

## HERBIVORY MORE LIMITING THAN COMPETITION ON EARLY AND ESTABLISHED NATIVE PLANTS IN AN INVADDED MEADOW

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**Abstract.** The dominance of nonnative plants coupled with declines of native plants suggests that competitive displacement drives extinctions, yet empirical examples are rare. Herbivores, however, can alter vegetation structure and reduce diversity when abundant. Herbivores may act on mature, reproductive life stages whereas some of the strongest competitive effects might occur at early life stages that are difficult to observe. For example, competition by perennial nonnative grasses can interfere with the establishment of native seeds. We contrasted the effects of ungulate herbivory and competition by neighboring plants on the performance of native plant species at early and established life stages in invaded oak meadows. We recorded growth, survival, and flowering in two native species transplanted as established plants, six native species grown from seed, and five extant lily species as part of two 2 × 2 factorial experiments that manipulated herbivory and competition. Herbivory reduced the performance of nearly all focal native species at early and established life stages, whereas competition had few measurable effects. Our results suggest that herbivory has a greater local influence on native plant species than competition and that reducing herbivore impacts will be required to successfully restore endangered oak meadows where ungulates are now abundant.

**Key words:** black-tailed deer; British Columbia; competition; conservation; exotic; grass; invasive; oak savanna; *Odocoileus hemionus*; sheep.

### INTRODUCTION

Nonnative species are increasing in abundance and distribution as native species decline, but the processes facilitating these changes remain poorly understood (Davis 2003, Levine et al. 2004). Resource competition between native and nonnative plant species has dominated studies of invasion ecology (Bruno et al. 2005) and increases in the abundance of nonnative species have been taken as evidence of competitive displacement (Wilcove et al. 1998). However, ecosystem processes are also influenced by herbivory. Increases in deer densities have shifted plant community composition (Martin and Baltzinger 2002, Horsley et al. 2003, Rooney and Waller 2003) and led to cascading effects in other taxa (Allombert et al. 2005a, b, Côté 2005). Native species declines are often the product of multiple related factors (Gurevitch and Padilla 2004) but estimating the relative contributions of herbivory and competition is complicated by their co-occurrence. Plant introductions, for example, often coincide with other human-related changes to landscapes, including the introduction of domestic livestock or increase in native herbivore

densities as a consequence of habitat modification and carnivore eradication (Côté et al. 2004). To identify the cause of declines in native plant species in an invaded ecosystem, we contrasted herbivory and competition for light and water on native species performance in oak meadows with abundant ungulates.

Three general ecological hypotheses describe the potential effects of herbivory and competition on native plant performance (Gurevitch et al. 2000, Chase et al. 2002). First, competition among neighboring plants may suppress seedling establishment and adult reproduction, hastening declines particularly in dispersal limited species (MacDougall and Turkington 2004, 2005). The accumulation of litter of nonnative grasses can also reduce establishment (Xiong and Nilsson 1999) and growth in native species (Foster 1999, Lenz et al. 2003). Second, abundant herbivores may limit plant growth and reproduction. Some species have been extirpated on islands where herbivore densities increased in the absence of predators (Terborgh et al. 2001, Hambäck et al. 2004). Third, herbivory and competition may interact. For example, herbivores might disrupt competitive interactions and facilitate species coexistence (Huston 1994). Alternatively, herbivores may cause shifts in dominance by reducing the relative abundance of palatable species thereby facilitating less palatable species (D'Antonio 1993, Buckley et al. 2006, Howe et al. 2006, MacDougall and Wilson 2007, Gonzales 2008).

Which process, competition or herbivory, limits a particular plant species may depend on the life stage of

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that species. Our study included two experiments with crossed manipulations of herbivory and competition to examine their effects on early and established life stages of several native plant species. We predicted that herbivory would reduce biomass and reproductive output in established plants that we transplanted into experimental plots. In contrast, we expected competition for light and water on control plots to reduce the establishment of native seeds and survival of seedlings. Therefore, it is possible that both herbivory and competition reduce native plant abundance in herbaceous plant communities.

