

Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders

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Abstract The ability of an exotic species to establish in a system may depend not only on the invasibility of the native community, but also on its interactions with other exotic species. Though examples of mutually beneficial interactions between exotic species are known, few studies have quantified these effects or identified specific mechanisms. We used the co-invasion of an endangered island ecosystem by exotic Canada geese (*Branta canadensis*) and nine exotic annual grasses to study the effects of an invading herbivore on the success of invading grasses. On our study islands in southwestern Canada, we found that geese fed selectively on the exotic grasses and avoided native forbs. Counter to current theory suggesting that the grasses should be limited by a selective enemy, however, the grasses increased in proportional abundance under grazing whereas forbs showed declining abundance. Testing potential mechanisms for the effects of grazing on grasses, we found that the grasses produced more stems per area when grazing reduced vegetation height and prevented litter accumulation. Forming dense mats of short stems appeared to be an efficient

reproductive and competitive strategy that the Eurasian grasses have evolved in the presence of grazers, conferring a competitive advantage in a system where the native species pool has very few annual grasses and no grazers. Germination trials further demonstrated that selective herbivory by geese enables their dispersal of exotic grass seed between heavily invaded feeding areas and the small islands used for nesting. In summary, the exotic geese facilitated both the local increase and the spatial spread of exotic grasses, which in turn provided the majority of their diet. This unexpected case of positive feedback between exotic species suggests that invasion success may depend on the overall differences between the evolutionary histories of the invaders and the evolutionary history of the native community they enter.

Keywords Annual grass · *Branta canadensis* · *Poa annua* · Seed dispersal · Selective herbivory

Introduction

As the rate of species introductions increases (Levine and D'Antonio 2003), the success of particular exotic species may increasingly be affected by their interaction with other non-indigenous flora and fauna. Simberloff and Von Holle (1999) raised the possibility of positive feedbacks between exotic species and reviewed qualitative reports of exotic animals pollinating or dispersing the seeds of exotic plants, and of one exotic plant or animal benefiting from habitat modification by another. To date, however, there have been relatively few quantitative or mechanistic studies of facilitation between exotic species (Simberloff 2006; Simberloff and Von Holle 1999). To uncover the mechanisms of interactions between exotic herbivores and exotic plant species, we studied the ongoing co-invasion of an

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endangered island ecosystem by an exotic herbivore (Canada geese, *Branta canadensis* (L.)) and nine exotic annual grass species. Counter to current theory, we show that the effect of an exotic herbivore on plant invasion success cannot necessarily be predicted from the target of herbivore attack. Instead, the outcome of interactions between exotic herbivores and exotic plants is likely to depend on the individual evolutionary histories of the exotic species and the native community.

Herbivores can have top-down effects on plant invasions both by opening spaces in the native vegetation for exotic plant species to germinate and spread (Hobbs and Huenneke 1992) and by failing to attack the exotic species themselves. The latter mechanism underlies the enemy release hypothesis, which predicts that exotic plants should benefit from the absence of their co-evolved enemies (Keane and Crawley 2002; Williamson 1996). In some circumstances, however, the opposite can be true. Exotic grasses benefit from the presence of their co-evolved grazers when those grazers do greater damage to grazing-intolerant native grasses (Crosby 1986; DiTomaso 2000; Hobbs 2001; Mack and Thompson 1982). To explain this observation, Colautti et al. (2004) formulated the “enemy of my enemy” hypothesis, which predicts that exotic plants may benefit from their exotic generalist enemies if they are more tolerant of these enemies than the native species are. Using the same logic, Mitchell et al. (2006) point out the opposite; plant invasions should be limited by specialist herbivores that consume only the invading species.

In our study system, grazing-tolerance may be a particularly important trait because the islands lack native vertebrate herbivores. The exotic *Branta canadensis* has been nesting in the islands only since the 1980s. These geese originate from the Giant and Great Basin subspecies, which were introduced to the lower Fraser Valley of southwestern British Columbia from Minnesota, Ontario, Saskatchewan, Alberta, and the grasslands of south central British Columbia in the 1960s (Banks et al. 2004; Hanson 1997; Smith 2000). We therefore hypothesized that if geese are generalist herbivores, their feeding should reduce the abundance of native plant species not adapted to grazing, and indirectly benefit the exotic grasses. Conversely, if geese selectively feed on the grasses this should limit their invasion success.

Using paired open and exclosed plots spread over island sites varying in grazing intensity, we tested (1) grazing selectivity, (2) the effects of grazing on the proportional abundance of native and exotic grasses and forbs, and (3) demographic mechanisms for these effects. We hypothesized two possible demographic mechanisms for the increase in the abundance of exotic annual grasses that we observed under grazing. First, grazing might reduce flower production by removing inflorescences or preventing their production. Second, grazing might increase grass stem

production, either through direct effects of injury or through indirect effects of reduced litter accumulation and increased light availability.

Finally, we determined the potential for seed dispersal by geese. Because the geese fly between their island nesting sites and cultivated feeding grounds on larger islands with more heavily invaded plant communities, geese may be a novel dispersal vector for the exotic grasses they consume. We tested the hypothesis that selective herbivory by geese may result in their dispersal of exotic propagules by collecting goose feces in the field and germinating viable seeds in a growth chamber.

In this paper, we provide quantitative evidence that the presence of a novel herbivore produced an overall demographic benefit to the exotic grasses even though they were selectively grazed. In addition, expanding populations of nesting geese are likely to benefit from their ability to increase both the abundance and the potential dispersal of their preferred food source. To explain this unexpected positive feedback between exotic species, we identify the underlying mechanisms and show how they may arise from similarities in the evolutionary history of the grasses and the grazer, and from the absence of equivalent species in the native community.

