Plant Diversity and Invasives in Blue Oak Savannas of the Southern Sierra Nevada[1]

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Abstract

Blue oak savannas were found to be substantially more diverse at all scales from localized point diversity to the community scale, than higher elevation shrubland and coniferous forests in the southern Sierra Nevada. Also, alien plants were more diverse and represented a substantial fraction of the understory flora in these blue oak savannas, comprising three-fourths of the species at the smallest scale (1-m^2) and about half at the largest scale (1,000-m^2). Either alien invasion has greatly increased species diversity in these savannas or it has displaced native annuals as opposed to native bunchgrasses as is commonly proposed. Livestock grazing is thought to have played a decisive role in the initial invasion of the blue oak savanna understory. Today there are differences evident between livestock grazed and ungrazed sites and between horse and cattle grazed sites. Grazed sites have slightly higher species richness and higher alien species richness and cover than ungrazed sites. The differences, however, are rather subtle and despite over a century of protection from livestock grazing, ungrazed sites are remarkably similar to sites with a continuing history of grazing.

Introduction

Blue oak (*Quercus douglasii*) woodlands are the most extensive hardwood cover type in California (Bolsinger 1988), often forming open savannas *(fig. 1)* with an understory dominated by annual grasses and forbs. Although these savannas have a rich flora of natives, a substantial portion of the herbaceous understory comprises non-native species (Borchert and others 1993). This alien understory is dominated by annual grasses and forbs endigenous to low elevation habitats in Eurasia (Baker 1989). It is generally assumed that this invasion is an extension of the alien invasion that occurred in native bunchgrass prairies, driven by a combination of livestock grazing and severe drought during the 19th century (Burcham 1957). Alternatively, it has been suggested that these savannas were formerly closed canopy blue oak shrublands that had been opened up by frequent anthropogenic fires (Cooper 1922, Griffin 1977).

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Abstract

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The fifth oak symposium was designed to provide a forum for current research and outstanding case studies on oak woodland conservation and sustainability in California. The previous conferences—held in 1979, 1986, 1990, and 1996—serve as rich sources of information about a wide range of subjects on oak ecology, management, uses, planning and conservation. This conference is aimed at natural resource managers, researchers, policy makers, and public and private interest groups. Seventy-two papers are presented in the proceedings. Topics covered include: grazing relations, soil relations, Garry oak conservation, oak regeneration and restoration, fire relations, wildlife relations, urban forestry, oak woodland policy, genetic factors, monitoring, ecology, and a special session on "Sudden Oak Death."

Retrieval Terms: hardwood rangelands, oak conservation policy, oak sustainability, oak woodland ecology and restoration, sudden oak death