#### MATERIALS AND METHODS

Garry oak meadows are part of a diverse, endangered, oak savanna complex stretching from central California, USA to southwestern British Columbia (BC), Canada. Approximately 80% of these meadows have been lost due to habitat conversion after the 1850s (Lea 2006), prompting recent conservation and restoration efforts (Fuchs 2001, Devine et al. 2007). Many remaining meadows, however, are dominated by nonnative perennial grasses (MacDougall and Turkington 2004) originating from farmed and urban areas. These grasses produce live material and litter that inhibit native seed establishment and survival (MacDougall 2005, MacDougall and Turkington 2005); whereas episodic biomass removals by cutting, weeding, or burning increase native species cover (MacDougall and Turkington 2007). It is believed that nonnative grasses have, therefore, competitively displaced native forbs (Garry Oak Ecosystem Recovery Team 2002); however, relationships between herbivory and native plants had yet to be examined. Ungulate densities have increased in the region (MacDougall 2008) from 7–15 deer/km<sup>2</sup> (Cowan 1945) to 10–25 deer/km<sup>2</sup> more recently (Hatter and Janz 1994; T. Martin and P. Arcese, *unpublished data*). Densities greater than 15 deer/km<sup>2</sup> produce overgrazed conditions (Cowan 1945). Habitat fragmentation, agriculture, declines in hunting and the eradication of predators have relaxed limits on the abundance of native black-tailed deer (*Odocoileus hemionus*). Domestic and feral ungulates (e.g., *Ovis aries*) also add to herbivore pressure in some locations.

#### Study sites

Our experiments took place on two sites in an oak meadow complex on Salt Spring Island (48°46'51" N, 123°27'23" W), BC, where climate is mild and wet from November to April (5°C, 128 mm) and moderate and drier from May to October (13°C, 43 mm). Soils are shallow with exposed bedrock and desiccate in summer. Soil moisture is thought to be a limiting resource that affects plant composition (MacDougall et al. 2006). The transplant experiment was located in 1.4 ha of oak meadow on Crow's Nest Ecological Research Area (CNERA). The seed-addition experiment was located in the Andreas Vogt Nature Reserve (AVNR) in 0.4 ha of

oak meadow that meets CNERA at its northwest corner. Nonnative perennial grasses dominate the plant community and both sites were visited by sheep and deer.

#### Experimental design

We tested the effect of herbivory and competition for light and water with two, 2 × 2 balanced factorial experiments: one with transplanted native plants (transplant experiment, see Appendix A: Fig. A1) and one with added native seeds (seed-addition experiment, see Appendix A: Fig. A2). Our focal native species have general habitat requirements and are found throughout the region (Gonzales 2008), but their abundances are declining relative to nonnative grasses (MacDougall and Turkington 2004, Gonzales 2008).

*Treatments.*—We tested the effects of herbivory by excluding or allowing access by ungulates and crossed this treatment with a “neighbor-reduced” treatment (extant, live vegetation and litter cut and removed) or an unmanipulated control. Because meadows are often heterogeneous, we used small plots to maximize plot number (Bonham 1989) and reduced the influence of abiotic drivers on variation by using the following criteria to select plots: <1% exposed rock, <10% slope, <5% canopy closure, and >10 m to a neighboring plot. Plots were selected or rejected by sequential coin toss and treatments were applied randomly.

Herbivory (H) treatment plots were left open (+) or fenced (–) (1.25-m<sup>3</sup> aluminum frame, open at top, large-celled net on sides to exclude ungulates but not light or small animals). The “neighbors-reduced” (C) treatment influenced competition for light and water by removing (–) or leaving (+) litter and live biomass. All above ground biomass was cut and removed twice annually when focal herbaceous species were senescent. Extant biomass in neighbor reduced plots was lower than in control plots throughout the growing season (Gonzales 2008). Garry oak seedlings were not cut. Neighbors-reduced (C–) plots were also spaded to a depth and distance of 25 cm from plot edges to sever roots and tillers.

To assess whether the neighbors-reduced treatment altered the availability of resources for the focal plants, we took four readings of soil moisture and ground light levels at each plot. Ground light level readings (LI-COR multi-point bar quantum sensor; LI-COR, Lincoln, Nebraska, USA) were taken three times in summer months between 10:00 hours and 13:00 hours on clear, sunny days. Soil moisture readings were taken monthly at a 12 cm depth (Hydrosense TDR meter, Campbell Scientific, Logan, Utah, USA) for a year. Manipulation of below ground competition was not tried because herbicides were locally prohibited and weeding may have caused soil disturbances and increased invasion.

