

## Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains

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Positive interactions among plants have been demonstrated in many communities around the world, and appear to play important roles in maintaining species coexistence, productivity, and species diversity. However, the potential for positive interactions to conserve biological diversity in ecosystems that are disturbed by humans is poorly understood and often overlooked. One of the most important positive effects one plant can have on another is protection from herbivory. By associating with an unpalatable neighbor, a tasty species may avoid being eaten and increase in size and reproductive fitness. We examined the role of two highly unpalatable plants, *Cirsium obvalatum* and *Veratrum lobelianum*, in subalpine meadow plant communities of the central Caucasus Mountains in the Republic of Georgia, where intense livestock grazing has occurred for over two thousand years. These two species are avoided by livestock because of spines and toxicity, respectively, and have increased dramatically in abundance recently due to seasonal trans-Caucasus migrations of vast herds of domestic sheep during the Soviet era. The Gudauri region, bisected by the Russian-Georgian Military Road, was a focal point of these migrations, and there we found that plant communities associated with *Cirsium* and *Veratrum* were very different in composition than open meadows. Forty-four percent (15/34) of all species at our site were found at only “trace” (< 1.0%) cover values in the open meadow, but at significantly higher covers under *Cirsium* or *Veratrum*. Of the 38 species that were reproducing sexually at our site, eight were found only under the unpalatable invaders. Communities associated with *Cirsium* and *Veratrum* had 78–128% more species in flower or fruit than open meadow communities, respectively, than open meadow sites. Furthermore, community composition and reproductive output differed substantially between *Cirsium* and *Veratrum*, indicating some degree of species-specificity in their effects. These results indicate that unpalatable plants, which are generally indicators of unhealthy rangelands, have the potential to preserve plant diversity in overgrazed plant communities.

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Intense grazing of grasslands often results in palatable species being replaced by less palatable species, which are often considered “less desirable or even worthless plants” (Vallentine 1990). These plants have been described as “invaders” (Sims 1988), and are considered to be indicators of unproductive, unhealthy grasslands (Vallentine 1990). However, invaders increase because they are unpalatable, and unpalatable species often

protect other, more palatable, species from herbivory (Atsatt and O’Dowd 1976, McNaughton 1978, Holmes and Jepson-Innes 1989, Callaway 1995). This facilitative relationship suggests that unpalatable invaders have the potential to play a more complex and important role in heavily grazed grasslands than is generally recognized. If invaders provide refugia for remnant populations of palatable plants, or “decreasers” (Sims

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1988), during periods of intense herbivory, then they may function to conserve some species of palatable plants.

Plants facilitate their neighbors via many mechanisms (Hunter and Aarssen 1988, Bertness and Callaway 1994, Callaway 1995, Callaway and Walker 1997), but protection from herbivores is primary. Plants protect other plants from herbivores in two general ways. Benefactors may have anti-herbivore characteristics such as spines or toxins, and other species benefit by being near heavily defended plants (McAuliffe 1984). Or palatable species may benefit from being hidden in a crowd, and by taking advantage of diverse neighbors they may be more difficult for predators to locate (Rausher 1981, Brown and Ewel 1987). However, we know little about the role such positive interactions may play during anthropogenic disturbances.

Grazing by domesticated animals is one of the most important human impacts on ecosystems throughout the world, with approximately 47% of the world's land surface currently used by livestock, and 80% of that considered degraded (National Research Council 1994). The central Caucasus Mountains in the Republic of Georgia provides an excellent natural laboratory for studying the long term effects of livestock on plant communities because alpine and subalpine meadows there have been used for pastures for cattle and sheep for over 2000 years (Gulisashvili et al. 1975, Radvanyi and Thorez 1977, Kikvidze 1987). During the Soviet era, large portions of the Caucasus Mts. experienced grazing intensities that were much higher than those previously maintained by the indigenous people. From the 1950's through the 1980's sheep herds numbering in the millions were driven on seasonal migrations from the southern steppes of Dagestan and Russia in the summer to the eastern plains of Georgia in the winter. (Rcheulishvili 1953, members of the Georgian Institute of Botany, Tbilisi, pers. comm.). These migrations caused severe overgrazing and erosion, and, as documented by Georgian and Soviet scientists, large-scale invasions of weedy plants (Gulisashvili et al. 1975). The two dominant unpalatable invaders, *Cirsium obvalatum* and *Veratrum lobelianum*, now occupy thousands of hectares in the central Caucasus. *Cirsium* is a thistle, and is defended by sharp spines on the leaves and stems, whereas *Veratrum* is poisonous to livestock until early fall when the defense chemicals are either retranslocated below ground or break down (Zamtaradze 1985). Once *Veratrum* loses its toxicity livestock will eat it (Zamtaradze 1985). The increased abundance of these species has been uniformly perceived as harmful because the forage productivity of invaded rangeland for livestock invariably decreases (Zamtaradze 1985). We tested the hypothesis that these unpalatable plants provide refugia from grazing for other meadow species by comparing species abundances and reproductive output in microsites occupied by *Cirsium* and *Veratrum*, to random sites in the meadow without these invaders.