Materials and methods

Study area

We conducted our study in the southern Gulf Islands of British Columbia, which comprise more than 100 smaller islands between the southwest corner of mainland Canada and the southern end of Vancouver Island (approximately 48°41'N, 123°23'W). The endangered Garry oak meadow ecosystem, also classified as Oregon white oak woodland or savannah, stretches north along the Pacific coast from southern California and covers the margins or the entirety of these islands (Fuchs 2001; Griffin 1977). Located in the rain-shadow of the Coastal Mountain Range, the ecosystem has a sub-Mediterranean climate, with mild wet winters and dry summers (di Castri 1973; MacDougall et al. 2006; Roemer 1972). The islands have shallow sandy to sandy loam soils that have accumulated in depressions and crevices sheltered from the wind (Ward et al. 1998). Germination begins in October or November and continues until April or May, and flowering begins as early as January but is concentrated between March and May. Severe drought stress leads to death of the annual species and dieback of the perennials in July and August. Native herbaceous vegetation is dominated by perennial and annual forbs, with a single native perennial grass species and no commonly found native annual grasses.

Although the exotic plant species in this system have certainly been present in the general area since before the 1980s, their distribution in the small islands where geese nest is still somewhat limited. On the smaller islands, ranging in size from 0.04 to 600 ha (Van Vliet et al. 1991), surveys completed in 2003–2005 show that 45–90% of the herbaceous plant biomass is native, compared to only 10–20% on the larger islands in the Gulf Islands archipelago (Gonzales 2008). Whereas remnants of the Garry oak ecosystem on larger, more accessible islands and Vancouver Island have been subject to disturbance by agriculture, livestock, and residential development, the small islands have only been visited by kayakers and boaters. The introduced species pool on these small islands is dominated by exotic annual grasses in the *Bromus*, *Aira*, *Vulpia*, and *Poa* genera, which tend to form dense grassy patches in the matrix of native vegetation. Exotic perennial forbs and grasses are present but more patchily distributed, with the perennial grasses being found at higher abundance in deeper soil meadows on larger islands. Exotic annual forbs are widely distributed throughout the islands.

Introduced Canada geese establish their territories and maintain nests on these islands between March and June. In contrast, native herbivores are largely limited to invertebrates. Deer are present on larger islands in the system, where they browse heavily on shrubs and some forbs, but they are absent from our study islands, perhaps because of their low shrub cover. Though groups of smaller, migratory sub-species of Canada geese native to western North America do stop over in southwest British Columbia while en route from Alaska to California, there are no resident Canada geese native to this region (Bellrose 1980; Delacour 1954). Furthermore, although the low abundance of terrestrial predators may make the smallest islands suitable for nesting by resident geese, their small size should make them unsuitable for large groups of migrants. Indeed, in over 25 years of avifaunal surveys, we have not observed fall or spring migrants stopping over on these islands to feed.

Experimental design

We selected 19 sites where we had previously observed geese to nest. These sites were located on eight islands ranging from 0.4 to 3.6 ha in size (Van Vliet et al. 1991) which are among the smallest vegetated islands in the archipelago. At each site, we established two to four pairs of 30 × 60-cm plots in mid-February 2005. Within a site, we distributed the pairs of plots to cover the range of vegetation types observed. For each pair, we identified two areas having similar vegetation composition and soil depth, where both areas were dominated by herbaceous vegetation, had <10% rock, and were on slopes <20°. We then randomly assigned one plot in each pair to be open and one

to be enclosed by a 75-cm-high fence of 2.5-cm-square wire mesh.

In 2005, we surveyed all plots between 23 March and 17 April, and between 11 and 24 May. There was sufficient overlap in phenologies that we surveyed only once in 2006, between 14 April and 2 May. For each survey, we recorded abundance as the number of stems of each species in the center 20 × 50 cm of each plot, leaving the edge as a buffer. Number of stems is an appropriate measure because the stem is the unit of reproduction, and the grasses in this system are able to flower at a range of heights. We also recorded grazed and flowering stems by species, average plant height by species, total percentage cover of litter, and three soil depth measurements per plot. Average soil depth in our plots ranged from 1 to 18 cm.

Germination trials

To test for the potential dispersal of exotic grass seed by geese, we collected a total of ten samples of fresh feces from seven islands between 25 April and 20 June 2005, a period coincident with both local seed production and the movement of geese between the islands and cultivated habitats on Vancouver Island. Each sample was composed of feces collected from multiple territories on each island, within approximately 6 h of their deposition on a rock surface. All feces were inspected to ensure they were free of windblown seed (Myers et al. 2004). We collected a total of 314 g dry weight, with individual sample weights ranging from 9 to 43 g. Feces were air dried, weighed, cold-dry stratified for 2 months at 4°C, then spread over 4 cm of Redi-Earth sterile medium (Sun Gro Horticulture, Vancouver, BC) and watered as needed. Growth chamber conditions simulated April to June temperatures in the islands, with 12 h of light (initially 17°C, increasing to 19°C after 1 month and 22°C after 2 months; dark temperature 2°C lower). Feces were initially left whole to simulate field conditions for germination. After 3 months, feces without emerging plants were gently crumbled apart, but no further germination occurred. All seedlings were grown to flowering for identification.

Analysis

Grazing selectivity

To assess goose foraging selectivity, we calculated a use-to-availability ratio for each group of plants, where a group is a unique combination of origin (native or exotic), life history (annual or perennial), and life form (grass or forb). As previously noted, the only group completely absent from our study plots was the native annual grasses. We used the forage index (\hat{w}_i), which is a group's proportion of

the grazed stems (o_i) divided by its proportion of the total stems ($\hat{\pi}_i$), as shown in Eq. 1 (Manly et al. 2002). We calculated a value for each group in all open plots where at least one stem was grazed.

$$\hat{w}_i = o_i / \hat{\pi}_i \quad (1)$$

Because the forage index data was clearly not normally distributed, we tested for selection or avoidance of each group using the non-parametric Sign test. A median value of \hat{w}_i significantly higher than 1 indicates selective grazing, while a median value less than 1 indicates avoidance.