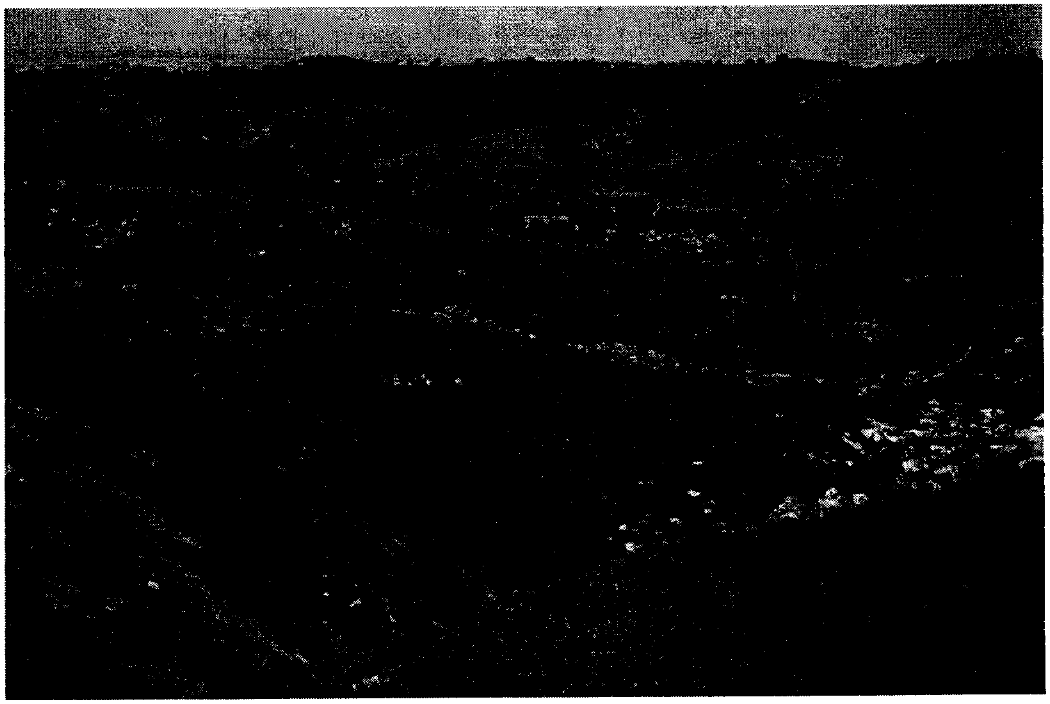

Figure 1—Blue oak savanna in the foothills of the southern Sierra Nevada. (Photo by author).

Disturbances in the form of intensive grazing and fire often favor invasion of natural ecosystems, although natural diversity patterns have long been considered to play a role in providing some level of resistance to invasion (Elton 1958). Thus, both patterns of disturbance and species richness are potential factors affecting community invasibility. Some communities are capable of closer species packing, and thus higher species richness than other communities, presumably making them less susceptible to invasion by alien species. Data both support (Fox and Fox 1986) and refute this prediction (Stohlgren and others 1999) and some of the potential explanations for community differences include differential impacts of various growth forms and different scales over which species richness is examined (Huston 1994). Propagule availability is also a potentially determining factor (D'Antonio 2000). For example, the proximity of alien populations may play a critical role in the invasion process. Thus, broad landscape patterns of alien distribution may be important in understanding the invasion process as concentrations of aliens in one community could influence invasion of adjoining communities.

Of particular concern to resource managers is how to predict which species are likely invaders, which communities are most at risk to invasion, and how land management practices influence the invasion process. In order to gain a picture of these patterns in the southern Sierra Nevada this study was undertaken to evaluate plant diversity and alien distribution across a broad scale from the localized point level to the community level and how they differ across the landscape. Specifically, patterns of species richness and alien plants were evaluated under cattle and horse grazing in blue oak savannas and these patterns were compared with other plant communities in and adjacent to Sequoia and Kings Canyon National Parks.

Study Sites and Methods

This study was conducted in the foothills and mid-elevation range of the southern Sierra Nevada, in or adjacent to Sequoia and Kings Canyon National Parks. All blue oak savanna sites were located within a 10 km radius of the Ash Mountain entrance station to Sequoia National Park, either on National Park land or Bureau of Land Management land. These blue oak savannas were dominated by oaks *(Quercus douglasii)* and buckeye (*Aesculus californicus;* nomenclature according to Hickman 1993). A total of 15 oak savanna sites between 440 and 680 m were sampled during the late spring and early summer of 1999. Sites differed with respect to their livestock grazing history: five had been grazed seasonally by horses, five grazed seasonally by cattle, and five with no livestock grazing since the founding of the national park in the 19th century. Fire history for the oak savanna sites was uncertain but none had burned recently. For comparison with the oak savanna sites, higher elevation chaparral, between 860 and 1,280 m, and mixed coniferous, between 1,400 and 2,400 m, were sampled. These sites had a complex fire history with many having burned in recent years and are described more fully in Keeley and others ([In press]).

Sites were selected from a GIS layer of plant association types and a layer of each of the required treatment conditions. Study sites were selected by picking random numbers for UTM coordinates between 50 and 200 m off a road. If ground truthing revealed sites had unanticipated disturbances, either natural, e.g., landslides, or anthropogenic, these were eliminated and new coordinates selected. Surface litter was collected within a 20-cm diameter hoop from three alternate plots at each site, dried and weighed. Three soil samples from the top 6 cm were collected from alternate plots and combined. Texture analysis was done according to Cox (1985). From a subsample, pH was determined in an equal mixture of soil and dH_2O. Soil nutrients, NO_3, NH_4, P, and K were determined on a subsample at the Soils Laboratory, University of California, Davis.