To describe the extant plant community, we dried and weighed clipped biomass from 14 1-m<sup>2</sup> plots (see Appendix B). Due to high water content, dry biomass

may underestimate the contribution of forbs relative to grasses (MacDougall 2005); thus, we also identified and counted stems in 16 0.5-m<sup>2</sup> plots (see Appendix A).

*Transplant experiment.*—Transplanted species (see Appendix C) were collected locally and kept in a common growth media at seasonal light and temperature regimes in a glasshouse for four months until transplanted into 56 experimental plots located in CNERA. In February 2003, we planted four common camas (*Camassia quamash*) bulbs, four 5 × 5 cm plugs of the annual, seablush (*Plectritis congesta*; see Plate 1) (mean = 60 stems/plot), and two Garry oak (*Quercus garryana*) acorns in each plot, spaced ≥15–20 cm from each other and the plot edges. Dry camas bulbs were weighed before and after the 3-year experiment; performance was assessed as the difference in mass. We counted the number of individual seablush (April) and the number of Garry oak seedlings (June) annually for three years to estimate performance. One arbutus (*Arbutus menziesii*) and two Garry oak saplings were also transplanted into the plots in 2003 but suffered >90% mortality due to drought and were discarded (rainfall data available online).<sup>2</sup>

In 2004, we also counted the number of flowers produced by five extant lily species observed in the plots of the transplant experiment (see Appendix C) because lilies have been used in forested ecosystems as an index of herbivory by deer (Anderson 1994).

Two plots with extant seablush were excluded from analyses for this species to avoid confusing their number with transplanted individuals. Seven exclosures were compromised by wildlife; those with evidence of substantial browsing were excluded from analysis in the year compromised.

*Seed-addition experiment.*—The seed-addition experiment, located in AVNR, followed the methods of plot selection and treatment application already described, except that the scale (seeds are smaller than transplanted plants) and meadow were smaller than the transplant experiment. Therefore, we used fewer (16), smaller (0.25-m<sup>2</sup>) plots. Seeds were collected locally in June 2003, cleaned of debris, air dried, counted, and then stored. Viability in yarrow (*Achillea millefolium*), great camas (*C. leichtlinii*), blue-eyed Mary (*Collinsia parviflora*), seablush, and bicolored lupine (*Lupinus bicolor*) (see Appendix D) was confirmed in a greenhouse before seeds were spread onto the surface of each plot. Seeds were added once in October 2003 and monitored annually in April to 2007. The number of seeds added per plot ranged from 35 to 200 seeds per species, approximating relative seed output (see Appendix D). Performance was assessed as the number of seedlings of each species. Oak seedlings were placed in transplant rather than seed-addition plots to maximize sample size without crowding; acorns are substantially larger than

forb seeds and the transplant experiment had larger, more numerous plots.

#### Data analyses

Mixed-effects models incorporate fixed and random factors and enable the modeling of the correlations that often exist with the spatially and temporally grouped data generated by ecological studies (Buckley et al. 2003). Soil moisture and ground light levels were compared in neighbors present (C+) and neighbors-reduced (C-) plots with general linear mixed models (Proc MIXED; SAS Institute 2003) with time as a random factor. To analyze the overall experiment, competition, herbivory, their interaction, and time were input as fixed effects. Models with time as a significant effect were further tested for second and third order interactions with time and treatment. If there were no interactions with time, we reported the simpler model.

Given that some data were collected on the same subjects through time, temporal measurements were input as random factors with autoregressive error-covariance structures. The initial number of seablush stems per plot was also input as a random factor. Multiple individuals of common camas, oak, and extant lilies were measured in each plot; thus, individuals of each species were categorized as random subjects. The subject designation produces a block-diagonal structure in the error-covariance matrix so that individuals in the same plot are not considered independent of each other (SAS Institute 2003). Residuals were assessed with Shapiro-Wilk and Bartlett's tests to test if assumptions of normality and homoscedasticity were met. When transformations failed to meet assumptions of normality, a non-normal distribution was used and fit was assessed by  $\chi^2/df$  ( $\approx 1$  indicates a good fit). Significance was assessed at  $\alpha \leq 0.05$ .