Model structure

For all analyses of the impacts of grazing on species, flower, or stem abundance, we used linear mixed models to test the similarity of open and exclosed plots along the gradient of grazing intensity. If goose herbivory impacts community dynamics, we should observe a large divergence between the exclosed and open plots in areas of heavy grazing, but no divergence where grazing was light. The principal approach for all analyses was therefore to test for an interaction between the exclosure treatment (open or exclosed) and the intensity of grazing. Grazing intensity was measured as the proportion of all stems in the open plot that were grazed and was roughly correlated through time, with the same plots experiencing either high or low grazing throughout the study. The grazing intensity gradient was therefore assumed to describe not only the difference in grazing experienced by the open and exclosed plots during our study, but also the relative level of grazing contributing to pre-existing plant community composition in our plots. As such, we assigned the same value of grazing intensity to the exclosed member of the pair so that we could examine the effects of the exclosure treatment along the grazing gradient. We also tested for interactions with survey year. We used linear mixed models because these models can account for random spatial and temporal autocorrelations in ecological data (Buckley et al. 2003; Schabenberger and Pierce 2002), and we needed to account for spatial clumping of plots within pairs within islands, as well as repeated measures over three sampling periods. We used the MIXED procedure in SAS (SAS Institute 2003) with the REML estimation method and the Satterthwaite method for estimating denominator degrees of freedom in models with multiple error terms (Littell et al. 1996).

Effects of grazing on abundance and diversity

We tested the effect of grazing on total abundance, richness, and total evenness (E_{var}) (Smith and Wilson 1996), and on the proportional abundance and richness of exotic annual grasses and native and exotic forbs, using a series of

similarly structured mixed models. Each model incorporated observations from all three sampling periods over 2 years using a two-banded unstructured variance covariance structure (i.e., different covariance within and between years). Fixed effects were Julian date of survey (where 1 = January 1); soil depth; grazing intensity; year; exclosure treatment; a year-by-exclosure interaction to test for equivalence of intercepts; and the year-by-grazing intensity, exclosure-by-grazing intensity, and year-by-exclosure-by-grazing intensity interactions to test for equivalence of slopes. For the forb proportional abundance and richness models, we coded forb type, (native annual, native perennial, exotic annual, or exotic perennial) as an additional fixed effect and included all possible interactions between forb type and grazing intensity, year, exclosure treatment, and soil depth. All models included island and plot pair as random effects. For the forb models, when there were multiple forb types from a single plot, we also included plot as a random factor.

For each model, we checked assumptions for the conditional residuals using residual versus predicted plots and normal probability plots, and used standard transformations (Krebs 1999), given in the legend notes for each table, to ensure that the assumptions of linearity and normality were met. We used likelihood ratio tests to test the covariance structure against a completely unstructured model and to eliminate non-significant random factors. We eliminated non-significant fixed effects based on type 3 hypothesis tests with $\alpha = 0.05$.

Mechanisms for effects of grazing on exotic annual grasses

We also used mixed models to identify mechanisms for the impacts of grazing on the exotic annual grasses. First, to test our hypothesis that grazing should reduce flower production, we assessed the impact of grazing intensity and exclosure on the proportion of exotic annual grass stems flowering in 2005, the first year of the experiment. Second, to test our hypothesis that grazing might increase grass stem (tiller) production, we assessed the impact of grazing and litter accumulation on the number of 2006 stems produced per 2005 inflorescence. For this model of 2006 stem production, we removed an outlying site, where five of the six plots (both open and exclosed) had less than 3% total cover in 2006.

Results

Composition of the island plant communities

We found a total of 60 species in our plots, of which 13 were grasses and 47 were forbs (Table 1; online supplement S1). Of the grasses, exotic annuals were by far the

Table 1 Number of species observed by origin and life history and percentage of plots in which each group was represented

Duration	Forbs		Grasses		Total
	Native	Exotic	Native	Exotic	
Annual (%)	15 (97)	10 (81)	0 (0)	9 (98)	34
Perennial (%)	16 (91)	6 (24)	1 (14)	3 (13)	26
Sub-total	31	16	1	12	
Total	47		13		60

most common, in particular, the following nine species: *Aira caryophylla* L., *A. praecox* L., *Bromus diandrus* Roth, *B. hordeaceus* L., *Cynosurus echinatus* L., *Hordeum murinum* L., *Poa annua* L., *Vulpia bromoides* (L.) S.F. Gray, and *V. myuros* (L.) K.C. Gmel. In contrast, the abundance of other grasses in our system was very limited. Only one species was a native perennial grass [*Festuca idahoensis* Elmer ssp. *roemeri* (Pavl.) S. Aiken], and only three were exotic perennial grasses. These were excluded from analyses due to their limited distribution. Native annual grasses were absent from all plots and were not observed elsewhere in the study area. Native perennial forbs, native annual forbs, and exotic annual forbs each occurred in over 80% of our plots (Table 1). Native perennials were mostly lilies (genera *Allium*, *Brodiaea*, *Triteleia*, *Camassia*, *Erythronium*, and *Fritillaria*) plus an aster (*Grindelia*) and a carrot (*Sanicula*). Native annuals included species of *Claytonia*, *Collinsia*, *Plectritis*, and *Trifolium*, and exotic annuals included species of *Cerastium*, *Senecio*, *Stellaria*, and *Vicia*. Exotic perennial forbs occurred in only 24% of plots and were thus omitted from analysis. A full species list is available as an online Appendix.

Overall, in both open and excluded plots, the total abundance of stems was positively related to the grazing intensity gradient ($F_{(1,174)} = 23.31$, $p < 0.0001$), but this did not differ between years, soil depths, or open versus excluded plots. In contrast, total species richness and total evenness (E_{var}) were each negatively related to grazing intensity (for richness: $F_{(1,212)} = 7.49$, $p = 0.0067$; for E_{var} : $F_{(1,166)} = 4.81$, $p = 0.030$). The estimated difference in species richness over the observed grazing gradient (i.e., the difference between the most heavily grazed plots and the plots with no grazing) was 1.65 species per plot.