## Methods

We established an approximately two-ha study site at 2000 m in elevation in the Gudauri area in the central Caucasus Mountains (42°40'N, 44°30'E) where isolated *Cirsium* and *Veratrum* are dispersed within a matrix of subalpine meadow dominated by much smaller grasses and forbs. Mature *Cirsium* and *Veratrum* average 38 cm and 61 cm in height, respectively, whereas the height of the vegetation canopy in grazed meadows ranges from 2 to 21 cm (R. M. Callaway unpubl.). Precipitation in the area averages between 75–100 cm per year (Nakhutsrishvili and Gamtsemidze 1984). The site is an subalpine meadow above the current treeline; however, treeline in the area has probably been altered by tree harvesting, and trees may have once naturally occurred at our site. We restricted our sampling to a north-facing, approximately 5° slope, and an area that was uniform in topography. Most *Cirsium* and *Veratrum* plants at our site did not form a closed canopy and were separated from one another by 50–200 cm. In other subalpine meadows in the region these species may be either much more abundant or absent. Heavy grazing by cattle and sheep was occurring during our sample period.

We sampled the vascular plant composition in mid-July, 1997, in 0.36 m<sup>2</sup> (60 × 60 cm) plots under *Cirsium*, *Veratrum*, and in adjacent open area by estimating cover of all species in 5% cover classes. These data were analyzed for differences in species diversity (Shannon-Wiener Index, Barbour et al. 1987), mean cover for each individual species among the three microsites with *t*-tests or Kruskal-Wallis comparisons, and for whole communities using detrended correspondence analysis (Hill 1979) in the PC-ORD 2.0 statistical package (McCune and Medford 1995). Species that occurred at less than 1% cover for all plots combined within a microsite were designated as "trace". We also constructed abundance-rank curves for species cover for all three microsites (see Whittaker 1975).

Based upon criteria for rangeland health suggested by National Research Council (1994) we counted all inflorescences in flower or fruit, or with vestiges of fruits, for each species in variable-sized plots that ranged from 9 to 4200 cm<sup>2</sup>. These plots spanned the size ranges of *Cirsium* and *Veratrum* at the site, allowed us to construct species-area curves for the three microsites, provided a examination of size-specific effects, and provided a different approach for sampling the effects of the unpalatable invaders. We used second-order regression curves to describe species-area relationships for sexually reproducing species in the three microsites. Rank-abundance curves were also calculated for inflorescences in the three microsites.

We also sampled the reproductive output of individuals of two species in the open microsites and under *Cirsium*. *Trifolium ambiguum* and *Agrostis planifolia*

were chosen because they were comparable in abundance in both of these microsites. All individual flowers on each of 25 individuals of each species were counted in each of the two microsites. Differences among microsites were tested using analysis of variance and post-ANOVA Tukey tests. These data were normally distributed and did not require transformation.

## Results

Multivariate analyses showed that the plant communities associated with *Cirsium*, *Veratrum*, and the open meadow were substantially different from each other (Fig. 1). The overlap of *Cirsium* and *Veratrum* samples on the x-axis of the ordination indicates that these samples were more similar to each other than either were to samples from the open meadow (Gauch 1982). However, the significant difference between *Cirsium* and *Veratrum* samples on the y-axis indicates that these invaders had strong, species-specific spatial associations with other meadow species.

Strong species preferences for each of the three microsites were also evident in univariate comparisons of

individual species (Table 1). Plant communities in the open meadow were dominated by *Alchemilla* spp. (34% cover) *Sibbaldia parviflora* (24%) and *Lerchenfeldia caespitosa* (20%). The genus *Alchemilla* is exceptionally complex and its taxonomy is controversial (Ivanishvili 1980); therefore we refer to all *Alchemilla* at our site as a single species complex. Four other species were relatively abundant in the open meadow but found only in trace amounts under the unpalatable plants. Communities under *Cirsium* had virtually no *Sibbaldia*, but were dominated by *Trifolium ambiguum* (30%), seven species that ranged from 3–8% cover under *Cirsium* but that were found only in trace amounts in both of the other microhabitats, four species that were also abundant in the open meadow but not under *Veratrum*, and four species (2–3% cover) that were found in common with *Veratrum* but not the open meadow. *Sibbaldia parviflora* was abundant under *Veratrum*, as it was in the open meadow, but virtually absent under *Cirsium*. Grasses were much more common under the unpalatable invaders, averaging 43.2% and 27.1% cover for *Cirsium* and *Veratrum*, respectively, versus 12.3% for the open meadow.