#### RESULTS

The plant communities at CNERA and AVNR were dominated by nonnative species. Nonnative species comprised 76% of the biomass ( $169 \pm 98$  g [mean  $\pm$  SD]) and 60% of the total number of stems ( $1712 \pm 673$  stems). Nonnative grasses were the dominant group within the community by biomass (59%,  $131 \pm 57$  g) and stem count (43%,  $1210 \pm 652$  stems). The extant plant community in the neighbors present (C+) treatment decreased available soil moisture ( $F_{1,155} = 6.27$ ,  $P = 0.01$ ) and ground light levels ( $F_{1,43} = 7.69$ ,  $P = 0.01$ ), but fencing (H) did not alter moisture ( $F_{1,155} = 0.22$ ,  $P = 0.64$ ) or light levels ( $F_{1,43} = 1.75$ ,  $P = 0.19$ ).

#### Transplant experiment

Herbivory (H+) reduced bulb mass in common camas and the number of stems of seablush, and these differences between treatments increased with time for seablush (Fig. 1, Table 1). In contrast, competition (C+) had no measured effect on common camas or seablush and no interactions between treatments were detected

<sup>2</sup> (<http://www.weatheroffice.ec.gc.ca>)

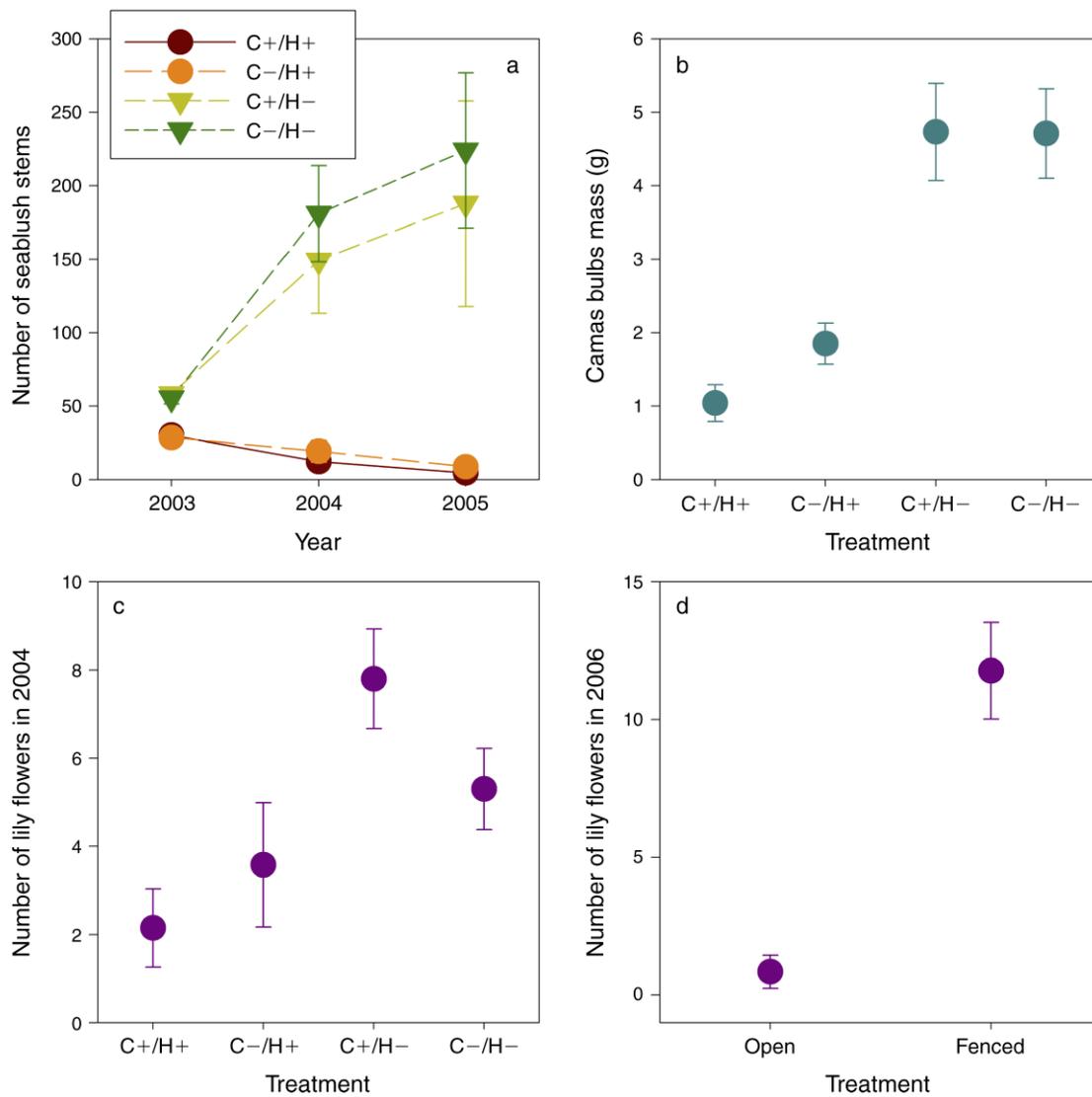


FIG. 1. (a) The number of seablush stems by treatment from 2003 to 2005, (b) the mass of common camas bulbs by treatment, and (c) the number of extant lily flowers in 2004 by treatment in a two-level (+/-), two-factor (competition [C] and herbivory [H]) transplant experiment in a Garry oak meadow. (d) Post-experiment (2006) number of flowers of extant lilies and experimental camas in open and fenced plots (neighbor-reduced treatment stopped in 2005). Error bars are  $\pm$ SE.

(see Appendix E: Table E1). Five lily species, fool's onion (*Triteleia hyacinthina*), nodding onion (*Allium cernuum*), harvest brodiaea (*Brodiaea coronaria*), chocolate lily (*Fritillaria affinis*), and white fawn lily

(*Erythronium oregonum*) were observed among the extant species in experimental plots and, as a group, these extant lilies produced more flowers in fenced (H-) than open (H+) plots (Fig. 1).

TABLE 1. Results of mixed models with significant values for a two-level, two-factor (competition and herbivory [herb]) transplant experiment in a Garry oak meadow.

Response variable	Fixed factors	Estimate	SE	df	Test	P	Random factors	Distribution
Seablush individuals (annual forb)	herb $\times$ time	-96.71	28.51	1, 149	$t = 19.15$	<0.0001	stems planted, year	normal
Mass change in common camas bulbs (perennial forb)	herb	-2.62	0.99	1, 136	$F = 23.00$	<0.0001	subject	normal
Extant lily flowers (perennial forbs)	herb	-1.56	1.01	1, 52	$F = 7.32$	0.01	subject	Poisson

Notes: There was no significant effect of competition; thus it does not appear in this table. See Appendix E: Table E1 for results of all transplant experiment models.