Grazing selectivity

Forage ratios for the plant groups in our system showed that geese fed selectively on exotic annual grasses. Only exotic annual grasses had a median forage ratio significantly above 1 among the seven groups tested (median = 1.28, $p < 0.0001$). These grasses were grazed

in 36 of the 39 plots where they occurred. Exotic perennial grasses were grazed in six of seven plots where they occurred, but with such a low sample size, their median forage ratio of 2.22 was not significantly different from 1 ($p = 0.45$). Native perennial grasses and exotic perennial forbs also had forage ratios equivalent to 1 ($n < 10$ plots, median = 0.00, $p > 0.07$). In contrast, native forbs and exotic annual forbs were significantly avoided ($n > 28$ plots, median = 0.00, $p < 0.0001$). We believe the 2006 data offer the best estimates of selectivity because the single survey for that year captured the middle of the goose grazing season, but analyses based on 2005 surveys yielded identical conclusions.

Effects of grazing on abundance and richness of exotic annual grasses

In both 2005 and 2006, we observed that the proportional abundance of exotic annual grasses in open plots was positively related to grazing intensity (Fig. 1a). This

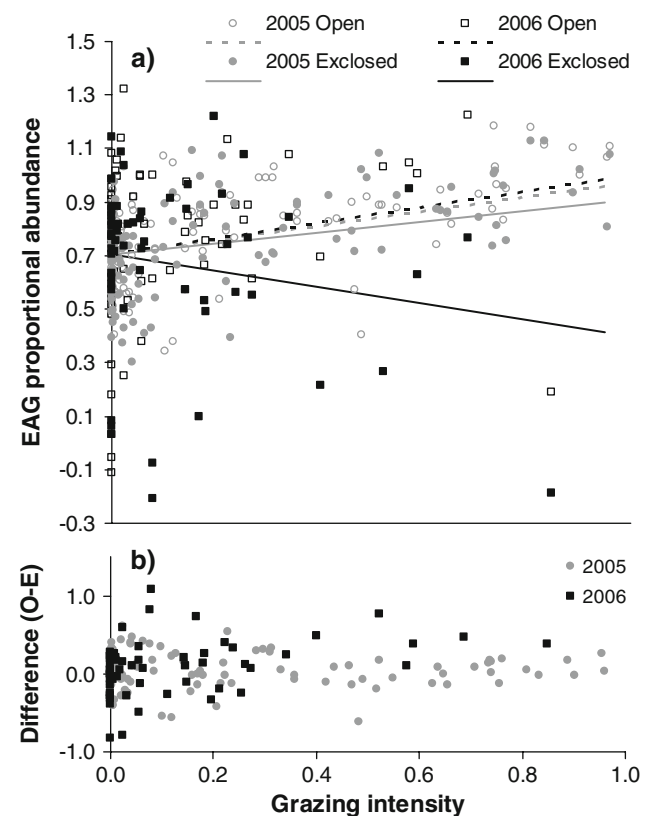


Fig. 1 Proportional abundance of exotic annual grasses (EAG) along the grazing intensity gradient. Grazing intensity is the total proportion of stems grazed measured in the open plots. **a** Data adjusted to the beginning of the survey period, to average soil depth, and to average levels of the random factors. EAG proportional abundance is arcsine square root transformed. Slopes are significantly different, with parameter estimates given in Table 2. **b** Pair-wise differences between the open (O) and excluded (E) plots in **a**

relationship was also positive in excluded plots in 2005, the year we established them. However, by the following year (2006), the relationship between grazing intensity and exotic grass abundance in the excluded plots had become negative (Fig. 1a and Table 2, graze intensity \times enclosure \times year term). We detected no difference in the intercepts of these relationships, where grazing intensity and, therefore, the magnitude of the treatment difference between open and excluded plots were zero (Table 2). The simultaneous observation of a single intercept but significantly different slopes is a strong indication that after a full year the relative abundance of exotic grasses was higher under grazing. This result is also apparent in the pair-wise differences between open and excluded plots. In 2006, the proportional abundance of exotic annual grasses in the open plot minus that in the excluded plot was consistently positive at grazing intensities over 0.3 (Fig. 1b). The increase of these grasses under grazing was counter to our hypothesis that selective grazing should limit grass abundance. Finally, we saw no effect of grazing on the species richness of the exotic annual grasses (Table 2).

Effects of grazing on abundance and richness of native and exotic forbs

Native perennial and annual forbs showed negative relationships with the grazing intensity gradient (Fig. 2). These relationships were steeper in 2006 and were different from that exhibited by the exotic annual forbs. In the full model, the graze intensity \times forb type \times year interaction term was significant (Table 3), and sub-analyses for each year produced significant graze intensity \times forb type interaction terms in both cases (for 2005: $F_{(2,467)} = 7.70$, $p = 0.0005$;

for 2006: $F_{(2,308)} = 8.54$, $p = 0.0002$). We did not observe an increase in forb abundance in excluded plots (Table 3, enclosure effect not significant). Rather, declines in the proportional abundance of exotic annual grasses inside enclosures were countered by increases in only a few patchily distributed exotic perennial forbs and grasses. We also observed interactions in both years between soil depth and forb type; native perennials increased with soil depth, whereas native annuals declined, and exotic annuals showed no pattern (Table 3).

Species richness of native forbs was also negatively related to grazing intensity, whereas exotic annual forb richness was relatively constant across the grazing gradient (Table 3: graze intensity \times forb type interaction term). Slopes were not different between years, and the enclosures did not produce any recovery in species richness of native forbs over our 2-year study.