Vegetation sampling was a modified Whittaker plot (Keeley and others 1995, Schwilk and others 1997); a 0.1 ha (20 x 50 m) site was subdivided into 10 non-overlapping 100-m^2 (10 x 10 m) plots and nested in the outer corner of each plot was a 1-m^2 (1 x 1 m) subplot, which was sampled for density and cover (in chaparral and forested sites with sparser herbaceous vegetation an additional subplot was sampled on the inside corner of each plot). Within the 100-m^2 plot, additional species not in the subplots were recorded. A total of 15 blue oak savanna sites, 10 chaparral sites and 103 coniferous forest sites were sampled. Comparisons between vegetation types were with one-way Analysis of Variance (ANOVA).

Results

Landscape Comparisons

These blue oak savannas were relatively open with generally less than 30 percent canopy coverage. The herbaceous understory was quite diverse and species richness was markedly higher than for chaparral and coniferous forests, at both the point (1-m^2) and community (1,000-m^2) scales *(fig. 2A-2B).* In blue oak savannas alien species comprised nearly three-fourths of the species at the smallest scale and about half at the largest scale *(fig. 2A-2B).* If alien species were subtracted from the total species richness then blue oak savannas and coniferous forests would be comparable in species richness at both the 1- and 1,000-m^2 scales.

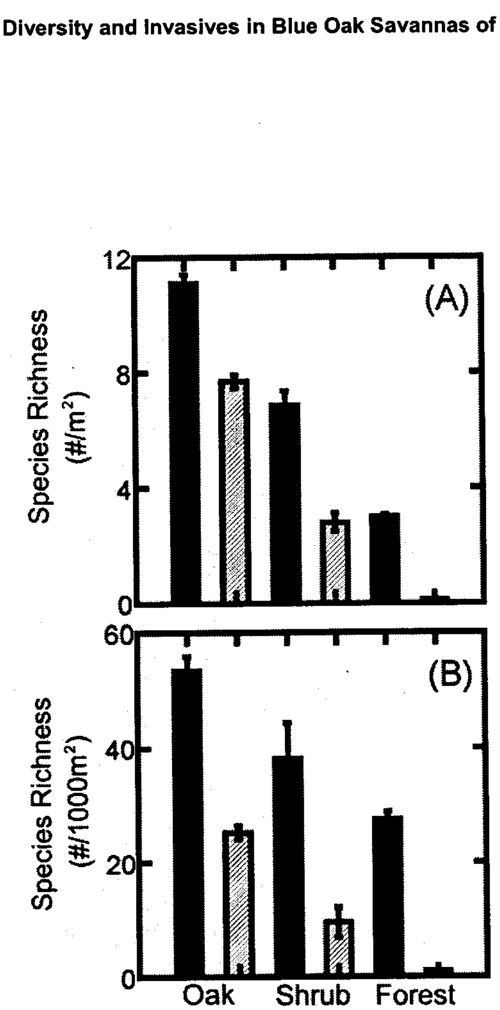

Figure 2—Total species richness (solid bars) and alien species (hatched bars) at the (A) 1-m^2 and (B) 1,000-m^2 scales in oak savanna (440-680 m), chaparral shrubland (860-1,280 m) and coniferous forests (1,400-2,400 m) in the southern Sierra Nevada.

These vegetation types differed greatly in the dominant life history type. Annuals dominated the blue oak savannas, both in terms of species *(fig. 3A)* and cover *(fig. 3B)*, and the bulk of these annuals were grasses *(fig. 3C)*.

The blue oak savannas differed from other communities in a number of soil parameters. They had a significantly lower sand content *(fig. 4A)*, markedly higher phosphorous levels *(fig. 4B)*, and substantially lower surface litter *(fig. 4C)*. Other soil parameters (pH, NO_3, NH_4, K) did not vary significantly between these vegetation types.

