

THE EFFECTS OF HERBIVORY, COMPETITION,  
AND DISTURBANCE ON ISLAND MEADOWS

by

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## Abstract

It is an unresolved paradox that non-native species are successful in novel environments whereas native species, presumably adapted to that environment, decline. This knowledge gap has persisted because third party processes in invasion ecology have been overlooked. Ungulate densities are increasing due to the eradication of predators and landscape change and I asked how herbivory and invasion might interact to cause declines of native species. In Garry oak meadows, Canada's most endangered ecosystem, native forbs have declined relative to non-native grasses and I tested the facilitatory role of herbivory in that degradation. My investigations, novel to the field, were conducted on islands spanning the Canada-US border. Islands served as natural experimental units in a mensurative study of abundance patterns in seven plant groups and 15 focal species along gradients of herbivory, biogeography, soil depth, and human activities. Increasing ungulate densities were related to declines in abundances of native forbs, and increasing abundances of non-native annual grasses. These regional patterns were upheld by two plot-based, 2x2 factorial experiments that contrasted the fitness of native species under manipulations of herbivory and competition for light. Specifically, I showed that ungulates limited the establishment, growth, survival and reproduction of seedlings and transplanted native forbs and shrubs and that competition from non-native species had little effect. I also calculated forage selectivity indices and tested the efficacy of fencing and cutting to reduce competition, for the restoration of native community biomass. Non-native annual grasses were rarely browsed and increased with increasing ungulate density. Non-native perennial grasses declined with herbivory, however, their regional abundances were unaffected by ungulate density despite being preferentially foraged. That non-native annual and perennial grasses differed in their responses to herbivory has consequences for restoration and illustrates

the challenge of developing a comprehensive theory of invasion. Reducing ungulates, necessary for the recovery of native forbs, also benefits non-native perennial grasses and therefore their removal speed recovery of Garry oak meadows. Despite advances in invasion ecology, scientists and managers are disconnected and research is rarely implemented. I conclude by proposing seven solutions to facilitate the integration of science into management.

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How does one measure impact?<sup>1</sup> Scientists quantify the world, so how do we measure the effect of a human being on the lives and thoughts of others? Is it through celebrity? A body of work? The number of publications? Some of the most profound and lasting impacts, such as the creation and care of National Parks, have been the products of many people, names unknown. Nevertheless, their efforts have and will continue to positively affect the lives of millions of people (and species). There will never come an end to the good they have done.<sup>2</sup>

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---

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<sup>2</sup> Modified from a phrase attributed to Stephen Tyng Mather, the first director of the National Park Service, United States of America.

Embarking upon a PhD at first seemed like a solo endeavour. Mine quickly became the product of many influential people: the financial and in-kind supporters that make the research possible; the community spirit of the property owners who shared their land and their homes with me and my crew; the crew itself; and the experienced researchers who guided my journey.

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## Dedication

To my mother, who has been an inspiration and mentor to me and many others. She embodies the spirit of one who gives of herself to the betterment of the greater community.

Through her professional career as an occupational therapist (1968-1997) and as a Senior Instructor in Psychology at the University of Victoria (1997-present), Dr. Valerie Anne Gonzales has enriched the lives of those around her. Her public policy work and mentorship have been exemplary.

Despite arthritis and the absence of athletic experience, she began tackling triathlons in her late-40's and has gone on to compete in numerous Olympic, Half, and full IronMan Triathlons around the globe. She now races as a member of Team Canada and has been on the podium at World Championship events in Florida and Hawaii.

Accomplishments at this scale can result in self-focused individuals, but she has an immense, giving spirit and is one of the most selfless people I know. I owe her so much more than life. She taught me independence, responsibility, the joy of adventure, to go against the grain, and the confidence that all that is needed to achieve the impossible is effort.



Dr. Valerie Gonzales at her first IronMan in Penticton, British Columbia, Canada 2003

## **Co-Authorship statement**

Chapter 2 was co-authored with Dr. Peter Arcese. I identified, designed and conducted the research. I am solely responsible for all data analyses. P. Arcese assisted with identification of the research question and manuscript preparation and revision.

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## **Chapter 1: General Introduction**

Non-native species are changing landscapes at an unprecedented rate, yet the mechanisms influencing the success of invasive species remain poorly understood (Levine et al. 2004) and efforts to slow the spread of non-native species have largely failed (Hulme 2003). The challenge of developing a general theory of invasibility is due to three ecological factors: the diversity of traits of non-native species (e.g., stress tolerance, physical defenses, allelopathy) that could confer advantages in a novel environment (Goodwin et al. 1999, Alpert et al. 2000), variability in physical and biological components among invaded communities (Hierro et al. 2005), and the complex direct and indirect effects inherent in multi-species interactions (White et al. 2006). Progress in invasion ecology and ecological restoration, however, has also been hampered by the way researchers and practitioners have perceived non-native species (Davis et al. 2001). What follows is an introduction to invasion ecology, a theoretical and applied field composed of unique concepts and history. The subsequent three chapters are comprised of data-driven research to understand the relationship among ungulate density and non-native plant species in the loss of native plant species in Garry oak meadows in the Georgia Basin archipelago. Equally important to understanding ecological problems, however, is the ability to implement solutions (Roux et al. 2006). Therefore, the final chapter addresses how management decisions based on sound scientific principles and theory would increase efficiency and efficacy and how to traverse the barriers that impede the integration of science into management.

One of the impediments to progress in invasion ecology has been the acceptance of untested hypotheses regarding the deleterious effects of non-native species (Hager and McCoy 1998, Slobodkin 2001), which are rooted in the history of the field. Invasion ecology is a relatively new sub-discipline in ecology (Davis 2005), despite the fact that theories related to



invasions date to Darwin's *Origin of the Species* (1859, Daehler 2001). Applied research in invasion ecology did not take off until in the 1980's (Davis 2005) and was highly influenced by Charles S. Elton, generally considered the "father of invasion ecology". His book, *The Ecology of Invasions by Animals and Plants* (1958), however, has "unintentionally handicapped the field's subsequent development" by identifying non-native species as distinct from native species thereby disassociating invasion ecology from related subdisciplines in ecology such as succession (Davis et al. 2001:98). Most non-native species are benign (Williamson 1996) and whether the presence of non-native species is undesirable in the absence of negative effects is a value judgment. Invasion ecology would be better served by a less biased perception of non-native species (Davis and Thompson 2000) and tests of multiple alternative hypotheses beyond simple, direct relationships between native and non-native species (Mitchell et al. 2006). For example, some non-native species have negative consequences for native communities and distinguishing those from relatively benign non-native species will increase the efficacy and efficiency of conservation and restoration (Alpert et al. 2000). Ultimately, bias in invasion ecology may be most detrimental if, by focusing on presumed negative influences of non-native species, a more potent driver of native species loss is overlooked. Therefore, to improve our understanding of the impacts of invasive species and mitigate threats to native species, we must be able to distinguish among different causal mechanisms of native population decline (Didham et al. 2005).

Studies of intratrophic interactions, such as plant-plant resource competition, dominate invasion ecology (Mitchell et al. 2006) because increases in the abundance of novel species have been taken as evidence of native species displacement (Hager and McCoy 1998, Wilcove et al. 1998). Intratrophic interactions are expected to result in replacement of species that are poor

competitors in stable environments at local scales (Tilman 1982). Most ecosystems, however, are spatially and temporally dynamic due to factors such as dispersal, environmental variation, and disturbances. These processes can promote invasion (Shea and Chesson 2002, Melbourne et al. 2007) but also promote regional coexistence (Huston 1994). Thus, it is possible that negative correlations between the abundance of native and non-native species simply reflect the fact that non-native species take advantage of ecosystem change, such as habitat disturbance, rather than being the drivers of changing native abundances (Gurevitch and Padilla 2004, MacDougall and Turkington 2005, Gonzales et al., in press). In contrast to intratrophic native/non-native relationships, introductions of predators, herbivores and pathogens have resulted in numerous cases of native species extinction (Rodda and Fritts 1992, Davis 2003, Nogales et al. 2006). The detrimental effects of introduced herbivores provide several particular examples of negative intertrophic interactions (Hobbs and Huenneke 1992, Fleischner 1994). However, our understanding of the effects of increased native herbivore density on native plant communities and the success of invaders remains very limited.

