kimball & Schiffman 2003). For example, accumulated biomass may have the opposite effect in xeric climates of what we found in our mesic system because it may provide protection to seedlings from intense sunlight and heat (Foster & Gross 1998). Soil conditions may also influence how plants respond to mammalian herbivory, as shown by Harrison et al. (2003), who demonstrated that cattle grazing on grasslands in northern California with serpentine soils increases the richness of native species and grazing on nonserpentine soils has the opposite effect. The difficulty in predicting how vegetation with distinct characteristics will respond to the reintroduction of herbivores underscores the importance of well-designed studies that assess the community-level consequences of these mammals. We strongly urge land managers to establish clear goals about what kind of system they wish to maintain prior to initiating reintroduction programs and to implement rigorous monitoring efforts to determine whether these goals are met.

The management implications of our results are complex because tule elk had an overall positive effect on native species composition, but this came at the cost of increasing the richness and abundance of exotic taxa in the community. Elk also appeared to play a critical role in maintaining open grasslands and preventing certain areas from being converted to less diverse, shrub-dominated systems. These results demonstrate that a reintroduced herbivore species can have profound effects on ecosystems and that land managers need to monitor not only the status of the reintroduced herbivore population, but also the diverse impacts that reintroduced herbivores have on different components of the community.

Acknowledgments

We thank C. Cumberland, A. Nadell, and T. Tierney for assistance in the field. Many staff at Point Reyes National Seashore provided logistical support, including M. Coppoletta, D. Schirokauer, and especially N. Gates. Special thanks go to V. and A. Johnson for all their support and encouragement throughout this project. This manuscript was improved substantially by comments from S. Benson, C. Christian, J. Coleman, M. Cooper, D. Crocker, E. Main, G. Meffe, D. Stokes, E. Stevens, and two anonymous reviewers. We also received invaluable statistical advice from C. Christian, D. Crocker, N. Rank, and K. Nielsen. Our research has been generously supported by

a grant from the National Science Foundation to J.H.C. (DEB-9981663).

Literature Cited

- Alvarez, M. E., and J. H. Cushman. 2002. Community level consequences of a biological invasion: effects of a non-native vine on three plant communities. *Ecological Applications* **12**:1434-1444.
- Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. *Science* **193**:24-29.
- Bonham, C. D. 1989. *Measurements of terrestrial vegetation*. John Wiley and Sons, New York.
- Brookshire, E. N. J., J. B. Kauffman, D. Lytjen, and N. Otting. 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. *Oecologia* **132**:559-566.
- Callaway, R. M., and F. W. Davis. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology* **74**:1567-1578.
- Carson, W. P., and C. J. Peterson. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia* **85**:8-13.
- Collins, S. L. 1987. Interactions of disturbances in tallgrass prairie: a field experiment. *Ecology* **68**:1243-1250.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. Blackwell Scientific, Oxford, United Kingdom.
- Cushman, J. H., T. A. Tierney, and J. M. Hinds. 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. *Ecological Applications* **14**:1746-1756.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madroño* **43**:316-333.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamic and effects on plant community and structure. *Botanical Review* **57**:1-32.
- Foster, B. L., and K. L. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* **79**:2593-2602.
- Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. *Journal of Range Management* **48**:327-335.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* **245**:477-480.
- Hamback, P. A., J. Agren, and L. Ericson. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology* **81**:1784-1794.
- Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native grasses in California. *Oecologia* **121**:518-526.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biological Conservation* **100**:45-53.
- Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* **17**:837-845.
- Hartnett, D. C., K. Hickman, and L. Fischer-Walter. 1996. Effects of bison grazing, fire and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* **49**:413-420.
- Hayes, G. E., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* **17**:1694-1702.
- Heady, H. F. 1988. Valley grassland. Pages 491-514 in M. G. Barbour and J. Mahor, editors. *Terrestrial vegetation of California*. John Wiley and Sons, New York.

- Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1992. California prairie. Pages 313–335 in R. T. Coupland, editor. *Ecosystems of the world: natural grasslands*. Elsevier, Amsterdam.
- Heady, H. F., T. C. Foin, J. J. Kektner, D. W. Taylor, M. G. Barbour, and W. J. Berry. 1988. Coastal prairie and northern coastal scrub. Pages 733–760 in M. G. Barbour and W. J. Berry, editors. *Terrestrial vegetation of California*. John Wiley and Sons, New York.
- Hickman, J. C., editor. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**:324–337.
- Hobbs, R. J., and H. A. Mooney. 1986. Community changes following shrub invasion of grassland. *Oecologia* **70**:508–513.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477–503.
- Kimball, S., and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* **17**:1681–1693.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* **49**:39–50.
- Lathrop, K. T., and J. P. Gogan. 1985. Plant communities of the tule elk range. Technical report 18. National Park Service, Davis, California.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**:975–989.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biological invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689–710.
- Maron, J. 1998. Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology* **79**:1281–1293.
- Maron, J. L., and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos* **95**:361–373.
- Martin, P. S., and R. Klein, editors. 1984. *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson.
- McCullough, D. R., J. D. Ballou, and J. K. Fischer. 1996. From bottleneck to metapopulation: recovery of the tule elk in California. Pages 375–410 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C.
- McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**:291–320.
- McNeil, S. G., and J. H. Cushman. 2005. Indirect effects of deer herbivory on local nitrogen availability in a coastal dune ecosystem. *Oikos* **110**:124–132.
- Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance to herbivory and plant diversity. *Oikos* **99**:113–130.
- Mooney, H. A., and R. J. Hobbs. 2000. *Invasive species in a changing world*. Island Press, Washington, D.C.
- Naiman, R. J. 1988. Animal influences on ecosystem dynamics. *BioScience* **38**:750–752.
- Nielsen, L., and R. D. Brown, editors. 1988. *Translocation of wild animals*. Wisconsin Humane Society, Milwaukee.
- Noss, R. F. 2001. Introduction: why restore large mammals? Pages 1–22 in D. S. Maehr, R. F. Noss, and J. L. Larkin, editors. *Large mammal restoration: ecological and sociological considerations on the 21st century*. Island Press, Washington, D.C.
- Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* **13**:261–265.
- Peinetti, H. R., R. S. C. Menezes, and M. B. Coughenour. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationships with plant water, carbon and nitrogen dynamics. *Oecologia* (Berlin) **127**:334–342.
- Phillips, W. E. 1976. *The conservation of the tule elk: a socioeconomic study of a survival problem*. The University of Alberta Press, Alberta, Canada.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**:2581–2592.
- Rebollo, S., D. G. Milchunas, I. Noy-Meir, and P. L. Chapman. 2002. The role of a spiny biogenic refuge in structuring grazed shortgrass steppe plant communities. *Oikos* **98**:53–64.
- Scheiner, S. M. 2001. MANOVA: multiple response variables and multi-species interactions. Pages 99–115 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, Oxford, United Kingdom.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* **100**:13384–13389.
- Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. *Wildlife Society Bulletin* **26**:419–428.
- Tierney, T. A., and J. H. Cushman. 2006. Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. *Biological Invasions* **8**:1073–1089.
- Toweill, D. E., and J. W. Thomas, editors. 2002. *North American elk: ecology and management*. Smithsonian Institution Press, Washington, D.C.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468–478.
- Wagner, F. H. 1989. Grazers, past and present. Pages 151–162 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Warner, P., and J. H. Cushman. 2002. Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. *Oecologia* **132**:77–85.