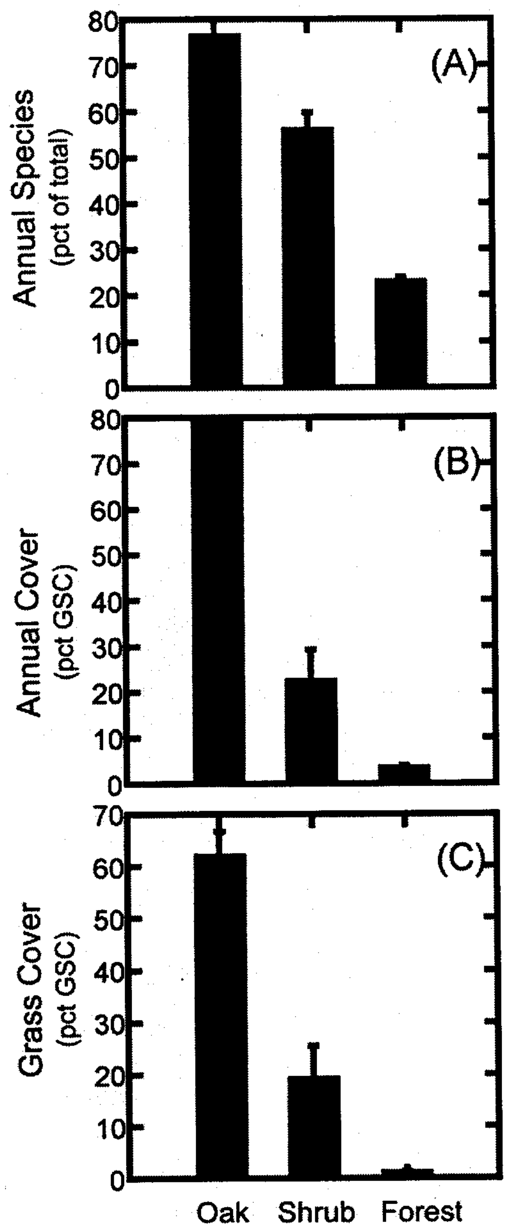

Figure 3—Annual species as (A) percentage of the total flora and (B) cover and (C) grass cover in blue oak savanna, chaparral and coniferous forests in the southern Sierra Nevada. Vegetation types with the same letter above the bar were not significantly different at (P>0.05; i.e., all bars are significantly different), middle line indicates the standard error.

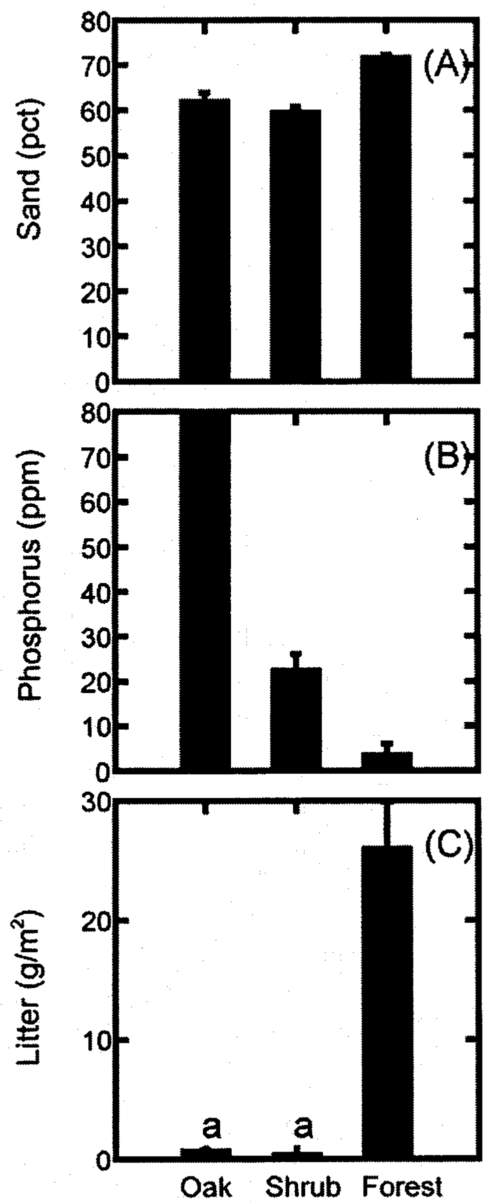

Figure 4—Comparison of soil characteristics between blue oak savanna, chaparral and coniferous forests in (A) percentage sand, (B) phosphorous content and (C) surface litter. Vegetation types with the same letter above the bar were not significantly different at (P>0.05), middle line indicates the standard error.