Theory and empirical results suggest that herbivores can either promote or reduce coexistence in plant communities depending on their consumption patterns and food preferences (Maron and Vila 2001, Klemola et al. 2002). Generalist herbivores are expected to consume both native and non-native species, whereas specialist herbivores have the potential to confer a competitive advantage to non-native species in the case that they feed preferentially on native species (Keane and Crawley 2002). As a consequence, the ‘enemy escape hypothesis’ of invasibility focuses on the relationship of specialists with focal prey species (Colautti et al. 2004). It is also possible, however, that competitive release facilitated by increasing populations of deer, which are generalist foragers, influences invasion success. To date few studies have

attempted to disentangle these potential mechanisms in any detail (D'Antonio 1993). Thus, there is a critical need for experiments involving the exclusion of generalist herbivores in invaded plant communities (Keane and Crawley 2002).

Mammalian herbivores are known to limit the biomass of diverse plant communities. Hester et al. (2000) has reviewed enclosure-based studies in forests in NW Europe and grassland enclosure studies over a range of productivity levels have been reviewed by Milchunas and Lauenroth (1993). A diversity of mammalian herbivores including moose (*Alces alces*), musk ox (*Ovibos moschatus*), zebra (*Equus spp.*), rabbits, voles, and lemmings reduce standing crop biomass relative to fenced areas. These results are consistent across multiple habitat types including African savanna (e.g., Sinclair 1975, McNaughton 1985, Goheen et al. 2004), temperate grasslands (e.g., Milchunas and Lauenroth 1993, Chase et al. 2000), tallgrass prairie (e.g., Keesing 2000, Howe et al. 2006), mountain pastures (Hill et al. 1992), arid lands (e.g., Brown and Heske 1990, Guo et al. 1995), woodlands (e.g., McInnes et al. 1992), forest edges (e.g., Manson et al. 2001), mountain snowbed (Virtanen 2000), forest tundra (Olofsson et al. 2004) and some subantarctic islands (Leader-Williams et al. 1987). There is little doubt that herbivores have significant impacts on vegetation in general, but the question of increasing herbivore densities has rarely been addressed.

Studies of increased herbivore densities have typically taken one of three approaches. Observational studies have been conducted during naturally occurring high densities of cyclic populations of snowshoe hares (*Lepus americanus*) (Krebs et al. 1992) and grey-sided voles (*Clethrionomys rufocanus*), Norwegian lemmings (*Lemmus lemmus*) and reindeer (*Rangifer tarandus*) (Grellmann 2002), or by sporadic outbreaks of grazers such as lesser snow geese (*Anser caerulescens*) (Jefferies et al. 1994). These have shown strong impacts by increasing

herbivores and in the case of snow geese almost complete destruction of the vegetation (Cooch et al. 1991). Second, using a combination of food additions and predator exclusion, Krebs et al. (1992) and Hodges et al. (2001) were able to increase population densities of snowshoe hares 6-fold which resulted in significantly increased herbivore impacts on vegetation. Third, comparisons of islands with and without predators has provided evidence of trophic cascades whereby predator-released herbivores erupt and plant damage significantly increases (Terborgh et al. 2001, Hamback et al. 2004, Terborgh et al. 2006). Increasing numbers of studies demonstrate that in the absence of wolves (*Canis lupus*) and/or cougars (*Felis concolor*), deer become abundant and consequently severely deplete vegetation (Rooney 2001, Ripple and Beschta 2006). Clearly, herbivores can have profound effects on vegetation but questions remain regarding how plant strategies to avoid or tolerate increased herbivory structure plant community composition.

To increase their abundance in the presence of a generalist forager, plant species may use herbivore avoidance or tolerance strategies (Zou et al. 2007). Avoidance can be achieved via the evolution of morphological defenses (thorns, spines, trichomes, lignin), low palatability or forage quality (Stoddart and Smith 1955), chemical and inducible defenses (Bryant et al. 1991, Hay 1991) or physical refuges (Milchunas and Noy-Meir 2002). Tolerance generally occurs through compensatory growth and the ability to reproduce after tissue removal (Rosenthal and Kotanen 1994, Hicks and Turkington 2000). Examples of intrinsic mechanisms promoting tolerance to herbivory are increased photosynthetic rate, increased branching or tillering and greater carbon storage below ground following herbivory (reviewed in Strauss and Agrawal 1999). The traits employed by some plant species to resist herbivory can affect populations of other plant species, thereby influencing plant community composition (Lonsdale 1999). For example, plants

defended with spines conferred protection to eight palatable species that were found exclusively underneath them in overgrazed meadows (Callaway et al. 2000). Alternatively, increasing herbivore densities can result in plant communities dominated by herbivore resistant species (Rooney and Waller 2003).

In addition to herbivory, plant community composition is also structured by extrinsic factors affecting the arrival, establishment and persistence of species and I present a simplified overview here (Fig. 1.1). Consequently, intrinsic factors are species traits that respond to the extrinsic factors (Ozinga et al. 2005). Extrinsic factors include patch size and isolation, available resources, competition, facilitation, herbivory, historical contingency and random factors that influence colonization and establishment and community ecology is, fundamentally, the study of when and where these processes predominate and at what scale (Gurevitch et al. 2002). In island systems, island size and isolation influence dispersal and filter plants with poor dispersal abilities and, typically, the composition of species on islands comprise a subset of the mainland plant community (*sensu* MacArthur and Wilson 1967, Whittaker 1998). However, in the case of invasive species, accumulation lags are likely to occur because founders require time to develop persistent populations before they are likely to spread further via dispersal (Crooks 2005). Moreover, upon their arrival at a novel site, environmental filters such as moisture and nutrient availability are likely to determine which species become established (Diaz et al. 1998). The resident plant community may also resist new arrivals (Levine and D'Antonio 1999). Persistence of species in the plant community is then dependent on intratrophic interactions such as competition and facilitation and intertrophic interactions such as herbivory (Olff and Ritchie 1998). If local conditions change, such as increases in herbivore densities, this may create niche opportunities for non-native species to become established (Keane and Crawley 2002).

Herbivory may further confer a competitive advantage to the persistence and spread of non-native species if they happen to be better at avoiding or tolerating the increased herbivore pressure relative to native species.

Invasion ecology has been criticized for being poorly integrated with related disciplines (Vermeij 1996, Davis et al. 2001). Therefore, I examine concepts that are infrequently incorporated into invasion ecology. Specifically, to test the effect of a native generalist herbivore on native/non-native plant assemblages, I measured:

- a) The relationship between native and non-native plant composition and herbivore abundance;
- b) Herbivore selectivity for native and non-native species;
- c) The effects of herbivory and competition on the establishment, growth, reproduction, and survival of focal native plants; and
- d) The response of plant community composition to manipulations of herbivory and disturbances to the plant community.

These four lines of inquiry were explored in Garry oak meadows located in an archipelago on the west coast of North America.