Microsites with *Cirsium* were richer in species ( $8.0 \pm 0.3$  per  $0.36 \text{ m}^2$ ) than either *Veratrum* or open microsites ( $6.6 \pm 0.2$  and  $5.7 \pm 0.3$ , respectively,  $F = 14.8$ ,  $df = 1,48$ ,  $P < 0.001$ , post-ANOVA Tukey,  $P = 0.005$ ), but the latter two microsites did not differ significantly (post-ANOVA Tukey,  $P = 0.059$ ). Diversity was also higher in communities associated with *Cirsium*. In the open meadow, the Shannon-Wiener Diversity Index was  $1.51 \pm 0.04$  (1 s.e.,  $n = 50$ ), versus  $1.91 \pm 0.04$  for *Cirsium* and  $1.66 \pm 0.05$  for *Veratrum*, but the only significant differences were between *Cirsium* and the other two microsites (post-ANOVA Tukey  $P < 0.05$ ). Abundance-rank curves demonstrated that species which were relatively rare were more important in the communities associated with the unpalatable plants than in open meadow communities (Fig. 2).

*Cirsium* and *Veratrum* also appeared to have had large impacts on sexual reproduction in these subalpine meadows (Table 2, Fig. 3). In plots designed to represent the range of sizes of both unpalatable species, and corresponding control plots for the open meadow, we found that reproductive diversity peaked in the open meadows at 6.5 species, under *Veratrum* at 9 species, and under *Cirsium* at 14.5 species. The total number of inflorescences of all species found with *Cirsium* was twice that found with *Veratrum* and almost four times higher than that in the open meadow (Table 2). Communities associated with *Cirsium* and *Veratrum* had 5.0 times and 2.4 times higher total reproductive output (number of flowering and fruiting stems, data not shown), and 78–128% more species in flower or fruit than open meadow communities. As for community composition, abundance-rank curves demonstrated much more evenly distributed and diverse assemblages

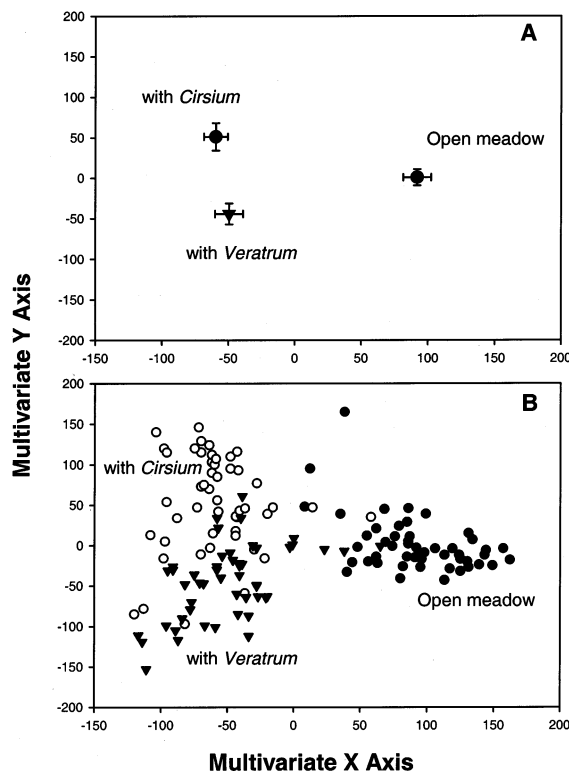


Fig. 1. (A) Distributions of the means and 95% confidence limits in a detrended correspondence multivariate analysis for samples collected under *Cirsium* and *Veratrum* and in the open meadow in the central Caucasus Mountains. (B) Distributions of all samples ( $n = 50$  for each) collected under *Cirsium* and *Veratrum* and in the open meadow.

Table 1. Means and one standard errors for cover of subalpine meadow plant species in open meadow microhabitats versus under the unpalatable invader weeds, *Cirsium obvallatum* and *Veratrum lobelianum*. Means that share a letter were not significantly different in *t*-tests (for normally distributed data) or Kruskal-Wallis tests (for non-normally distributed data) at  $P < 0.05$ . T = "trace", or less than 1% cover.