Grazing Impacts on Blue Oak Savannas

Species richness in the blue oak savanna sites ranged from an average of 10-15 species per m^2 to 50-60 species per 1,000 m^2 *(fig. 5)*. Grazing history in the blue oak savanna tended to increase total species richness at all scales but this was not statistically significant (P>0.05, n=5). The scaling relationship between species richness and area was similar between grazed and non-grazed sites. All exhibited a substantially better fit to a log-log regression (r^2=0.90, 0.83, 0.96, for control, cattle, and horse grazed, respectively) than a semi-log regression (r^2=0.75, 66, 84) and all deviated slightly from a linear relationship by being slightly depauperate in species richness at the intermediate scale *(fig. 5)*.

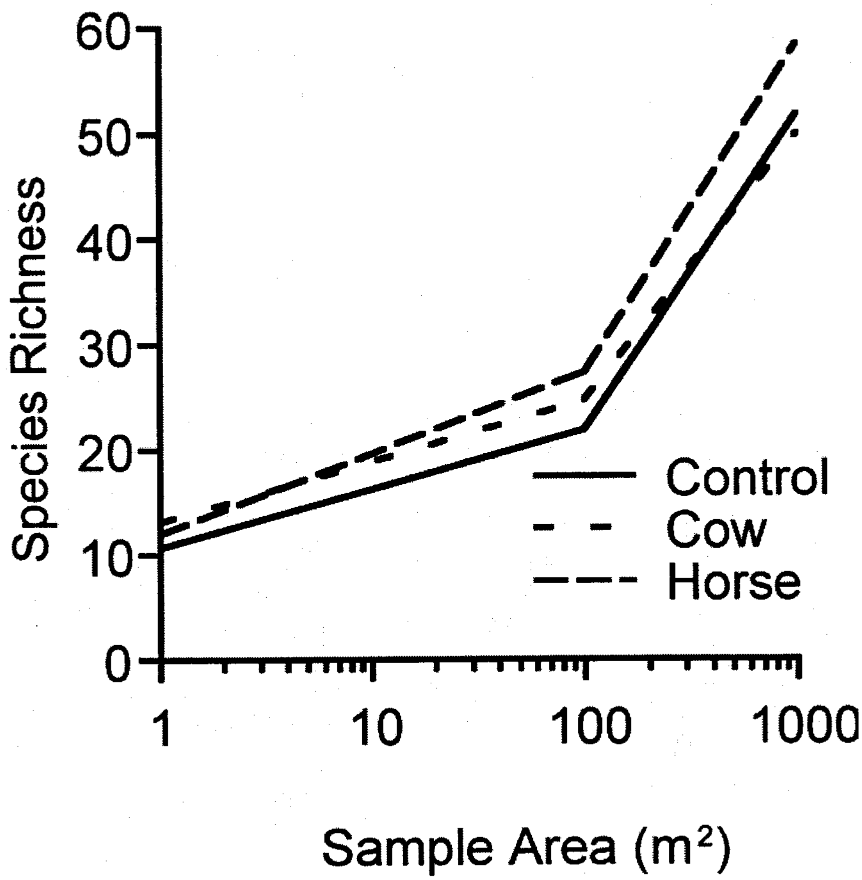

Figure 5—Log-log species area curves for blue oak savanna "controls" (no livestock grazing), cattle grazed, and horse grazed sites, based on nested plots.