#### THESIS OVERVIEW

In this thesis, I ask if increasing population densities of large ungulates [Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and sheep (*Ovis aries*)] facilitate non-native plant species, and explore the implications for restoration of endangered Garry oak meadows in an island system. Garry oak ecosystems encompass a variety of habitats including coastal bluffs, herbaceous meadows, vernal pools, grasslands, rock outcrops, and transitional forests (Fuchs 2001). The distribution of the Garry oak ecosystem extends from southwestern

British Columbia, Canada, to central California in the United States. My study sites were located in the Georgia Basin archipelago which includes the Southern Gulf (Canada) and San Juan (USA) Islands, a region that extends 43 km latitudinally and 52 km longitudinally.

Paleoecological records suggest that Garry oaks (*Quercus garryana*) and herbaceous plants associated with the ecosystem type arrived to Vancouver Island around 10 000 BP (Pellatt et al. 2001). After 5750 B.P., the climate generally became cooler and favoured an increase in Douglas-fir (*Pseudotsuga menziesii*) forest (Pellett et al. 2001). Garry oak meadows are presently interspersed with other ecosystems, mainly conifer forest (Gedalof et al. 2006). At a landscape level, Garry oak meadows are naturally fragmented by being on islands and by intervening conifer forest. Meadows are also isolated into patches through agricultural and urban development. Land conversion has reduced the previous range of Garry oak ecosystems in Canada by approximately 80% (Lea 2006). Of more than 100 plant and animal species designated as at-risk in British Columbia, 23 are threatened or endangered globally and 21 are listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as being at-risk nationally (GOERT 2007). Few of the meadows that remain are thought to represent the native species richness of historical levels due to dominance by non-native grasses (MacDougall and Turkington 2004).

Some of the most uninvaded examples of Garry oak meadows occur on small, isolated islands (Photo 1.1) and a central question of this thesis is: are these islands relatively pristine because non-native species have yet to arrive and establish, because they are relatively undisturbed by humans, or because herbivore populations are low or absent? The transition from native forbs to non-native grasses has prompted detailed studies of the competitive relationships between native and non-native plants as well as the role of disturbance in maintaining meadow

conditions (MacDougall 2005, MacDougall and Turkington 2004, 2005, 2006). Shading and litter accumulation by non-native grasses (Photo 1.2) have suppressive effects on native forbs (MacDougall and Turkington 2004, 2007, MacDougall et al. 2006). However, the abundance of non-native grasses could also be related to abundant herbivores selectively foraging on native forbs, in turn conferring a competitive advantage to non-native grasses.

Black-tailed deer are the most ubiquitous herbivores in the region although other large herbivores include sheep, feral goats (*Capra hircus*), and fallow deer (*Dama dama*). The introduced herbivores are only found on one or two islands each; therefore, native deer are the focal herbivore in the regional scale investigations whereas both deer and sheep occur on the experimental sites. Both deer (Cowan 1945) and sheep (Bartolomé et al. 1998) are typically thought of as generalists as they eat a variety of plant types. Sheep were introduced to some islands in the Georgia Strait from the 1850's to 1940's. Most were eradicated from islands in the 1970's and 1980's (personal interviews) but a small flock continues to range near the location of my three experiments on Salt Spring Island. Estimates of deer densities on Vancouver Island, British Columbia, which serves as the "mainland" for the Southern Gulf Island research area, vary from 7-15 deer/km<sup>2</sup> in the past (Cowan 1945) to 10 to 20 deer/km<sup>2</sup> more recently (Hatter and Janz 1994), suggesting increasing densities in some areas. Wolves are the primary predator on deer (Hatter and Janz 1994) and are still present in undeveloped areas on Vancouver Island. Wolves were actively poisoned on the Gulf islands when cattle were introduced in the 1850's and were presumed extirpated by the 1880's (Wilson 1906) although transients visited occasionally until the 1940's. Cowan (1945) estimated that densities greater than 15 deer/km<sup>2</sup> produced overgrazed conditions and estimates on some islands exceed those values (T. Martin, N. Scheerder and P. Arcese, unpub. data). If herbivory increased due to introduced sheep,



carnivore extirpations and land conversion, niche opportunities may have been created for certain non-native plant groups through increased herbivore pressure, increased spread of non-native seeds via endo/ectozoochory, changes in nutrient levels through increased feces deposition, and disturbance by trampling.

My research objectives were to:

- a) Determine if there was a relationship between ungulate density and abundances of seven plant groups and 15 focal species;
- b) Establish ungulate foraging preferences and whether they were related to abundances of the seven plant groups;
- c) Test the consequences of ungulates (intertrophic) and shading (intratrophic) effects on added native seeds and transplanted plant species;
- d) Examine the effects of fencing and cutting on the proportional biomass of plant community groups;
- e) Make recommendations for restoration of Garry oak meadows and discuss strategies for implementing science into management.

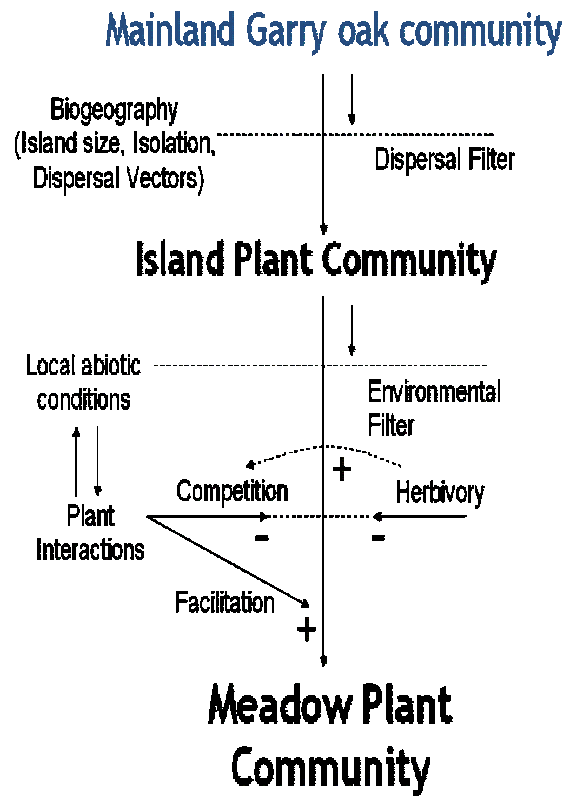
To determine if it is possible that the success of non-native grasses in Garry oak meadows have been facilitated by ungulate herbivory, I asked four key research questions:

- a) Are patterns of plant community composition related to the densities of deer **(Chapter 2)**?
- b) Do ungulates avoid non-native plant groups and select native plant groups **(Chapter 2)**?
- c) Does herbivory, rather than shading by non-native grasses and litter, limit native plants planted into experiments as transplanted plants or as seeds **(Chapter 3)**?

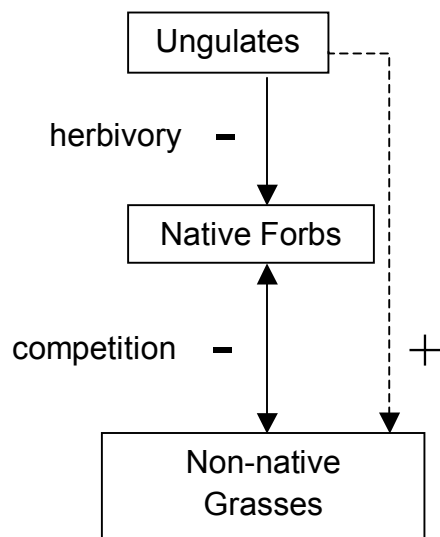
- d) Does fencing, rather than cutting and removing non-native grasses and litter, increase biomass of native plants (**Chapter 4**)?

Under this scenario, ungulates are a generalist herbivore that feeds on both native and non-native plant species, but that non-native grasses are more adept than native forbs at avoiding or tolerating herbivory which, in part, accounts for their dominance in Garry oak meadows today (Fig. 1.2).