Mechanisms for effects of grazing on exotic annual grasses

Grazing by geese had a measurable effect on the demographic processes underlying the success of the exotic annual grasses. In 2005, the proportion of grass stems flowering in open plots exposed to grazing declined with increasing grazing intensity (Table 4; Fig 3a). In contrast to this negative relationship, grazing increased the rate at which grasses converted their reproductive output in 2005 into tiller production in 2006. This relationship between conversion rate and 2006 grazing intensity was positive in open plots and negative in excluded plots (Fig. 3b; Table 4: graze intensity \times enclosure term). Over all plots, the conversion of flowers to tillers was also negatively related

Table 2 Models for proportional abundance and species richness of exotic annual grasses

Response variable	Effect	<i>df</i>	<i>F</i>	<i>p</i>	Estimate ^a
Proportional abundance	Graze intensity \times year \times enclosure	1, 81	3.96	0.049	$b_{\text{graze}(2005 \text{ O})}$: 0.27 $b_{\text{graze}(2005 \text{ E})}$: 0.20 $b_{\text{graze}(2006 \text{ O})}$: 0.29 $b_{\text{graze}(2006 \text{ E})}$: -0.31
	Enclosure	1, 64.6	0.05	0.83	
	Year	1, 136	0.04	0.84	
	Survey date	1, 106	26.85	<0.0001	b_{date} : 0.0011
	Soil depth	1, 150	5.17	0.024	b_{soil} : -0.015
	Species richness	Graze intensity	1, 223	1.53	0.22
Enclosure		1, 87.6	0.24	0.62	
Year		1, 142	2.80	0.097	
Survey date		1, 114	2.61	0.11	
Soil depth		1, 161	2.79	0.097	

^a Parameter estimates (slopes and intercepts) are for $\text{Asin}\sqrt{(\text{proportional abundance})}$. Bracketed notation before the estimate denotes the year (2005 or 2006) and enclosure treatment (O, open; E, excluded)

Fig. 2 Proportional abundance of forbs along the grazing intensity gradient in 2005 (a) and 2006 (b). Grazing intensity is the total proportion of stems grazed measured in the open plots. Slopes are significantly different; parameter estimates are given in Table 3. Data are displayed adjusted to the beginning of the survey period, to average soil depth, and to average levels of the random factors. Forb proportional abundance is arcsine square root transformed

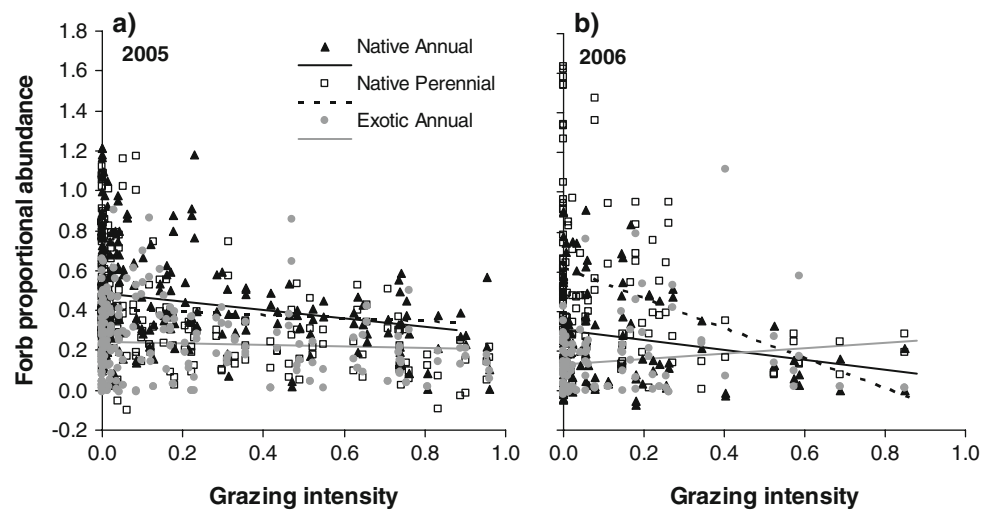


Table 3 Models for proportional abundance and species richness of native and exotic forbs

Response variable	Effect	df	F	p	Estimate ^a
Proportional abundance	Graze intensity × forb type × year	2, 350	10.65	<0.0001	$b_{\text{graze}(2005 \text{ na})}$: -0.21
					$b_{\text{graze}(2005 \text{ np})}$: -0.07
					$b_{\text{graze}(2005 \text{ ea})}$: -0.03
					$b_{\text{graze}(2006 \text{ na})}$: -0.25
					$b_{\text{graze}(2006 \text{ np})}$: -0.75
					$b_{\text{graze}(2006 \text{ ea})}$: 0.13
	Year × forb type	2, 438	31.55	<0.0001	$b_{\text{o}(2005 \text{ na})}$: 0.62
					$b_{\text{o}(2005 \text{ np})}$: 0.27
					$b_{\text{o}(2005 \text{ ea})}$: 0.29
					$b_{\text{o}(2006 \text{ na})}$: 0.45
Exclosure	1, 577	0.43	0.51	$b_{\text{o}(2006 \text{ np})}$: 0.49	
				$b_{\text{o}(2006 \text{ ea})}$: 0.20	
Survey date	1, 281	26.71	<0.0001	b_{data} : -0.00066	
				$b_{\text{soil}(na)}$: -0.012	
Soil depth × forb type	2, 585	16.27	<0.0001	$b_{\text{soil}(np)}$: 0.027	
				$b_{\text{soil}(ea)}$: 0.00019	
				$b_{\text{graze}(na)}$: -0.18	
Species richness	Graze intensity × forb type	2, 792	3.75	0.024	$b_{\text{graze}(np)}$: -0.23
					$b_{\text{graze}(ea)}$: 0.052
					$b_{\text{graze}(na)}$: -0.18
	Year × forb type	2, 479	31.34	<0.0001	$b_{\text{o}(2005 \text{ na})}$: 1.98
					$b_{\text{o}(2005 \text{ np})}$: 1.75
					$b_{\text{o}(2005 \text{ ea})}$: 1.64
					$b_{\text{o}(2006 \text{ na})}$: 1.59
					$b_{\text{o}(2006 \text{ np})}$: 1.89
					$b_{\text{o}(2006 \text{ ea})}$: 1.41
	Exclosure	1, 580	1.74	0.19	$b_{\text{o}(2006 \text{ ea})}$: 1.41
b_{data} : -0.0021					
Survey date	1, 328	42.16	<0.0001	b_{data} : -0.0021	
				$b_{\text{soil}(na)}$: -0.012	
Soil depth	1, 263	3.05	0.082	$b_{\text{soil}(na)}$: -0.012	
				$b_{\text{soil}(np)}$: 0.027	