Grazing did not significantly affect total cover (P>0.05, n=5) but there were differences in proportions of growth (and possibly functional) forms. Grass cover was significantly greater on horse grazed plots (P<0.05, n=5) and the density of herbaceous perennials was higher on the cattle grazed plots (P<0.05, n=5). In addition, grazing had a statistically significant impact on alien species richness *(fig. 6A and 6B)* and cover *(fig. 6C)*. Cattle grazed pastures had a greater proportion of their cover and flora contributed by aliens than did horse grazed pastures, although this was only significant at the 1-m^2 scale.

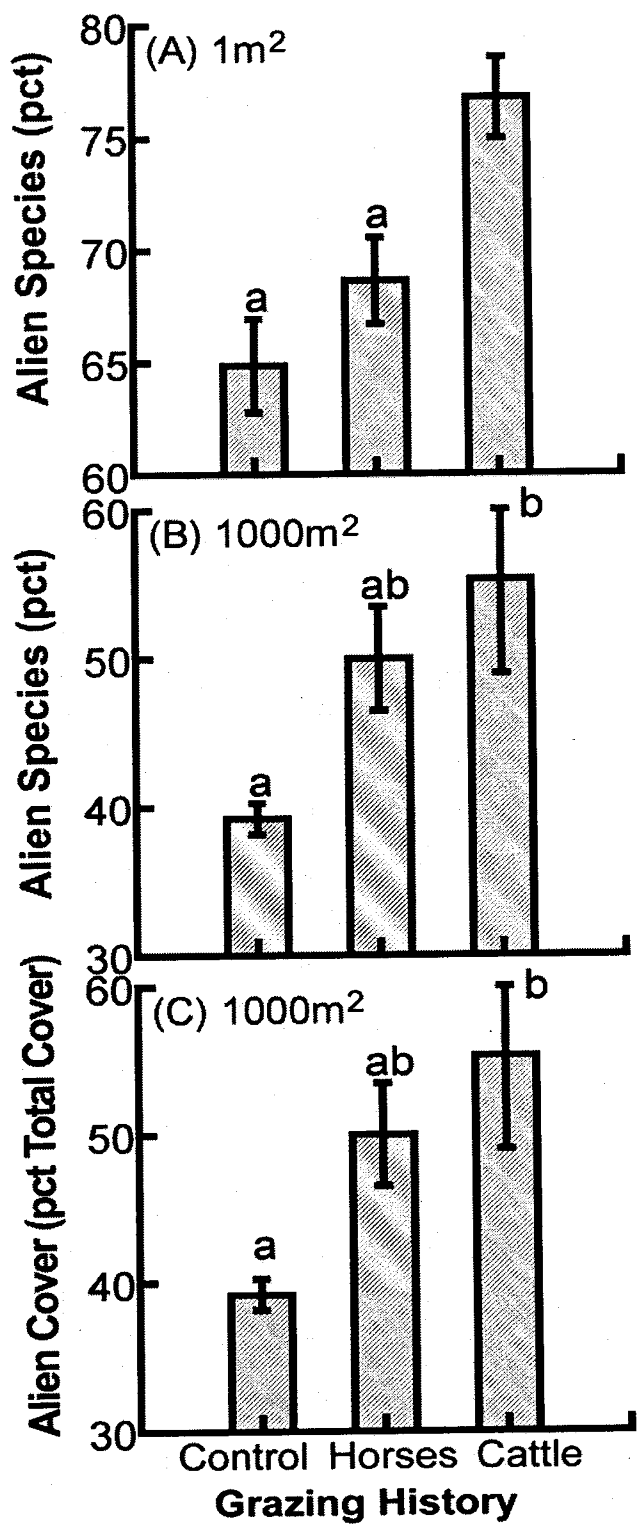

Figure 6—Impact of horse and cattle grazing on alien species richness at (A) 1-m^2 and (B) 1,000-m^2 and (C) proportion of total cover contributed by alien species. Treatments with the same letter above the bar were not significantly different at (P>0.05), middle line indicates the standard error.