## FIGURES



**Figure 0.1:** General factors and simplified relationships influencing plant community composition. Island size and isolation, as well as species traits, determine propagule arrival. Local abiotic conditions influence establishment. Herbivory, competition, and facilitation influence persistence and these relationships can be positive, negative and interact.



**Figure 0.2:** Hypothesized relationship between black-tailed deer and native and non-native plant species in Garry oak meadows. Solid arrows indicate direct effects. Dashed arrows indicate indirect effects. In this scenario, herbivory has a direct negative effect on native plant species and a positive indirect effect on non-native plant species. Deer are also expected to avoid browsing on non-native annual grasses, which, in general, compete for the same resources as native forbs.



**Photo 0.1:** Garry oak meadow with abundant native species such as chocolate lily (*Fritillaria affinis*).





**Photo 0.2:** Garry oak meadow invaded with non-native species such as sweet vernal grass (*Anthoxanthum odoratum*).

## LITERATURE CITED

- Alpert P., Bone E., and Holzapfel C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* **3**(1):52-660.
- Bartolome, J., J. Franch, J. Plaixats, and N. G. Seligman. 1998. Diet selection by sheep and goats on mediterranean heath-woodland range. *Journal of Range Management* **51**(4):383-391.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**(4988):1705-1707.
- Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. T. Dutoit. 1991. Interactions between woody-plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* **22**:431-446.
- Callaway, R. M., Z. Kikvidze, and D. Kikodze. 2000. Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus mountains. *Oikos* **89**(2):275-282.
- Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* **81**(9):2485-2497.
- Coblentz, B. E. 1990. Exotic organisms - a dilemma for conservation biology. *Conservation Biology* **4**(3):261-265.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* **7**(8):721-733.
- Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1991. Long-term decline in body size in a snow goose population - evidence of environmental degradation. *Journal of Animal Ecology* **60**(2):483-496.
- Cowan, I. M. 1945. The ecological relationships of the food of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the coast forest region of southern Vancouver Island, British Columbia. *Ecological Monographs* **15**(2):109-139.
- Crooks, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* **12**(3):316-329.
- Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. *American Naturalist* **158**(3):324-330.
- D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant-communities by the alien succulent *Carpobrotus-edulis*. *Ecology* **74**(1):83-95.
- Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London, England.

- Davis, M. A. and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* **81**: 226–230.
- Davis, M. A., K. Thompson, and J. P. Grime. 2001. Charles S. elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* **7**:97-102.
- Davis, M. A. 2005. Invasion Biology 1958-2004: The Pursuit of Science and Conservation Chapter 2. in M. W. Cadotte, S. M. McMahon and T. Fukami, editors. *Conceptual ecology and invasions biology: reciprocal approaches to nature*. Kluwer Publishers, London.
- Davis, M. A. 2003. Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience* **53**(5):481-489.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* **88**(3):528-534.
- Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**(1):113-122.
- Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* **20**(9):470-474.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. The University of Chicago Press, Chicago, Illinois.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629-644.
- Fuchs, M. A. 2001. *Towards a Recovery Strategy for Garry Oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review*. Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region. GBEI/EC-00-030.
- Gedalof, Z., M. Pellatt, and D. J. Smith. 2006. From prairie to forest: Three centuries of environmental change at rocky point, Vancouver Island, British Columbia. *Northwest Science* **80**(1):34-46.
- GOERT 2007. Garry Oak Ecosystem Recovery Team website. Available from [www.goert.ca](http://www.goert.ca) (accessed November 24 2007).
- Goheen, J. R., F. Keesing, B. F. Allan, D. L. Ogada, and R. S. Ostfeld. 2004. Net effects of large mammals on acacia seedling survival in an African savanna. *Ecology* **85**(6):1555-1561.
- Gonzales, E. K., Y. F. Wiersma, A. I. Maher, and T. D. Nudds. in press. Positive relationship between non-native and native squirrels in an urban landscape. *Canadian Journal of Zoology*.



- Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology* **13**(2):422-426.
- Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* **98**(2):190-204.
- Guo, Q. F., D. B. Thompson, T. J. Valone, and J. H. Brown. 1995. The effects of vertebrate granivores and folivores on plant community structure in the Chihuahuan desert. *Oikos* **73**(2):251-259.
- Gurevitch, J., Samuel M. Scheiner, and Gordon A. Fox. 2002. *The ecology of plants*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**(9):470-474.
- Hager, H. A., and K. D. McCoy. 1998. The implications of accepting untested hypotheses: A review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation* **7**(8):1069-1079.
- Hambäck, P. A., L. Oksanen, P. Ekerholm, A. Lindgren, T. Oksanen, and M. Schneider. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos* **106**(1):85-92.
- Hatter, I. W., and D. W. Janz. 1994. Apparent demographic-changes in black-tailed deer associated with wolf control on northern Vancouver-Island. *Canadian Journal of Zoology* **72**(5):878-884.
- Hay, M. E. 1991. Marine terrestrial contrasts in the ecology of plant-chemical defenses against herbivores. *Trends in Ecology & Evolution* **6**(11):362-365.
- Hester, A. J., L. Edenius, R. M. Buttenschon, and A. T. Kuiters. 2000. Interactions between forests and herbivores: The role of controlled grazing experiments. *Forestry* **73**(4):381-391.
- Hicks, S., and R. Turkington. 2000. Compensatory growth of three herbaceous perennial species: The effects of clipping and nutrient availability. *Canadian Journal of Botany* **78**(6):759-767.
- Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology* **93**(1):5-15.
- Hill, M. O., D. F. Evans, and S. A. Bell. 1992. Long-term effects of excluding sheep from hill pastures in North Wales. *Journal of Ecology* **80**(1):1-13.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion - implications for conservations. *Conservation Biology* **6**(3):324-337.

- Hodges, K.E., C. J. Krebs, D. S. Hik, C. I. Stefan, E. A. Gillis and C. E. Doyle. 2001. Snowshoe hare dynamics. In *Ecosystem dynamics of the boreal forest*. Edited by C. J. Krebs, S. Boutin, and R. Boonstra. Oxford University Press, New York. pp. 141–178.
- Howe, H. F., B. Zorn-Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* **87**(12):3007-3013.
- Hulme, P. E. 2003. Biological invasions: Winning the science battles but losing the conservation war? *Oryx* **37**(2):178-193.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, New York.
- Jefferies, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and northern plant-communities - reciprocal influences and responses. *Oikos* **71**(2):193-206.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**(4):164-170.
- Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. *Bioscience* **50**(3):205-215.
- Klemola, T., M. Tanhuanpaa, E. Korpimaki, and K. Ruohomaki. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* **99**(1):83-94.
- Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin. 2001. Estimating snowshoe hare population density from pellet plots: A further evaluation. *Canadian Journal of Zoology* **79**(1):1-4.
- Kuijper, D. P. J., D. J. Nijhoff, and J. P. Bakker. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. *Oecologia* **141**(3):452-459.
- Larson, B. M. H. 2005. The war of the roses: Demilitarizing invasion biology. *Frontiers in Ecology and the Environment* **3**(9):495-500.
- Lea, T. 2006. Historical Garry oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. *Davidsonia* **17**(2):34-50.
- Leader-Williams, N., R. I. L. Smith, and P. Rothery. 1987. Influence of introduced reindeer on the vegetation of south-Georgia - results from a long-term exclusion experiment. *Journal of Applied Ecology* **24**(3):801-822.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**(10):975-989.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* **87**(1):15-26.