| Species                                      | Microhabitat            |                         |                         |
|--|-------------------------|-------------------------|-------------------------|
|  | Open meadow             | <i>Cirsium</i>          | <i>Veratrum</i>         |
| <i>Alchemilla</i> spp. <sup>P</sup>          | 33.8 ± 2.5 <sup>a</sup> | 17.6 ± 1.9 <sup>b</sup> | 20.8 ± 1.5 <sup>b</sup> |
| <i>Lerchenfeldia caespitosa</i> <sup>u</sup> | 20.1 ± 2.0 <sup>a</sup> | 4.3 ± 1.0 <sup>b</sup>  | 8.8 ± 1.7 <sup>b</sup>  |
| <i>Luzula spicata</i> <sup>u</sup>           | 7.1 ± 1.2 <sup>a</sup>  | T <sup>b</sup>          | T <sup>b</sup>          |
| <i>Matricaria caucasica</i>                  | 3.4 ± 0.9 <sup>a</sup>  | T <sup>b</sup>          | T <sup>b</sup>          |
| <i>Myosotis alpestris</i>                    | 5.6 ± 1.5 <sup>a</sup>  | T <sup>b</sup>          | 1.5 ± 0.6 <sup>b</sup>  |
| <i>Lotus caucasicus</i> <sup>P</sup>         | 3.1 ± 0.9 <sup>a</sup>  | T <sup>b</sup>          | 1.2 ± 0.5 <sup>b</sup>  |
| <i>Carex cuspidata</i>                       | 3.4 ± 1.0 <sup>a</sup>  | T <sup>b</sup>          | T <sup>b</sup>          |
| <i>Cerastium arvense</i>                     | 1.7 ± 0.6 <sup>a</sup>  | T <sup>a</sup>          | T <sup>a</sup>          |
| <i>Sibbaldia parviflora</i>                  | 23.9 ± 1.7 <sup>a</sup> | T <sup>b</sup>          | 21.8 ± 1.7 <sup>a</sup> |
| <i>Colpodium versicolor</i>                  | T <sup>a</sup>          | 6.6 ± 1.2 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Leontodon hispidus</i> <sup>P</sup>       | T <sup>a</sup>          | 2.4 ± 0.8 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Picris caucasica</i>                      | T <sup>a</sup>          | 2.9 ± 0.9 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Phleum alpinum</i> <sup>P</sup>           | T <sup>a</sup>          | 8.2 ± 1.2 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Ranunculus oreophyllus</i>                | 3.5 ± 1.0 <sup>a</sup>  | 8.6 ± 1.3 <sup>b</sup>  | T <sup>c</sup>          |
| <i>Trifolium ambiguum</i> <sup>P</sup>       | 5.1 ± 1.2 <sup>a</sup>  | 30.3 ± 1.5 <sup>b</sup> | T <sup>c</sup>          |
| <i>Trifolium trichocephalum</i> <sup>P</sup> | 4.7 ± 1.1 <sup>a</sup>  | 9.2 ± 1.5 <sup>b</sup>  | T <sup>c</sup>          |
| <i>Plantago caucasica</i> <sup>P</sup>       | 3.1 ± 0.9 <sup>a</sup>  | 4.5 ± 1.2 <sup>a</sup>  | T <sup>b</sup>          |
| <i>Taraxacum porphyranthum</i> <sup>P</sup>  | 0                       | 7.9 ± 1.2 <sup>b</sup>  | 1.9 ± 0.7 <sup>a</sup>  |
| <i>Plantago lanceolata</i> <sup>P</sup>      | T <sup>a</sup>          | 1.4 ± 0.6 <sup>a</sup>  | T <sup>a</sup>          |
| <i>Dactylis glomerata</i> <sup>P</sup>       | T <sup>a</sup>          | 3.0 ± 0.4 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Nardus stricta</i> <sup>u</sup>           | T <sup>a</sup>          | 1.9 ± 0.6 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Chaerophyllum roseum</i> <sup>P</sup>     | T <sup>a</sup>          | 1.0 ± 0.5 <sup>a</sup>  | T <sup>a</sup>          |
| <i>Carum meifolium</i> <sup>P</sup>          | T <sup>a</sup>          | 1.0 ± 0.5 <sup>a</sup>  | T <sup>a</sup>          |
| <i>Carum caucasicum</i> <sup>P</sup>         | 0                       | 2.2 ± 0.8 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Urtica dioica</i> <sup>u</sup>            | T <sup>a</sup>          | 3.3 ± 0.6 <sup>b</sup>  | T <sup>a</sup>          |
| <i>Anthoxanthum odoratum</i> <sup>P</sup>    | T <sup>a</sup>          | 1.8 ± 0.6 <sup>b</sup>  | 2.1 ± 0.6 <sup>b</sup>  |
| <i>Bromopsis variegata</i> <sup>P</sup>      | T <sup>a</sup>          | 3.1 ± 0.4 <sup>b</sup>  | 2.4 ± 0.6 <sup>b</sup>  |
| <i>Agrostis planifolia</i> <sup>P</sup>      | 11.1 ± 1.7 <sup>a</sup> | 18.4 ± 1.8 <sup>b</sup> | 21.1 ± 2.4 <sup>b</sup> |
| <i>Astrantia maxima</i>                      | T <sup>a</sup>          | 1.8 ± 0.5 <sup>b</sup>  | 2.0 ± 0.5 <sup>b</sup>  |
| <i>Betonica macrantha</i>                    | T <sup>a</sup>          | 2.2 ± 0.7 <sup>b</sup>  | 2.7 ± 0.7 <sup>b</sup>  |
| <i>Campanula trautvetterii</i> <sup>P</sup>  | T <sup>a</sup>          | T <sup>a</sup>          | 6.0 ± 1.0 <sup>b</sup>  |
| <i>Cruciata laevipes</i> <sup>P</sup>        | T <sup>a</sup>          | 2.4 ± 0.7 <sup>b</sup>  | 5.3 ± 1.0 <sup>b</sup>  |
| <i>Cynosurus cristatus</i>                   | 1.2 ± 0.4 <sup>a</sup>  | 1.2 ± .5 <sup>a</sup>   | 1.5 ± 0.5 <sup>a</sup>  |
| <i>Veronica gentianoides</i> <sup>P</sup>    | T <sup>a</sup>          | T <sup>a</sup>          | 0                       |