The dominant natives on most blue oak sites were forbs: *Amsinckia menziesii, Claytonia perfoliata, Holocarpha heermannii, Plagiobothrys nothofulvus,* and *Trifolium microcephalum.* In contrast, the dominant aliens were mostly grasses: two species of *Avena,* seven species of *Bromus,* predominantly *B. diandrus* and *B. hordeaceous,* two species of *Hordeum, Lolium multiflorum* and *Vulpia myuros*; although some alien forbs were dominant as well: *Centaurea melitensis, Geranium molle, Cerastium glomeratum,* four species of *Erodium, Silene gallica,* and two species of *Torilis*). The total alien flora recorded from the blue oak savanna sites comprised 56 species, all of which were annuals. Of the total alien flora, 10 species showed significant differences in response to grazing pressure *(fig. 7)*. Horse or cattle grazed sites were dominated by alien annual grasses such as *Bromus diandrus, Hordeum murinum,* and *Vulpia myuros.* Control sites had significantly greater cover by alien forbs, particularly *Geranium molle, Hypochoeris glabra,* and *Trifolium dubium.*

Discussion

Relative to chaparral shrublands and coniferous forests, blue oak savannas in the southern Sierra Nevada foothills are markedly different, not only in physiognomy, but in diversity and magnitude of alien plant invasion. While this pattern comes as no surprise to those familiar with this region, the causal factors have not been widely explored.

Most of the diversity in these oak savannas is contributed by annual species and thus the low overstory canopy levels are important in allowing the persistence of these heliophylic (light-loving) species. In associated shrublands and forests, open canopies are a temporary phenomenon due to fires and thus high light conditions favoring annuals are transient habitats that require frequent colonization. The species-rich flora of annual genera in the California Floristic Province (Raven and Axelrod 1978) is likely one important factor in the higher diversity of blue oak savannas.

The extraordinary alien flora in the understory of blue oak savannas is striking, particularly when contrasted with the limited invasion of associated communities. The transient open canopy conditions in other communities may explain the lack of alien annuals but do not stand as an adequate explanation for fewer aliens per se. Past and present human activities may explain some of this pattern. The majority of invasive species in California have their origins in the Mediterranean Region, including southern Europe, North Africa, and Eurasia (Shmida 1981), where they potentially have been in association with anthropogenically altered landscapes through a significant portion of the Holocene (Atherden and Hall 1999). Valleys and foothills in the Old World have had the longest history of intensive land use and present the greatest opportunity for co-evolution with human-perturbed landscapes. In California, these valley and foothill habitats were also the ones most immediately and thoroughly exploited by Europeans, creating favorable sites for the establishment of exotics pre-adapted to such disturbed landscapes.