^a Parameter estimates (slopes and intercepts) are for $\text{Asin}\sqrt{(\text{proportional abundance})}$ and $\sqrt{(\text{species richness})}$. Bracketed notation before the estimate denotes the year (2005 or 2006) and forb type (na, native annual; np, native perennial; ea, exotic annual)

Table 4 Models for exotic annual grass (EAG) flowering and stem production

Response variable	Effect	df	F	p	Estimate ^a
Proportion of EAG stems flowering in 2005	Graze intensity × enclosure	1, 51	25.81	<0.0001	$b_{\text{graze(O)}}: -0.88$ $b_{\text{graze(E)}}: -0.042$
	Enclosure	1, 51	4.28	0.044	$b_{\text{o(O)}}: 1.17$ $b_{\text{o(E)}}: 1.04$
Number of EAG stems in 2006 per 2005 inflorescence	Graze intensity × enclosure	1, 49.2	14.26	0.0004	$b_{\text{graze(O)}}: 0.86$ $b_{\text{graze(E)}}: -1.16$
	Enclosure	1, 57.3	4.24	0.044	$b_{\text{o(O)}}: 1.24$ $b_{\text{o(E)}}: 1.52$
	Percentage cover litter	1, 88.3	14.42	0.0003	$b_{\text{litter}}: -0.018$

^a Parameter estimates (slopes and intercepts) are for $\text{Asin}\sqrt{(\text{proportion flowering})}$ and $\text{Ln}(\text{stems per inflorescence})$. Bracketed notation before the estimate denotes the enclosure treatment (O, open; E, enclosed)

to the percentage cover of litter, which was much higher in enclosed than open plots (Fig. 3c; note right-skewed distribution of closed circles). This latter finding also explains why the conversion rate declined in enclosed plots as grazing intensity increased. Sites with high grazing intensity in the open plots experienced higher rates of litter accumulation in paired enclosed plots, given the similar vegetation composition within pairs at the outset of our experiment. Thus, reduced litter accumulation appears to be a key factor underlying the increased production of grass stems under grazing. In addition, grazing also increased light availability by reducing the average vegetation height. In open plots, average vegetation height declined with increasing grazing intensity ($F_{1,102} = 9.49$, $p = 0.003$, $b_{\text{graze}} = -0.62$ for \ln -transformed vegetation height).

Propagule dispersal

We observed 25 germinants from 314 g of dried feces, 80% of which were exotic annual grasses (72% *Poa annua* L.; 8% *Aira praecox* L.). The remainder included one exotic annual forb (12% *Silene gallica* L.), one native annual forb (4% *Myosurus minimus* L.), and one native perennial forb (4% *Epilobium ciliatum* Raf.). *Poa annua* was by far the most common species overall, at an estimated density of one viable seed per 18.7 g of dry feces. Only the smallest sample failed to produce any germinants.

Discussion

Our results show a pattern of increasing abundance of exotic annual grasses and decreasing abundance and richness of native forbs under grazing by geese (Figs. 1, 2). Our experimental comparison of paired open and enclosed plots further indicates that grazing by geese directly

facilitated the spread of their preferred food source. In addition, our germination trials show that geese may have contributed to the colonization phase of grass invasion in this system and that they are now clearly capable of dispersing exotic grass seed to areas still dominated by native vegetation. In return, geese appear to obtain most of their diet from these same exotic grasses. Overall, these results describe a positive feedback loop wherein proliferating grasses are likely to attract more grazing pressure.

The occurrence of a positive feedback cycle wherein one invader is the selected target of another is unexpected under current theory. The “enemy of my enemy” hypothesis states that novel herbivores that consume native plant species may indirectly benefit grazing-tolerant grasses, whereas herbivores that selectively feed on the grasses should limit their abundance. To understand why grasses were more abundant when exposed to selective herbivory, we first consider the mechanisms for the increased demographic success of the grasses under grazing. We then ask how these mechanisms might arise, based on the similarities and differences in the evolutionary histories of the species now interacting in our study system.

Grasses under grazing

We found that exotic grasses were not limited by reduced flower production under grazing (Fig. 3a). Instead, exotic grasses increased in abundance when grazing reduced vegetation height and litter accumulation (Fig. 3b, c). Increased light availability might be expected to elevate germination rates to benefit all annual species. However, the observed increase in proportional abundance of exotic grasses suggests that they received an additional benefit relative to annual forbs, perhaps because grazed annual grasses produced more tillers per individual prior to flowering. This mechanism has been documented in annual grasses with other grazers (Gutman et al. 2002; NoyMeir