- Lodge, D. M. 1993. Biological invasions - lessons for ecology. *Trends in Ecology & Evolution* **8**(4):133-137.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**(5):1522-1536.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- MacDougall, A. S. 2005. Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology* **86**(12):3354-3363.
- MacDougall, A. S., J. Boucher, R. Turkington, and G. E. Bradfield. 2006. Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science* **17**(1):47-56.
- MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology* **92**(3):422-434.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**(1):42-55.
- MacDougall, A. S., and R. Turkington. 2006. Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology* **87**(7):1831-1843.
- MacDougall, A. S., and R. Turkington. 2007. Does the type of disturbance matter when restoring disturbance-dependent grasslands? *Restoration Ecology* **15**(2):263-272.
- MacDougall, A. S., and S. D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* **88**(5):1105-1111.
- Manson, R. H., R. S. Ostfeld, and C. D. Canham. 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* **82**(12):3320-3329.
- Maron, J. L., and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* **95**(3):361-373.
- McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**(6):2059-2075.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem - the Serengeti. *Ecological Monographs* **55**(3):259-294.
- Melbourne, B. A., H. V. Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H.

- Yokomizo. 2007. Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? *Ecology Letters* **10**(1):77-94.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**(4):327-366.
- Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* **99**(1):113-130.
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin, and D. P. Vazquez. 2006. Biotic interactions and plant invasions. *Ecology Letters* **9**(6):726-740.
- Nogales, M., J. L. Rodriguez-Luengo, and P. Marrero. 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review* **36**(1):49-65.
- Odonoghue, M., and C. J. Krebs. 1992. Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. *Journal of Animal Ecology* **61**(3):631-641.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**(2):240-261.
- Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* **155**(6):703-723.
- Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* **13**(7):261-265.
- Olofsson, J., P. E. Hulme, L. Oksanen, and O. Suominen. 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* **106**(2):324-334.
- Ozinga, W. A., J. H. J. Schaminee, R. M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J. Bakker, and J. M. van Groenendael. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* **108**(3):555-561.
- Pellatt, M. G., R. J. Hebda, and R. W. Mathewes. 2001. High-resolution Holocene vegetation history and climate from hole 1034B, ODP leg 169S, Saanich inlet, Canada. *Marine Geology* **174**(1-4):211-226.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**(1):53-65.
- Ripple, W. J., and R. L. Beschta. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion national park. *Biological Conservation* **133**(4):397-408.

- Rodda, G. H., and T. H. Fritts. 1992. The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam lizards. *Journal of Herpetology* **26**(2):166-174.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* **74**(3):201-208.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**(1-2):165-176.
- Rosenthal, J. P., and P. M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution* **9**(4):145-148.
- Roux, D. J., K. H. Rogers, H. C. Biggs, P. J. Ashton, and A. Sergeant. 2006. Bridging the science–management divide: moving from unidirectional knowledge transfer to knowledge interfacing and sharing. <http://www.ecologyandsociety.org/vol11/iss1/art4/> edition.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**(4):170-176.
- Simberloff, D. 1981. Community effects of introduced species. Pages 53-81 in M. Nitecki, editor. *Biotic Crises in Ecological and Evolutionary Time*. Academic Press, New York.
- Sinclair, A. R. E. 1975. Resource limitation of trophic levels in tropical grassland ecosystems. *Journal of Animal Ecology* **44**(2):497-520.
- Slobodkin, L. B. 2001. The good, the bad and the reified. *Evolutionary Ecology Research* **3**(1):1-13.
- Soule, M. E. 1985. What is conservation biology. *Bioscience* **35**(11):727-734.
- Stoddart, L. A., and A. D. Smith. 1955. *Range Management*. 2nd edition. McGraw-Hill, New York.
- Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution* **14**(5):179-185.
- Terborgh, J., K. Feeley, M. Silman, P. Nunez, and B. Balukjian. 2006. Vegetation dynamics of predator-free land-bridge islands. *Journal of Ecology* **94**(2):253-263.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**(5548):1923-1926.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, N.J.
- Vermeij, G. J. 1996. An agenda for invasion biology. *Biological Conservation* **78**(1-2):3-9.

- Vila, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* **105**(2):229-238.
- Virtanen, R. 2000. Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. *Oikos* **90**(2):295-300.
- White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: A neglected concept in invasion biology. *Diversity and Distributions* **12**(4):443-455.
- Whittaker, R.J. 1998. *Island Biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford, UK. 285pp.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperilled species in the United States. *Bioscience* **48**(8):607-615.
- Williamson, M. H. 1996. *Biological Invasions*. Chapman and Hall, London, U.K.
- Wilson, E. F. 1906. From Barnsbury, England in 1868 to Barnsbury, Canada 1906. <http://www.saltspringarchives.com/wilson.pdf> edition.
- Zou, J., W. E. Rogers, and E. Siemann. 2007. Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Functional Ecology* **21**(4):721-730.

## Chapter 2: Herbivores facilitate non-native grasses in island Garry oak meadows\*

### INTRODUCTION

Increases in distributions and densities of deer worldwide have caused economic and ecological losses (Côté et al. 2004) and altered forest ecosystem structure and function where their abundances are high (McShea et al. 1997, Waller and Alverson 1997). Heavy browsing reduces plant cover and diversity (Rooney 2001, Martin and Baltzinger 2002), alters nutrient and carbon cycling (Wardle et al. 2002), and by transforming habitats, can lead to extirpation of songbirds (Allombert et al. 2005a), invertebrates (Allombert et al. 2005b), and black bears (*Ursus americanus*) (Côté 2005). Non-native grasses bring about economic and ecological costs (Pimentel et al. 2000) by altering carbon sequestration (Litton et al. 2006), fire regimes (Rossiter et al. 2003), nitrogen cycling (Evans et al. 2001, Mack et al. 2001), and soil biota (Belnap and Phillips 2001). These ecosystem altering changes can have profound effects on native plant diversity (e.g., Ferdinands et al. 2005, Mayer et al. 2005, Gabbard and Fowler 2007).

Herbivores such as deer and non-native grasses can alter ecosystem function and native species diversity (e.g., Lambrinos 2000, Rooney et al. 2004, Gabbard and Fowler 2007), but the interactions of deer, non-native grasses and native species composition have not been explored in detail within a single system. Whereas the effects of abundant herbivores and non-native grasses on plant communities are generally well-described, the potential role of ungulates in facilitating invasion by non-native grasses has not been studied. Invasive grasses are ubiquitous to grass-dominated systems worldwide and are often assumed to dominate by competition. However,

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they also can differ widely in their palatability, suggesting that herbivory could influence success. Agronomic grasses were introduced for their forage quality and have spread extensively throughout the landscape, but some are limited by overgrazing (e.g., *Lolium perenne*) and others appear highly tolerant (e.g., *Dactylis glomerata*) despite extensive defoliation (Cullen et al. 2006). Numerous annual grasses of the *Bromus* genera, by contrast, are also pernicious but can be highly unpalatable to grazers at certain life stages such as aptly named ripgut brome (*Bromus diandrus*). Or, some may have such limited forage quality that they are ignored thereby increasing their abundance relative to palatable species (e.g., *Aira sp.*). These contrasts in palatability suggest that herbivory could influence invasion success, even when it looks like competition. We therefore used a comparative analysis of surveys on 40 island sites subject to different levels of herbivory to ask if deer facilitate the invasion of less palatable, non-native grasses by foraging selectively on native plants.

We used Garry oak meadows on islands for our comparison of plant community composition along a gradient of herbivory. The main herbivore, the black-tailed deer (*Odocoileus hemionus*), is a generalist, but selects forbs and shrubs over grasses (Cowan 1945, Hanley 1997) and can limit reproduction and abundance of forbs at high deer densities (Anderson 1994, McNaughton and Augustine 1998, Kirby 2001). The abundance of annual grasses, in particular, is predicted to increase under increasing deer densities and, therefore, deer density was considered as a natural, large-scale experimental treatment effect. We further recognised that three other factors, island biogeography, environmental conditions, and human activities, can also influence plant community composition. Two aspects of island biogeography, island size and isolation, affect colonization and dispersal which may limit the presence and abundance of recent invaders on small, isolated islands (Lomolino et al. 2006).