p = palatable, u = unpalatable, after Grossheim (1952). The absence of a letter indicates that no data are available.

of sexually reproducing species under the unpalatable invaders than in the open meadow, and suggested that *Cirsium* and *Veratrum* had species-specific effects (Fig. 4). Individual *Trifolium ambiguum* and *Agrostis planifolia* under *Cirsium* produced more flowers per plant than conspecifics in the open meadow (Fig. 5; two-way

ANOVA, species × microsite;  $F_{\text{microsite}} = 41.36$ ,  $df = 1,97$ ,  $P < 0.001$ ).

## Discussion

Our results suggested that there were strong positive effects of unpalatable "invaders" on the abundance and sexual reproduction of many other subalpine meadow species. Forty-four percent (15/34) of all species in the vegetation samples at our site were found at only "trace" (< 1.0%) abundances in the open meadow, but at significantly higher abundances under *Cirsium* or *Veratrum*. Of the 35 species that were found reproducing sexually in a second set of plots, 21 were found only under the unpalatable invaders and other subalpine meadow plant species showed higher reproductive output under unpalatable plants. Only four species showed higher sexual reproduction rates in the open than when associated with the invaders. These results are correlative, but they suggest that the unpalatable weeds *Cirsium obvallatum* and *Veratrum lobelianum* may preserve plant diversity in heavily grazed areas, and provide focal points from which palatable species can recolonize overgrazed pastures by seed. By providing refugia in which sexual reproduction is possible for many other species, unpalatable invaders also have the potential to maintain genetic variation in species that are protected (see Kelley and Clay 1987), and give strong selective advantages to genotypes that can tolerate the microclimate and biotic conditions near *Cirsium* and *Veratrum*.

Because our results are correlative, it is possible that invaders do not cause the spatial relationships that we have described, but that invaders preferentially occupy microsites that already have diverse, highly sexually reproductive communities occupied by particular assemblages of plant species. Experiments are necessary to separate biological from microsite effects. However, we suggest several lines of evidence to support the hypothesis that biological causes (protection from herbivory rather than microsite preference) account for the spatial associations described here. First, *Cirsium* and *Veratrum* are highly interspersed with respect to each other on similar topography at our site. Therefore, they did not seem to have strong, large-scale site preferences. Second, of the species that were found in trace amounts or missing in intensely grazed meadows, but that occurred with one or both of the invaders, all occurred in small patches of open meadow in similar, nearby sites that are used for hay meadows by local villagers and are protected from heavy grazing (Z. Kikvidze and R. Callaway pers. obs.). Of the species found flowering in association with either *Cirsium* or *Veratrum*, but not in the open meadow, these too were found in flower and widely distributed in protected hay meadows. This suggests that the spatial association between unpalatable

invaders and other species only occurs when grazing is intense, and that palatable species do not require benefactor plants when intense grazing does not occur. Third, the effects of *Cirsium* and *Veratrum* on sexual reproduction were highly size-dependent, and highly nonlinear for *Veratrum*. It is unlikely that invader size, invader species, microsite conditions, and community composition all co-varied in such a predictable manner. Fourth, one of the abundant species in the open meadow, *Lerchenfeldia caespitosa*, is known to be highly unpalatable, and many species that were abundant in *Cirsium* and *Veratrum* microsites (*Trifolium ambiguum*, *Taraxacum porphyranthum*, *Campanula trautvetterii*, *Agrostis planifolia*, *Bromopsis variegata*, *Anthoxanthum odoratum*, *Phleum alpinum*) are known to be preferred by livestock (Grossheim 1952). Finally, the effects of the weeds on associated plant communities ended sharply and consistently at the edges of the canopy of the unpalatable plants (pers. obs.), and it is unlikely that particular abiotic microsite conditions also ended as abruptly.