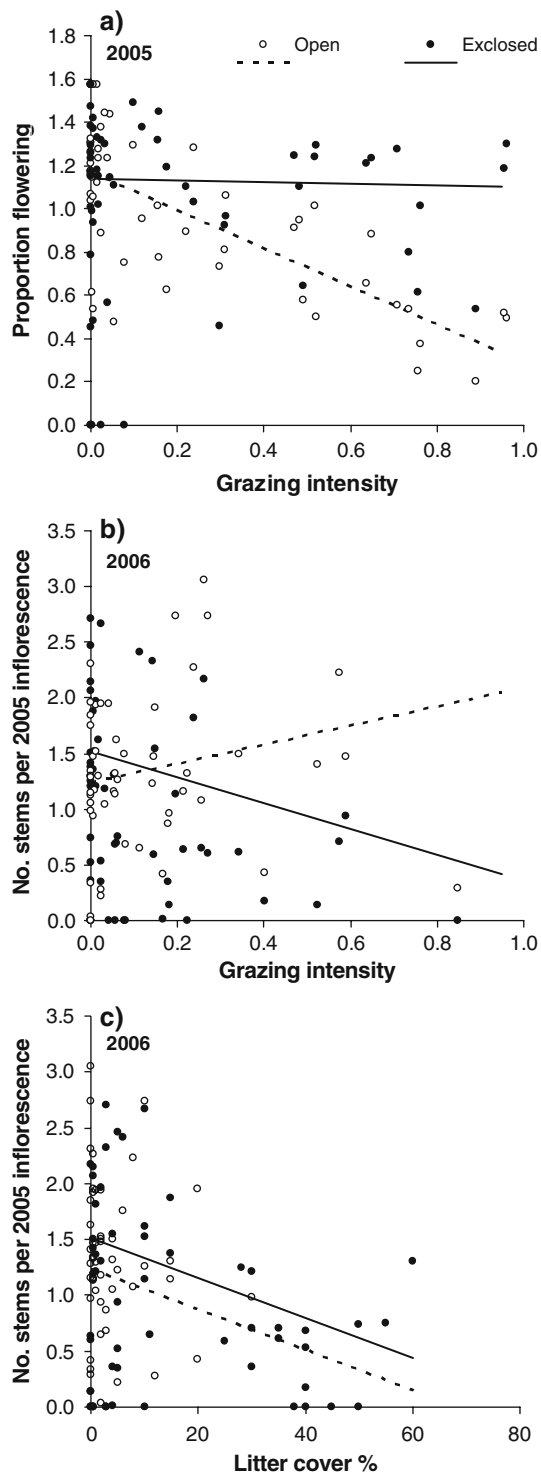


Fig. 3 Direct and indirect effects of grazing on exotic annual grass population growth. Effect of grazing on flower production in 2005 (**a**) and effects of grazing (**b**) and reduced litter cover (**c**) on stem production in 2006. Grazing intensity is the total proportion of stems grazed measured in the open plots. In **a**, **b**, slopes of regressions shown are significantly different (Table 4). Proportion flowering is arcsine square root transformed, and stems per inflorescence is log transformed

and Briske 1996) and under mowing (Lush 1988), and may be a direct response to leaf injury or an indirect response to light availability. Van der Graaf et al. (2005) also showed an increased production of branches in the perennial grass *Festuca rubra* under grazing by Barnacle geese (*Branta leucopsis*). It is important to note, however, that we do not interpret our results as evidence of compensatory biomass production under grazing, as has been demonstrated in other systems with goose herbivory (Cargill and Jefferies 1984; Van der Graaf et al. 2005), because we did not measure total production of biomass in the presence and absence of grazing. Instead, our results suggest that grazing by geese facilitated their demographic success by increasing the number of tillers.

In systems where grazing prevents litter build-up and shading, the production of many short stems may evolve as an efficient strategy for space occupation and reproduction. Under grazing, early-germinating annual grasses tend to form short, highly branched mats that occupy a large percentage of available space. *Poa annua*, for example, is a common golf course weed known for its ability to move into disturbed patches and create an impenetrable cover that prevents invasion by other species (Bergelson 1990; Hutchinson and Seymour 1982; Lush 1988). Falster and Westoby (2003), in their review of theoretical work on plant height strategies, point out that the production and maintenance of tall stems is an inefficient use of resources resulting from the “evolutionary arms race” of light competition. Larger size requires the diversion of resources to the maintenance of structural and transport tissues, away from reproductive output and away from the production of additional lateral shoots to occupy additional space. Again, *Poa annua* is a persistent weed in golf courses in part because of its ability to flower even at very low mowing height (Johnson and White 1998). Reviewing ten studies of grazing systems in Scotland, Pakeman (2004) showed that plant traits that consistently increased under grazing included low minimum height and an annual life history strategy. The short stem strategy has also been demonstrated in systems where biomass is frequently removed by fire, creating a niche space for short, efficient reproducers to thrive immediately following disturbance (Falster and Westoby 2005).

Grazed grasses and ungrazed forbs

Because the grazing we observed was almost entirely on exotic annual grasses (the median forage ratio for all forb groups was 0.00), any impact of grazing on forbs must have occurred through a modification of the interactions between plant species. Given our experimental demonstration that exotic annual grasses were more abundant under grazing and our observational evidence that native

forbs declined along the spatial gradient of grazing intensity, it is possible that by stimulating grasses to produce dense mats of stems, grazing also conferred a competitive advantage to exotic annual grasses. Moreover, if annual grasses are, in general, better adapted to compete under grazing than forbs, then the absence of annual grasses from the native species pool we studied (Table 1) may contribute to the invasion success of exotic grasses in this system. This idea is consistent with the theory predicting that similarity in function (Fox's assembly rule 1987) or phylogeny (Daehler 2001) should decrease invasion success when species from the same functional or taxonomic group are already present. In our system, both the grazer and the species adapted to thrive under grazing are introduced. Consequently, the benefits of grazing for the efficient production of stems accrue only to exotic members of the species pool.

In addition, whereas our results indicate that exotic annual grasses are limited by litter cover, the native species in this forb-dominated system do not produce litter that persists and accumulates over multiple growing seasons. Native forbs therefore cannot have the same suppressive effect on exotic annual grasses that other grasses might produce. Evidence from other systems also suggests that native perennial grasses can limit the demographic success of exotic annual grasses under grazing. Quigley and Ford (2002) reported that the abundance of *Vulpia myuros* and *Poa annua* was more strongly associated with sheep grazing in the absence of perennial grasses. Similarly, Whitson and Koch (1998) found that native perennial grasses reduced *Bromus tectorum* establishment through the suppressive effects of litter. The only native perennial grass found in our plots, however, is *Festuca idahoensis* ssp. *roemerii*, which is limited to clumps in rock crevices. Overall, therefore, our results suggest that differences between the native and exotic species pools, themselves the products of different evolutionary histories, may make the islands vulnerable to invasion by exotic species with novel strategies.