Environmental conditions also influence plant species composition in Garry oak meadows, which are generally structured along soil moisture gradients (MacDougall and Turkington 2004). Perennials, particularly non-native grasses, replace annuals, particularly native forbs, as soils increase in depth (MacDougall et al. 2006). Human activities can also facilitate invasion of plant species by direct introduction (Mack et al. 2000), and by creating favourable conditions for non-native species through disturbance and habitat alteration (Alpert 2006).

To explore relationships between herbivory and plant community composition, we developed and evaluated several multivariate models to estimate how plant groups and focal species responded to gradients of island size, meadow isolation, soil depth, human population density, and the duration of European settlement. We calculated species-specific forage selectivity indices to ask if particular plant species were browsed more or less often than expected by their availability. If herbivory by deer facilitates non-native species or groups in the oak meadows we studied, we predicted that 1) non-native annual grasses would increase with herbivory and 2) native perennial forbs would decline with herbivory. We further predicted that deer would avoid non-native annual grasses, but select native perennial forbs.

## METHODS

### **Study Sites**

Coastal meadows in the Georgia Basin of western North America (Fig. 2.1) are one of several habitats considered as part of the Garry oak ecosystem (Fuchs 2001). These meadows typically occur as shallow soil openings with exposed bedrock interspersed with herbaceous vegetation. Garry oak meadows occur mainly in populated regions of southwestern British Columbia, Canada, and extend south to central California, USA. Our study islands occur in the

San Juan and Gulf Island archipelagos (Photo 2.1), at the border of the USA and Canada in western North America.

Land conversion has reduced the extent of Garry oak meadows by *c* 80% in Canada since 1800 (Lea 2006) and non-native grasses have replaced native species in many sites (MacDougall et al. 2004). Agricultural and silvicultural activities that increase food for native deer (Alverson et al. 1988), the local extirpation of carnivores (McCullough 1997) via poisoning (Wilson 1906) and hunting, and declines in deer hunting (Riley et al. 2003) have all contributed to high deer densities on some islands in the region. Deer density on Vancouver Island, British Columbia, which serves as a ‘mainland’ for the islands we studied, varies from 10-20/km<sup>2</sup> (Hatter and Janz 1994). Cowan (1945) estimated that densities exceeding 15/km<sup>2</sup> produced overgrazed conditions, and estimates on some islands substantially exceed those values (T. Martin, N, Scheerder and P. Arcese, unpub. data).

### **Sampling Design**

We surveyed vegetation from May to June, 2003-06, in coastal meadows identified via reconnaissance and digital ecosystem maps (Ward et al. 1998). We assigned islands as our sampling unit except on two large islands where meadows separated by > 20 km were treated separately, for a total of 40 island sites (Appendix A). Survey plots were each 1-m<sup>2</sup> and were selected randomly after identifying candidate plots meeting the following criteria: < 5% exposed rock, < 10% slope, no canopy closure, > 10 m to an adjacent plot, and < 200 m to the high tide line. We identified all plant species and estimated their cover in each plot (Photo 2.2) by using a 1-m<sup>2</sup> quadrat divided into one hundred 10 cm x 10 cm cells and estimating the area covered by each species rooted in the plot to the nearest ½ cell. Sampling effort was approximately one plot/200 m<sup>2</sup> of meadow and all islands had a minimum of three plots. Plots were marked with

metal spikes for subsequent visits to confirm the identification of late-maturing grasses.

Seasonal effects on composition were minimized by surveying plots from south to north within the study area. Analyses of spring (May to mid-June) and summer (mid-June to July) surveys, conducted to control for varied plant phenology yielded similar results, thus, seasonal data were pooled and the mean values for plots on each island used as a response variable.

We recorded evidence of browsing by deer on each plant species to estimate selectivity. Plants were classed as ‘browsed’ if we observed straight or diagonal excisions of leaf or stem, as opposed to small, rounded excisions typical of insects or gastropods. Only islands with deer present were included in estimates of forage selectivity.

### **Response Variables**

Seven plant groups and 15 common focal species comprised the response variables. Plant groups were defined by three general features: ‘geographic origin’ (native or non-native), ‘life history strategy’ (annual or perennial), and ‘plant type’ (forb or ‘grass,’ including sedges and rushes). Shrubs and ferns were not evaluated due to low abundance. Native annual grasses were absent from our plots and rarely occur in meadows along the west coast of North America (MacDougall et al. 2006, Cushman and Johnson 2007). To minimize bias due to rarity or specialized habitat requirements, our focal species analyses only included species occurring in > 20% of all plots which ensured that species were found on at least three different islands.

### **Explanatory Variables**

We employed six explanatory variables in our analyses: island size, herbivore density, meadow isolation, soil depth, and two measures of human influence. ‘Island size’ was estimated from 1: 50,000 digital maps based on orthophotos taken during summer low tide. ‘Neighbouring land area’ is an inverse measure of meadow isolation, estimated by taking Universal Transverse

Mercator (UTM) coordinates at the centre of each plot (Garmin eTrex;  $\pm 5\text{-}15$  m precision), and then estimating via GIS the terrestrial area within a 500 m radius of the plot centre. ‘Herbivore density’ was estimated as the number of pellet (feces) groups per meadow area ( $\#/m^2$ ). The size of pellet groups can be variable depending on season and diet quality (McCullough 1982), here  $>10$  pellets in close proximity to each other comprised one group. On islands  $< 6$  ha in size, we surveyed entire islands by walking parallel transects in search of pellets. On larger islands transects only included meadows. Meadows were free of tree canopy and typically had well defined edges where they abutted forest or ocean. Meadow area was estimated by measuring the length and width of the meadow and estimating area ( $m^2$ ) based on meadow shape. ‘Soil depth’ was estimated as the mean of four measurements taken at the edges of each plot by driving a 90 cm steel rod into the ground until reaching bedrock. ‘Human population density’ was estimated as the number of residents recorded in Canadian (2001) and United States (2000) censuses divided by island size. Estimates for private islands were obtained by interview. ‘Duration of European settlement’ was estimated based on historical records and interviews on each island.

### **Data Analyses**

The effect of herbivory on plant communities was estimated in two stages. First, to determine whether island size, herbivory, neighbouring land area, soil depth, and humans was correlated with plant groups and focal species, we used multimodel inference to develop a set of best approximating models from a set of candidates based on the literature and our prior experience with the system (*cf* Burnham and Anderson 2002). Second, to test if deer preferentially selected particular plant groups, we calculated forage selectivity indices for species occurring in  $> 20\%$  of plots. All analyses were conducted using SAS 9.1 (SAS Institute 2003, Cary, NC).

Herbivory and Plant Group/Species Cover: We used multimodel inference to assess which of our candidate variables was sufficiently influential to include in potential explanatory models. This approach is particularly useful in observational studies where several potentially related variables are predicted to be correlated with patterns of interest (Whittingham et al. 2006). We then attempted to identify the best approximating model or set of models given our data (Burnham and Anderson 2002). To do so, we calculated likelihood estimates from general and generalized linear models to input into Akaike's Information Criterion ( $AIC_c$ ) corrected for small sample sizes. Relative likelihoods, used to identify models best approximating the data, were based on Akaike weights for models with  $AIC_c$  values ( $\Delta_i$ ) that differed by  $< 2$ . Because information theory-AIC algorithms can result in over-fitting (Guthery et al. 2005), all plant groups and focal species lacking bi-variate relationships with any of the explanatory variables were excluded from our model selection procedure.