Unpalatable plants that increase or invade under intense grazing pressure may play facilitative roles in other grasslands. In the early 1900's there were unsubstantiated claims that weed-grass relationships were crucial for rebuilding grasslands after overgrazing, droughts and "dust-bowl" conditions in the midwestern United States in the 1930's (in Cocannouer 1950). Canfield (1948) observed that range recovery was often due to improvement of the grass cover "under an established shrub or sub-shrub". Weaver and Albertson

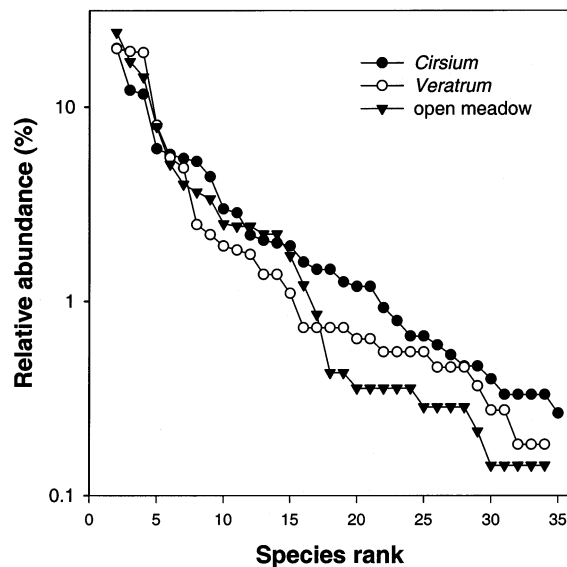


Fig. 2. Abundance-rank curves for species cover associated with *Cirsium* and *Veratrum* and in the open meadow in the central Caucasus Mountains.

Table 2. Mean number of inflorescences in flower or fruit per m<sup>2</sup> for subalpine meadow plant species in open meadow microhabitats versus under the unpalatable invader weeds, *Cirsium obvallatum* and *Veratrum lobelianum*. Standard errors are not presented because inflorescences were counted in variable-sized plots designed for species area curves. Bold indicates highest mean.

| Species                        | Microhabitat |                |                 |
|--------------------------------|--------------|----------------|-----------------|
|                                | Open meadow  | <i>Cirsium</i> | <i>Veratrum</i> |
| <i>Plantago lanceolata</i>     | <b>4.2</b>   | 0              | 0.5             |
| <i>Trifolium ambiguum</i>      | <b>17.4</b>  | 10.5           | 8.4             |
| <i>Plantago caucasica</i>      | <b>2.6</b>   | 1.0            | 0.2             |
| <i>Poa alpinum</i>             | <b>6.8</b>   | 3.1            | 3.4             |
| <i>Alchemilla</i> spp.         | 9.9          | <b>27.1</b>    | 12.3            |
| <i>Agrostis planifolia</i>     | 11.2         | <b>92.5</b>    | 22.0            |
| <i>Phleum alpinum</i>          | 1.8          | <b>13.7</b>    | 7.3             |
| <i>Colpodium versicolor</i>    | 0.4          | <b>6.9</b>     | 6.0             |
| <i>Taraxacum porphyranthum</i> | 0.3          | <b>2.6</b>     | 0.3             |
| <i>Carum causicum</i>          | 3.3          | <b>7.0</b>     | 6.5             |
| <i>Prunella vulgaris</i>       | 0.7          | <b>2.4</b>     | 1.8             |
| <i>Cynosurus cristatus</i>     | 0.1          | <b>15.4</b>    | 1.2             |
| <i>Ranunculus oreophyllus</i>  | 0            | <b>16.3</b>    | 0               |
| <i>Myosotis alpestris</i>      | 0            | <b>6.8</b>     | 0               |
| <i>Picris caucasica</i>        | 0            | <b>4.7</b>     | 0               |
| <i>Campanula trautvetterii</i> | 0            | <b>1.4</b>     | 0               |
| <i>Juncus effusus</i>          | 0            | <b>0.6</b>     | 0               |
| <i>Cruciata laevipes</i>       | 0            | <b>3.1</b>     | 0               |
| <i>Arenaria rotundifolia</i>   | 0            | <b>0.7</b>     | 0               |
| <i>Lotus causicus</i>          | 0            | <b>0.6</b>     | 0               |
| <i>Platanthera chlorantha</i>  | 0            | <b>0.1</b>     | 0               |
| <i>Cerastium purpurascens</i>  | 0            | <b>0.1</b>     | 0               |
| <i>Bromopsis variegata</i>     | 0            | <b>6.5</b>     | 0.2             |
| <i>Veronica gentianoides</i>   | 0            | <b>1.1</b>     | 0.1             |
| <i>Euphrasia hirtella</i>      | 0            | <b>0.6</b>     | 0.1             |
| <i>Veronica minuta</i>         | 0            | <b>0.6</b>     | 0.5             |
| <i>Cerastium arvense</i>       | 0            | <b>2.0</b>     | 1.1             |
| <i>Lerchenfeldia flexuosa</i>  | 1.8          | 5.7            | <b>9.4</b>      |
| <i>Nardus stricta</i>          | 2.0          | 2.3            | <b>4.0</b>      |
| <i>Rumex alpinus</i>           | 0            | 0.1            | <b>0.9</b>      |
| <i>Carex cuspidata</i>         | 0            | 0.8            | <b>3.6</b>      |
| <i>Dactylis glomerata</i>      | 0            | 0.1            | <b>3.4</b>      |
| <i>Urtica dioica</i>           | 0            | 0.7            | <b>2.1</b>      |
| <i>Polygonum carneum</i>       | 0            | 0              | <b>0.8</b>      |
| <i>Galeopsis tetrahit</i>      | 0            | 0              | <b>0.2</b>      |
| Total inflorescences           | 62.5         | 237.1          | 96.3            |