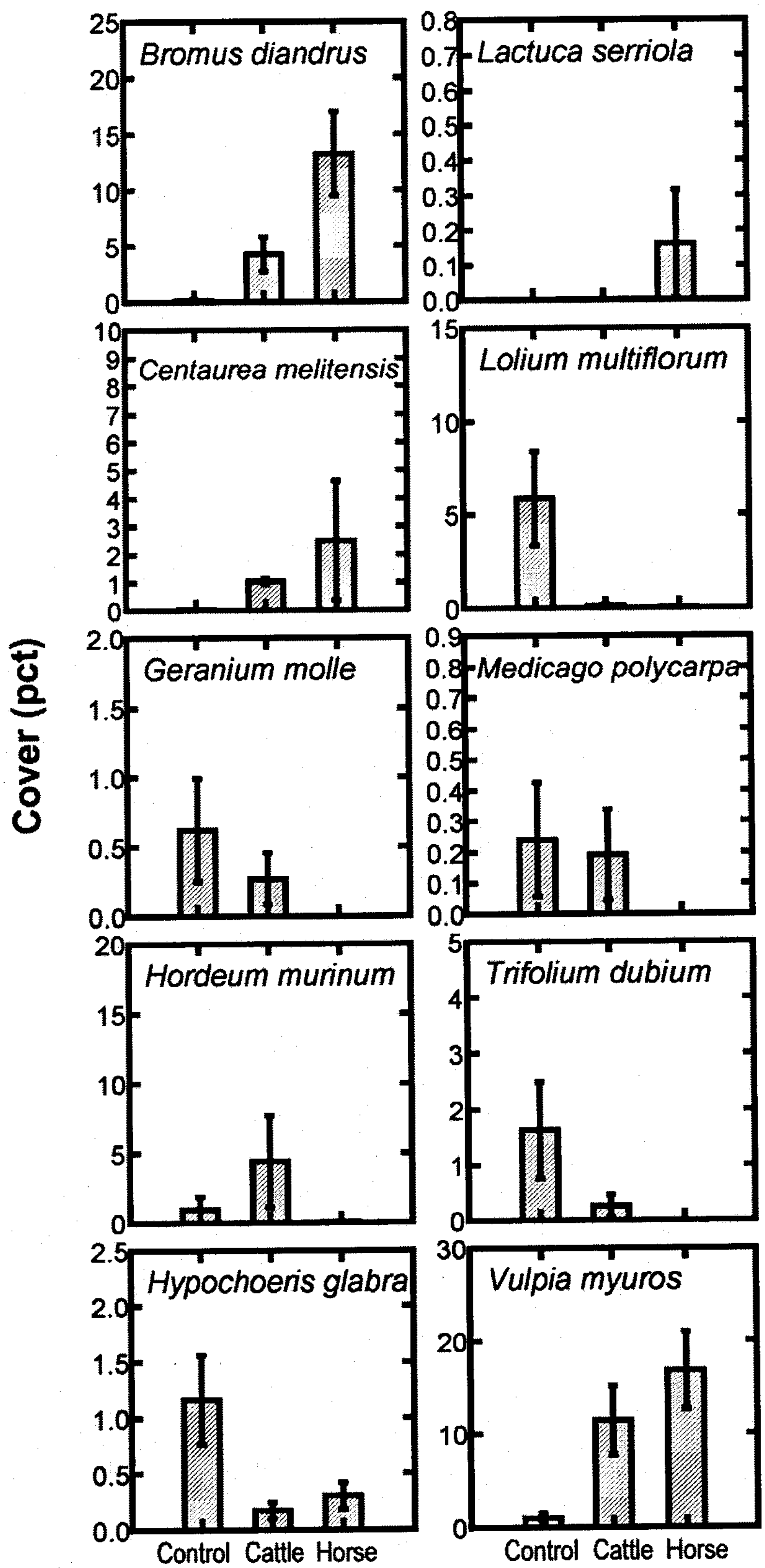

Figure 7—Alien species with cover significantly affected by grazing in blue oak savannas (lines indicate standard errors).

The present dominance of blue oak savannas by alien species raises a number of interesting questions. At the scale of 1-m^2, the majority of species are aliens *(fig. 2A)* and nearly half of the flora at each site is composed of aliens *(fig. 2B)*. Either, these oak savannas are much richer in diversity today than prior to EuroAmerican colonization, or these aliens have displaced a large component of the native flora. Commonly it is thought that these aliens, most of which are annual grasses, have displaced native perennial bunchgrasses. If that is true, then in light of the rather limited number of native bunchgrass species in our flora (Hickman 1993), natural diversity prior to EuroAmerican settlement, was much lower. Alternatively, native annuals, of which there is a rich regional flora may have dominated these communities, and thus alien invasion may not have greatly changed species richness.

Another interesting facet of this massive alien invasion of blue oak savannas is its apparent permanence. The controls in this study have not had livestock grazing in at least 100 years and may never have been intensively grazed. These sites also have never been plowed, which is often associated with a more or less permanent alien presence (Stromberg and Griffin 1996) Today the floristic differences between our control sites and the currently grazed sites are rather subtle. Hypotheses that may explain the persistence of the alien flora in these long undisturbed blue oak savannas are: (1) the native flora that formerly made up the understory has been so severely decimated in the region that dispersal is a major limitation to reestablishment, (2) these savannas are an anthropogenic artifact due to accelerated fire frequency that has converted a closed canopy woodland/shrubland into a savanna, and thus elimination of the alien flora requires return to the closed canopy condition, and (3) due to Holocene climatic changes, the more arid adapted alien annual grasses, through pre-adaptation, are better adapted to these sites and consistently out compete the native flora. These are testable hypotheses that await further experimentation.

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