Model fit and the distribution of residuals was assessed by running full models (all six explanatory variables) using Proc REG (SAS 9.1). Assumptions of normality were tested with the Shapiro-Wilk test ( $W$ ; for samples  $< 50$ ) and homoscedasticity was assessed visually. All explanatory variables were transformed by  $\log_e(x+1)$  except soil depth. Models that failed to meet assumptions of ordinary least squares were subsequently fit to a negative binomial distribution to accommodate overdispersion in residuals. Systematic site selection minimized collinearity of island size and isolation, human influences and herbivore density. Collinearity diagnostics (SAS 9.1) estimated condition indices in full models and variance inflation factors (VIF) for individual variables. Although no firm thresholds exist for collinearity, our values were less than those recommended as upper limits by rules of thumb (e.g., maximum condition index = 4.33; maximum VIF = 3.9).

Plant Selectivity by Deer: To test deer foraging preferences, we calculated forage selectivity indices for all plant species found on islands with herbivores. The forage selectivity indices ( $f_i$ ) were based on the proportion of individuals of each species browsed ( $o_i$ ) given the proportion of plots in which they occurred ( $\mu_i$ ) relative to the total number of occurrences of all species in all plots (Manly et al. 2002):

$$f_i = o_i / \mu_i \quad \text{eqn 1}$$

Indices greater than 1 indicate selection while indices below 1 indicate avoidance. Species were then categorized into their plant groups and we used Fisher's Exact to test whether deer favoured particular plant groups.

## RESULTS

We identified 138 species in 340 plots, 59.4% of which were natives. Native perennial forbs comprised the richest plant group (23.9% or 33 spp), followed by native and non-native annual forbs (16.7% (23) and 15.9% (22) spp, respectively). All other groups contributed 10% or fewer of species identified (Fig. 2.2A). Richness was unrelated to cover averaged over islands because non-native annual grasses often dominated plots, but were represented by only 11 species compared to the next most abundant plant group, native perennial forbs, which were represented by 33 species (Fig. 2.2A). Patterns of cover (Fig. 2.2B), however, do not appear to be related to herbivore density (Fig. 2.3A and B).

### **Herbivory and Plant Group Cover**

The cover of native annual and perennial forbs declined as herbivore density increased (Fig. 2.3A), whereas the cover of non-native annual grasses and perennial forbs increased (Fig. 2.3B). However, cover was rarely well-described by a single best approximating model (Appendix B). Thus, to illustrate patterns across all plant groups, we highlight sets of variables

appearing in our best approximating models and the strength of their relationships (Table 2.1a), and describe those relationships generally below.

The cover of native annual and perennial forbs was greatest on small, isolated islands with few or no herbivores and a brief duration of European settlement (Table 2.1a). In contrast, the cover of non-native perennial forbs declined with these same four factors whereas none of the variables predicted non-native annual forbs. Cover of non-native annual and perennial grasses were related to different suites of variables: non-native annual grasses were abundant on islands with high herbivore densities and shallow soils; whereas non-native perennial grasses were more abundant on islands with high human population densities and longer durations of European settlement. None of the variables explained cover of native perennial grasses.

### **Herbivory and Focal Species Cover**

We observed 30 plant species in > 20% of the plots and found that the cover of 15 of these were related to one or more of explanatory variables (Table 2.1b). Three native species (*Achillea millefolium*, *Camassia leichtlinii* and *Trifolium willdenowii*) declined in cover with increasing herbivore density (Fig. 2.3C) whereas three non-native species increased with herbivore density (*Bromus hordeaceus*, *Hypochaeris radicata*, and *Trifolium dubium*; Fig. 2.3D). Similarly, cover of non-native annual and perennial grasses were best predicted by contrasting models (Table 2.1b). The non-native annual grass, *Bromus hordeaceus*, was the most widespread plant in the community. This species was most abundant on large, non-isolated islands with abundant herbivores but unaffected by human density or duration of European settlement. In contrast *Poa pratensis*, a non-native perennial grass, was abundant on islands with high human density and long durations of settlement. However, cover of *P. pratensis* was unrelated to herbivore density.

Half of the 30 focal species showed no relationship to our explanatory variables. Several pairs of these species were of the same genera. Pairs were considered to be similar in morphology and ecology and so were pooled to test if their combined covers were related to our variables of interest; *Aira* (*A. caryophylla* and *A. praecox*), *Bromus* (*B. diandrus* and *B. sterilis*), *Vicia* (*V. hirsuta* and *V. sativa*), *Vulpia* (*V. bromoides* and *V. myuros*). Of these, only *Aira* displayed clear relationships, being more abundant on islands with higher herbivore density and shallower soils (Table 2.1b).

### **Plant Selectivity by Deer**

Deer chose species non-randomly with respect to cover in the community ( $p=0.006$ ) by selecting native perennial forbs and non-native perennial grasses. This result is interesting given that cover of non-native perennial grasses and herbivore density was unrelated suggesting that non-native perennial grasses are tolerant of browsing. Deer avoided non-native annual grasses and forbs (Fig. 2.4). On islands with herbivores, native annual forbs occurred in less than 20% of the plots, and were represented by only 1 species (of 23 identified) in our analyses of selectivity. Of the next five most common native annual forbs, four had forage indices  $>1$  indicating preferential selection by deer (Appendix C). Individually, these five species occurred in 9% to 17% of the plots.

### **DISCUSSION**

Theories explaining the successful invasion of non-native plant species have historically focused on traits of the invader that confer competitive advantages over native species (Rejmanek and Richardson 1996) or characteristics of the invaded community such as the ability of diversity to repel or minimize the abundance of invaders (Levine et al. 2004). In this natural landscape experiment, our findings suggest that a native herbivore, black-tailed deer, facilitates



the invasion of an endangered ecosystem by non-native grasses. Present densities of deer exceed historical levels (MacDougall, in review) which gives a competitive advantage to less palatable plant species such as non-native annual grasses. Given that native analogues to non-native annual grasses are absent or rare, our results are consistent with the Limiting Similarity Theory of invasibility in which non-native species that are ecologically, functionally, and/or phylogenetically distinct are more likely to invade communities (Abrams 1983). This concept dates back to Darwin's naturalization hypothesis (Daehler 2001) and has been supported by recent phylogenetic analyses (Strauss et al. 2006). What limits most earlier studies is a confirmation of mechanism – being functionally unique was determined to influence successful invasion but the causes were not identified (Emery 2007, but see Fargione et al. 2003). Here, we show that persistent high herbivory is one way this can occur.

Native plant species may be ill prepared for increased herbivore densities or may lack adaptations to novel herbivores relative to non-native grasses (Mack and Thompson 1982, Westoby 1989, McIntyre et al. 2003). In contrast, non-native grasses exhibited avoidance and tolerance strategies to herbivory. Grasses, which have co-evolutionary histories dating back to grazing dinosaurs (Prasad et al. 2005), often produce silica or secondary compounds to avoid herbivory (Vicari and Bazely 1993). Some perennial grasses can also tolerate intense herbivory by tillering, high relative growth rates, ability to shunt carbon stores from roots to shoots after damage, and increased net photosynthetic rate after damage (Strauss and Agrawal 1999). Most introduced perennial grass species that are widespread invaders in North America were intentionally introduced to improve grazing opportunities. These species therefore were selected non-randomly from Old World plant communities to be productive under livestock grazing (Williams and Baruch 2000) and further altered through breeding and genetic transformation for

productivity and fecundity (Casler and Vogel 1999, Wang and Ge 2006). Non-native annual grasses appear to avoid herbivory as they were rarely browsed, presumably because of low nutritional content or avoidance mechanisms such as spiked seeds (e.g., *Bromus diandrus* and *Cynosurus echinatus*). Conversely, non-native perennial grasses were browsed by deer but appear to tolerate defoliation as herbivore density did not affect their cover. Land conversion, limited or no hunting, and predator eradication on some of the islands favour abundant deer and increased herbivore pressure would favour species possessing strategies to avoid or tolerate those conditions. The distinct strategies of non-native annual and perennial grasses to avoid or tolerate herbivory have consequences for restoration. Although protection from herbivory increased reproduction in native forbs (Gonzales and Arcese, in prep), the biomass of non-native perennial grasses also increased (Gonzales and Clements, in review). This suggests that reductions of deer alone may not result in increased abundances of dispersal limited native forbs; instead, non-native perennial grasses may replace non-native annual grasses.