(1956) argued for an important conservation role for prickly pear cacti in North American shortgrass prairie, claiming that this well-defended species provided refugia for grasses during drought and overgrazing, and supplied "local sources of seed supply on many ranges almost devoid of [grass] vegetation". These claims, however, were not supported with quantitative studies. McNaughton (1978), however, found that *Themeda triandra*, a highly palatable East African savanna grass, experienced  $\approx 80\%$  mortality from native ungulate grazers when it was not associated with other, less palatable grass species; however, as the abundance of

unpalatable species increased with grazing, the mortality rate of intermixed *Themeda* rapidly decreased.

Facilitative effects produced by protection from herbivory have been shown in other grasslands (Holmes and Jepson-Innes 1989), but are also common in other plant communities (Atsatt and O'Dowd 1976, Callaway 1995). McAuliffe (1986) found that far more paloverde

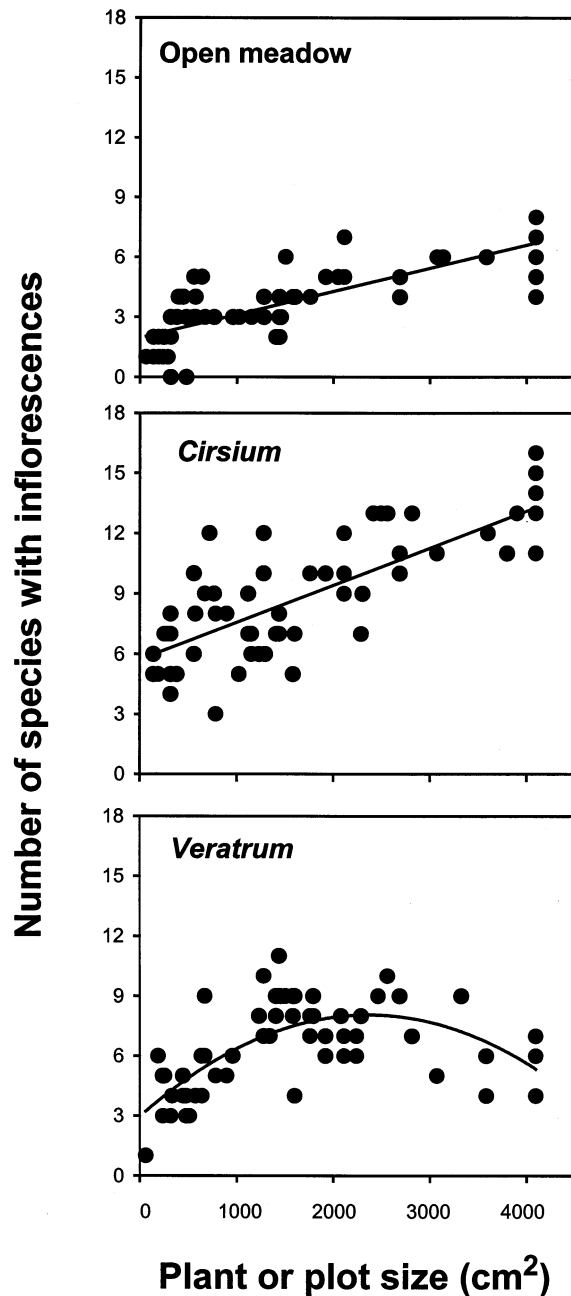


Fig. 3. Area curves for variable-size plots and plant species in flower or fruit under *Cirsium* and *Veratrum* and in the open meadow in the central Caucasus Mountains. All curves are fit with quadratic (2nd-order) regressions.