Propagule dispersal

In addition to increasing the proportional abundance of grasses by grazing, Canada geese are capable of transporting seeds of exotic annual grasses in their feces. Exotic grasses are ubiquitous in the lawns, golf courses, and fields of adjacent Vancouver Island and the larger Gulf Islands, all of which act as feeding areas for geese. Thus, geese are likely to disperse grass seed to the small islands where they now nest as well as between these small islands which as yet display varying degrees of invasion by exotic grasses. Of the 25 individuals germinating from seeds in goose feces, 80% were exotic annual grasses, either *Poa annua* or *Aira praecox*. In addition, many of the other annual grass

species proliferating in the islands (e.g., *Bromus diandrus*, *Hordeum murinum*, *Vulpia* spp.) have long, rough awns, an adaptation that can facilitate external transport by animals (Romermaun et al. 2005; Sorensen 1986). Both internal and external dispersal by animals has been an important factor in the spread of exotic plant species in other systems (Malo and Suarez 1997; Simberloff and Von Holle 1999). Furthermore, grass seed production in this system is seasonally coincident with the inter-island movement of geese flying between their nesting sites and additional feeding grounds on larger islands. Since seasonal timing and short flight distances are important determinants of viable seed dispersal by birds (Clausen et al. 2002), these geese are likely vectors for the spread of exotic grass propagules to the small islands where they nest. Whereas herbivores in many systems may have simultaneous positive and negative effects on their food source via dispersal and biomass removal, respectively (Vellend et al. 2006), in this system both dispersal and herbivory appear to contribute to population growth in the grasses.

Although areas already dominated by exotic annual grasses are not likely to be affected by further seed input, many sites in our study area still harbor some of the most intact examples of native coastal bluff ecosystems (Gonzales 2008). While the dispersal of grass seed by geese is very unlikely to account for the entire history of grass invasion on these islands, it does currently represent an ongoing threat to remaining intact areas. Furthermore, even though the effect is far more patchily distributed than grazing in this system, greenhouse experiments have shown that nutrient addition from goose feces may also facilitate dominance by the exotic annual grasses (Best 2008). Finally, grazing by geese at the edges of the island meadows appears to be contributing to rapid erosion of the shallow soils overlying the bedrock. Soil disturbance within our study plots did not appear to be significant compared to grazing, but it does act at a larger scale to reduce the extent of the vegetated area on these islands.

Implications for biotic resistance theory

The most surprising aspect of the joint success of geese and grasses in this system is that it occurred despite the grazers' preference for exotic grasses as food and their avoidance of forbs. Instead of doing better in the absence of their enemies, the grasses appeared to benefit from the herbivory. Our finding differs from earlier demonstrations that generalist herbivores can facilitate exotic grasses by grazing on intolerant native species (DiTomaso 2000; Hobbs 2001) because the native forbs we observed appear to decline without being grazed. Our results also suggest that, for at least some types of herbivores, high attack rates do not necessarily indicate that exotic plant species are limited by

enemies, especially in the case that herbivores also disperse seed. Overall, these findings reaffirm the importance of quantitative studies of the demographic impacts of interactions between exotic species. Qualitatively, the relationship between geese and grasses would likely have been interpreted as a (+/−) relationship in Simberloff and Von Holle's (1999) inventory because grasses are consumed by geese. In contrast, our experimental approach uncovered what we interpret to be a mutually beneficial relationship (i.e., +/+).

Much theory about community invasibility has considered the escape from evolutionary constraints to be a distinct advantage for invading species. The enemy release (Keane and Crawley 2002; Williamson 1996), evolution of increased competitive ability (Blossey and Notzold 1995), and novel weapons (Callaway and Aschehoug 2000) hypotheses are all based on this premise. More recently, Parker et al. (2006) also showed that exotic plants may be more limited by novel native herbivores than by co-evolved exotic herbivores. In our study system, however, it is likely that the introduced European grasses we studied evolved under grazing pressure, and it is certain that the large-bodied forms of Canada geese, which are native to the central prairies of North America (Hanson 1997), evolved with grasslands. Thus, although these species originate from different continents, it is plausible that similarities exist in the species interactions involved in the evolution of the grasses and geese we studied. In contrast, the native forb community we studied evolved without grazers and with few grasses. The success of the exotic annual grasses in this system may therefore be a consequence of their interaction with a familiar type of enemy, and novel, dissimilar competitors. Instead of the grasses bringing novel abilities to a new game, they appear to do better playing their old game against a community of inexperienced opponents.

As the co-occurrence of multiple exotic species increases globally, it becomes more likely that invasion success will depend on interactions between invaders as well as on a single invader's ability to escape competitors or enemies. This possibility underlies the potential for the “invasional meltdown” scenarios suggested by Simberloff and Von Holle (1999) and recently reviewed (Simberloff 2006). In our study, we have not demonstrated that the interaction between an exotic herbivore and a group of exotic grasses facilitates further invasion by other species. Furthermore, without additional experiments to test for competition between exotic grasses and native forbs in the presence and absence of grazing, we can only speculate that the grazer and grass combination has a larger negative impact on native species persistence than either exotic on its own. However, we have shown that exotic grasses derive a clear demographic advantage from grazing by geese and that

geese also appear to benefit from the presence of the exotic grasses that form the bulk of their diet.

We have also shown that exotic species from similar systems can create mutual benefits by making an invaded system more—rather than less—like home. While Simberloff (2006) found that co-evolution of multiple invaders was not necessary to produce a positive interaction in the invaded range, it remains possible that similarity in evolutionary history may promote such interactions. Ecologists have recently recognized the importance of biogeographical comparisons of invaders' native and exotic ranges (Hiero et al. 2005); we suggest this approach needs to be expanded to consider the home ranges of multiple co-occurring invaders.

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