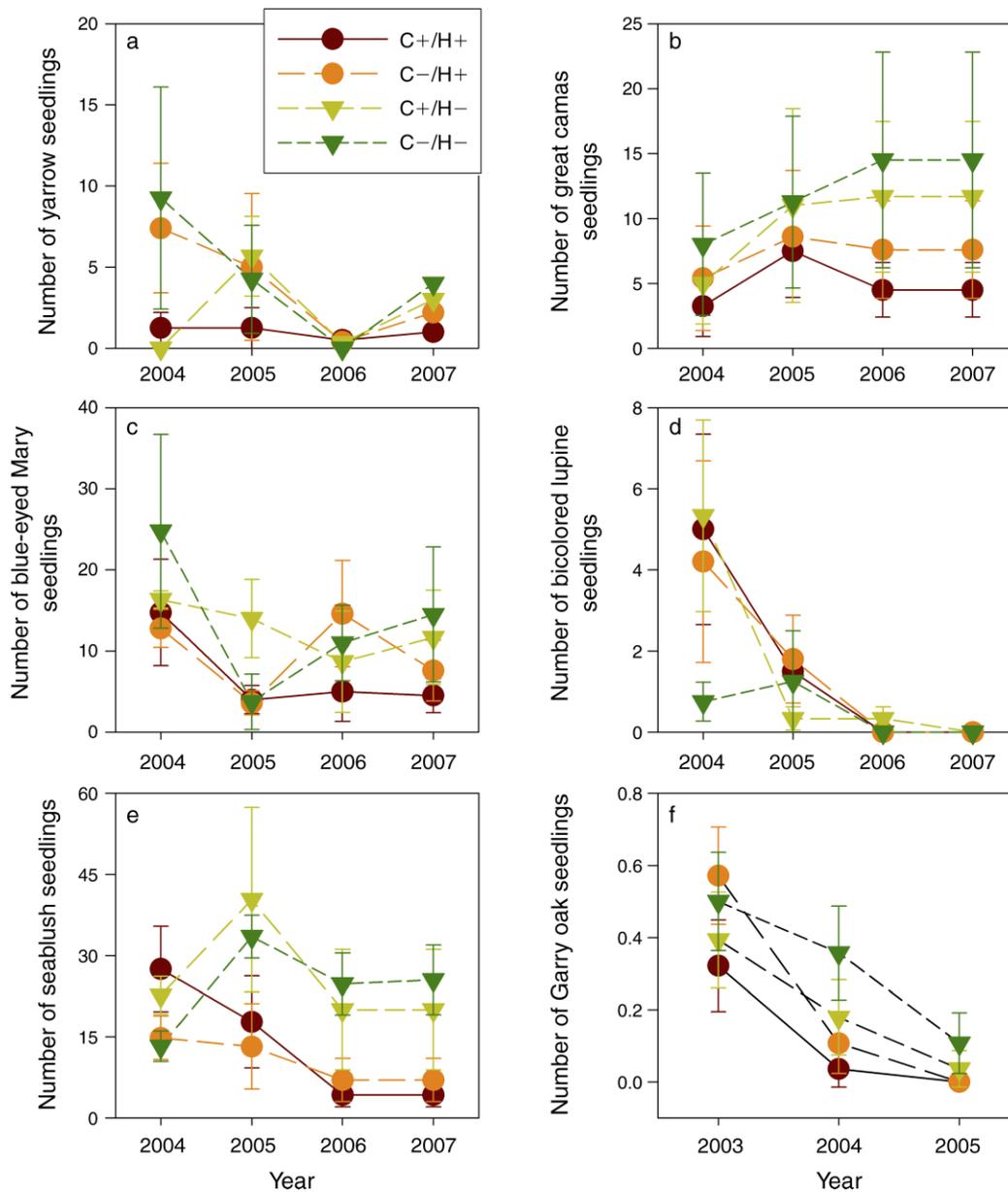


FIG. 2. The number of (a) yarrow, (b) great camas, (c) blue-eyed Mary, (d) bicolor lupine, and (e) seablush seedlings from 2004 to 2007 and (f) Garry oak seedlings from 2003 to 2005 by treatment in a two-level (+/-), two-factor (competition [C] and herbivory [H]) seed-addition experiment in a Garry oak meadow. Error bars are  $\pm$ SE.

TABLE 2. Results of mixed models with significant values for a two-level, two-factor (competition [comp] and herbivory [herb]) seed-addition experiment in a Garry oak meadow (see Appendix E: Table E2 for results of all seed-addition experiment models).

Response variable	Fixed factors	Estimate	SE	df	F	P	Random factors	Distribution
Yarrow (perennial forb)	comp	-0.47	0.52	1, 57	4.86	0.03	year	negative binomial
Great camas (perennial forb)	herb	-4.76	3.15	1, 57	4.08	0.05	year	normal
Blue-eyed Mary (annual forb)	herb	-0.28	0.33	1, 57	4.21	0.04	year	negative binomial
Bicolor lupine (annual forb)	time	-2.00	0.58	1, 57	12.12	0.00	year	negative binomial
Seablush (annual forb)	herb $\times$ time	-0.44	0.24	1, 54	7.83	0.01	year	negative binomial
Garry oak seedlings (tree)	herb $\times$ time	-1.30	0.63	1, 327	3.98	0.05	subject	negative binomial



PLATE 1. Unbrowsed seablush (*Plectritis congesta*) in a west coast Garry oak meadow on Salt Spring Island, Canada. Photo credit: David R. Clements.

This experiment ended in 2005 and the above ground biomass from all plots was cut in spring and summer (flowering season) for another study (Gonzales 2008), but all exclosures were left in place. When counted again in 2006, extant lily flowers occurred much more often in fenced (H-) ( $11.77 \pm 1.75$  flowers [mean  $\pm$  SE]) than open (H+) plots ( $0.85 \pm 0.61$  flowers; Fig. 1).