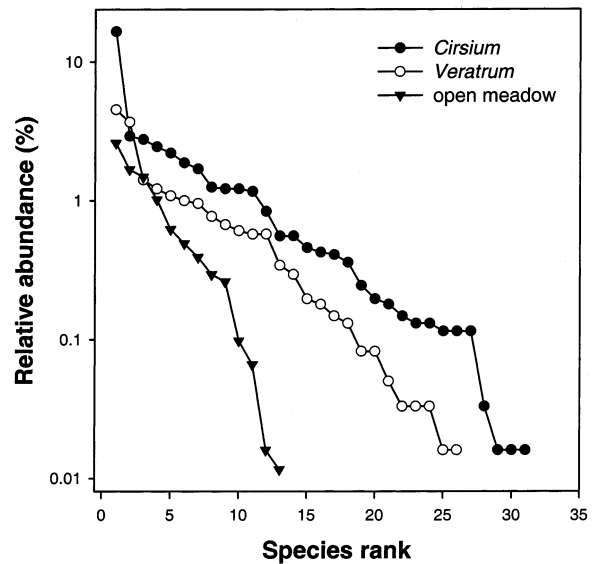


Fig. 4. Abundance-rank curves for plants species in flower or fruit, or with vestiges of fruits, under *Cirsium* and *Veratrum* and in the open meadow in the central Caucasus Mountains.

seedlings were consumed by herbivores when they were in the open than when they were under various shrub species. McAuliffe hypothesized that shrubs provided concealment, and that the unpalatability of the most common nurse species, *Ambrosia deltoidea* and *A. dumosa*, deterred browsing. McAuliffe (1984) also found that young barrel-shaped cacti (*Mammillaria microcarpa* and *Echinocereus englemannii*) were protected from herbivores by spine-covered stem joints accumu-

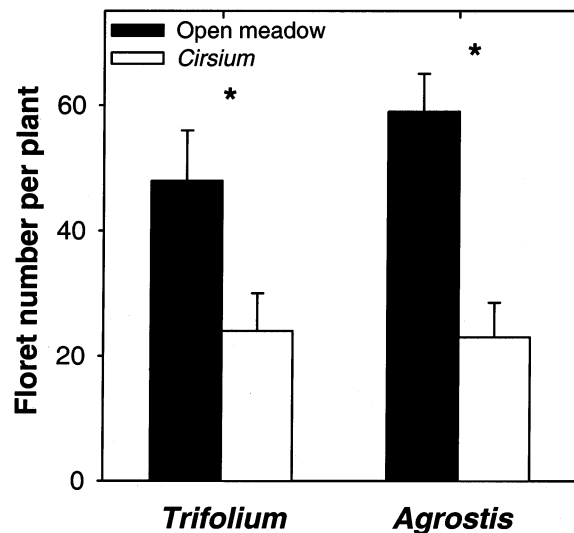


Fig. 5. Means and one standard error for the number of flowers per individual *Trifolium ambiguum* and *Agrostis planifolia*. \*indicate significant differences between microsites.

lating near *Opuntia* nurse-plants. Facilitation via protection from herbivores has also been shown in oak woodlands (Callaway 1992), mixed northern forests (Hjälten et al. 1993), and mediterranean-climate scrub (Jaksic and Fuentes 1980).

Species-area curves and plant community composition differed between *Cirsium* and *Veratrum*, suggesting that the positive effects of the two unpalatable invaders may have been somewhat species-specific. The richness of sexually reproducing species associated with *Cirsium* individuals increased linearly with *Cirsium* up to the size of the largest individual *Cirsium* plants that we sampled. For *Veratrum*, however, the reproductive diversity of associated plants peaked at lower levels and for medium-sized individuals that were approximately 2000 cm<sup>2</sup> in area, and then declined. This may have been due to strong competition between the largest *Veratrum* plants and other species for light, as the larger *Veratrum* individuals were taller than the largest *Cirsium*, and appeared to create deeper shade in their understories. As has been shown in other systems, the balance of facilitation and competition may change with the age or density of the interacting plants (Valiente-Banuet et al. 1991, Callaway and Walker 1997, Callaway 1998a, b).

Positive interactions suggest a higher level of interdependence in plant communities than has been generally recognized by plant ecologists (see Callaway 1997, 1998a, Jones et al. 1997). It is important to note that *Cirsium* and *Veratrum* are not exotic weeds in the Caucasus, such as are altering many plant communities elsewhere. Our results suggest that facilitative interactions among plants may be important for the conservation of subalpine meadows in the Caucasus. The unpalatable invaders, *Cirsium* and *Veratrum*, may have decreased forage quality in the short term for livestock, but their positive effects on other species may be preserving the long-term grazing quality of subalpine meadows and much of the regional plant diversity.

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