#### Seed-addition experiment

Herbivory (H+) reduced the number of seedlings of great camas, blue-eyed Mary, and seablush, and this difference between treatments increased with time for seablush (Fig. 2, Table 2). Bicolored lupine declined with time in all treatments whereas yarrow was the only species that responded positively to the reduction of neighbors (C-; Fig. 2, Table 2). More oak seedlings survived in fenced (H-) than open (H+) plots (Fig. 2, Table 2) but their overall survival was low.

#### DISCUSSION

Herbivory had the greatest effect on the performance of two transplanted native species, a suite of native extant lilies, and four of six experimentally added seeds of native species. In contrast, competition only affected yarrow seedlings negatively (see also MacDougall and Turkington 2006). Overall, our findings suggest strongly that herbivory had a greater influence on the performance of native species at both early and established life stages relative to competition in Garry oak meadows. Consequently, herbivores may have played a greater role in the decline of palatable native species in Garry oak meadows than competition by nonnative grasses.

We expected that local competition for seed establishment would be the dominant process limiting seedlings. Stem densities in our plots were high and native plant cover and flowering increased with neighbor reductions in Garry oak meadows on Vancouver Island, BC (MacDougall and Turkington 2007). It is possible that herbivory is higher, and/or soils shallower on our Salt Spring Island study area than on Vancouver Island. Plant communities in resource-poor sites are often structured by disturbance, herbivory, and stress rather than competition for resources (Huston 1994). Prior to this study, herbivory was unexplored in Garry oak meadows and our results suggest that herbivory has a stronger role in limiting some native species at early life stages than anticipated. Whether herbivory has influenced native species declines in richer, deep, soil sites remains to be tested.

The effects of herbivory on vegetation structure are widely observed. However, in ecosystems dominated by nonnative species, competitive displacement has frequently been presumed to be the driving factor in the decline of native plant species (Gurevitch and Padilla 2004, Bruno et al. 2005), perhaps because herbivory can be more "cryptic" relative to shifting abundances of plants. Most studies highlighting the dramatic impacts of deer herbivory have also focused on forested ecosystems (Côté et al. 2004, Rooney et al. 2004). Relatively speaking, forests have few nonnative species and declines of native plant species are more clearly attributable to deer. In herbaceous ecosystems, which are the most invaded ecosystem type, it has been parsimonious to attribute declines of native plant species

to invaders rather than herbivores and we tested this assumption. Because our results indicate that herbivores limit native plant species more than competition, we suggest that the restoration of Garry oak meadows will require reductions of herbivores and not just nonnative plants. However, because the current dominance of nonnative grasses in many sites may confer a “weighted lottery” advantage via propagule pressure (Lavorel and Lebreton 1992), the reduction of nonnative species and augmentation of native species may also hasten overall restoration goals.

Biotic homogenization is occurring at a global scale and is characterized by increasing abundances of nonnative species and the loss of native species (Rooney et al. 2004, McKinney and La Sorte 2007). The processes facilitating this shift, however, are likely to interact in complex ways (White et al. 2006) and restoration may be inhibited if the mechanisms driving losses of native species are incorrectly identified (Gurevitch and Padilla 2004, Didham et al. 2005). Although competitive displacement of native forbs by nonnative grasses would explain the shift in plant community composition observed in Garry oak meadows, our results suggest that nonnative dominance could be an indirect consequence of herbivory limiting native plant establishment, growth and reproduction. Identifying factors that enhance ecosystem invasibility will lead to more effective, integrated ecological restoration (Hobbs and Humphries 1995).

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#### APPENDIX A

Views of neighbor-reduced and fenced plots in the transplant and seed-addition experiments (*Ecological Archives* E089-188-A1).

#### APPENDIX B

Native and nonnative extant species in experimental plots in Garry oak meadows on Salt Spring Island, British Columbia (BC), Canada (*Ecological Archives* E089-188-A2).

#### APPENDIX C

Characteristics and measures of the focal plant species measured in the transplant experiment (*Ecological Archives* E089-188-A3).

#### APPENDIX D

Species added to each plot in the seed-addition experiment, their plant type, and the number of seeds per plot (*Ecological Archives* E089-188-A4).

#### APPENDIX E

Tables of the results of all mixed models for two-level, two-factor competition and herbivory transplant and seed-addition experiments in Garry oak meadows and Salt Spring Island, British Columbia, Canada (*Ecological Archives* E089-188-A5).