Herbivory had negative effects on the native plant community in our shallow soil, Garry oak meadows, however, herbivore impacts can vary according to site quality. According to the exploitation ecosystem hypothesis (Oksanen et al. 1981, Oksanen and Oksanen 2000), strong effects of herbivory should be prevalent in unproductive environments. In contrast, herbivores should exert much weaker control of primary production in productive systems. This may be because competition becomes a more influential mechanism in more productive sites and the effects of herbivory depend on the herbivore avoidance/tolerance strategies and competitive abilities of plants in the community. For example, *Schizachyrium scoparium* is replaced by other grasses with the same herbivore tolerance abilities when herbivore pressure is high. However, *S. scoparium* maintains dominance under herbivory when resources are available and consistent

(Anderson and Briske 1995). Given that annual grasses in Garry oak meadows are replaced by perennial grasses as soils get deeper (MacDougall et al. 2006), the effects of herbivory along with the dominance of non-native grasses may vary along productivity gradients (Huston 2004). Therefore, herbivores may be beneficial in reducing non-native perennial grass biomass in deep soil Garry oak sites. Given that herbivores are likely to also reduce native forbs in deep soil sites, manual removal of non-native perennial grasses coupled with fencing is likely to increase native forb abundance.

Black-tailed deer are native to this community, and thus it is reasonable to ask how native forbs have persisted, we imagine the following scenario. Historically, deer populations may have fluctuated locally through shifting human hunting pressure and the movement of wolves and cougars between the islands. Dispersal limitation, ubiquitous to most forbs in this system (MacDougall and Turkington 2006), interacted with island area and isolation and created considerable patch-by-patch variability in species composition (beta diversity). Nomadic deer had two positive effects on the community. Deer maintained species coexistence by limiting dominant species and facilitated species occurrences and abundance by acting as a vector of seed dispersal. Following carnivore removal, landscape change and non-native species introductions, meadows became browsed by deer at higher density. The intensity of herbivory on palatable native plants increased, providing favourable conditions through disturbance and selective browsing for some unpalatable non-native annual grasses and herbivore tolerant non-native perennial grasses.

There are disadvantages to natural experiments, in particular, the challenge of deducing causation, but there are several advantages for studies of herbivory. Experimental studies quantifying the effects of herbivores on plant communities typically create artificial settings

using exclosures with binary effects that do not mimic real herbivore gradients (Wisdom et al. 2006, but see Horsley et al. 2003). Experimental sites also tend to be located in plant communities that have already been affected by increased herbivory for an extended period of time and reducing herbivory may not reconstruct the historical plant community if palatable species have been extirpated or if other factors have influenced changes in the plant community (Valone et al. 2002, Holmgren 2002). The comparative absence of native annual forbs on islands with herbivores may provide a signal of this phenomenon that may not have been detected in an experiment on a site with a history of herbivory. Natural experiments can also increase the spatial extent and, therefore, broader applicability of a study. With increased spatial extent, we were able to incorporate tests of island size and isolation that influence dispersal and composition that are difficult to manipulate in experimental settings.

Our results illustrate relationships among the dominant native and non-native plant groups and herbivory. Island size and isolation and human activities were influential for non-native perennial forbs and grasses suggesting that these new arrivals are still dispersing into the archipelago via human dispersal and disturbance. Smaller, isolated islands are providing a refuge for native Garry oak meadow species for what is becoming a relictual community. In Australia (Burbidge et al. 1997) and New Zealand (Towns and Ballantine 1993), islands have been important refuges for conservation and restoration. Protection and management of these islands will be critical in maintaining seed sources for restoration as well as their value as relatively pristine examples of Garry oak meadows.

## CONCLUSIONS

Theories explaining the successful invasion of non-native plant species have historically focused on either the traits of the invader (Rejmanek and Richardson) 1996 or characteristics of

the invaded community (Levine et al. 2004). We described patterns among herbivore density, island biogeography, soil depth and human activities for four plant groups and 15 species plus 1 genera of the 30 species examined. Increasingly, studies of invasibility are becoming more comprehensive (Shea and Chesson 2002). They consider the characteristics of the invader and native competitors simultaneously (Fargione et al. 2003, Von Holle and Simberloff 2004, Emery 2007) as well as the role of the community on the invader, such as generalist herbivores (D'Antonio 1993, MacDougall and Wilson 2007). Here we demonstrate that a generalist herbivore, black-tailed deer, facilitates the abundance of a functionally and phylogenetically distinct non-native plant group through selective browsing.

Developing general principles to explain invasion success are further complicated by the variability within non-native species as a group. Globally, non-native species come from a variety of locations and would be expected to have different evolutionary histories although many successful invaders share traits that dispose them to succeed in disturbed environments (Alpert 2006). Native species share the same evolutionary history, but have evolved strategies for coexistence. These strategies, however, may be less effective under new disturbance regimes resulting from increased herbivore density that create opportunities for invasion of non-native species.

TABLES

**Table 0.1:** Correlations of plant groups with herbivory, human population density, soil depth, island size, neighbouring land area, and duration of European settlement. We calculated Pearson Product Moment Correlation Coefficients (P) for models that met ordinary least squares (OLS) assumptions and Spearman (R) correlations for those that did not between plant groups (a), focal native species (b), focal non-native species (c) and the six explanatory variables. Shaded boxes indicate variables kept in models using information theory model selection and illustrate patterns in variable selection for different plant groups and species. Grey shading indicates negative relationships and black shading indicates positive relationships between the response and explanatory variables.

Explanatory Variables	a)						b)						c)					
	Native Annual Forbs			Non-native Annual Forbs			Native Perennial Forbs			Non-Native Perennial Forbs			Native Perennial Grasses			Non-native Annual Grasses		
	R	p		R	p		P	p		P	p		R	p		R	p	
Herbivory	-0.41	0.01		0.17	0.28		-0.57	0.00		0.31	0.05		0.00	0.99		0.34	0.03	
Human Population Density	-0.23	0.15		0.15	0.35		-0.12	0.46		0.18	0.28		0.17	0.30		-0.17	0.29	
Soil depth	-0.16	0.34		-0.14	0.39		0.05	0.77		-0.02	0.89		0.14	0.40		-0.34	0.03	
Island Size	-0.47	0.00		0.29	0.07		-0.62	<.0001		0.46	0.00		0.06	0.70		0.22	0.16	
Neighbouring Land Area	-0.36	0.02		0.18	0.26		-0.58	<.0001		0.45	0.00		0.02	0.89		0.15	0.37	
Duration of European Settlement	-0.34	0.03		0.27	0.09		-0.49	0.00		0.41	0.01		0.08	0.62		0.10	0.54	
																0.31	0.05	

b) Explanatory Variables	<i>Achillea millefolium</i>		<i>Camassia leichtlinii</i>		<i>Festuca rubra</i>		<i>Galium aparine</i>		<i>Sanicula crassicaulis</i>		<i>Trifolium willdenowii</i>	
	R	p	P	p	R	p	R	p	R	p	R	p
Herbivory	-0.32	0.04	-0.50	0.00	-0.09	0.57	-0.14	0.39	-0.23	0.16	-0.51	0.00
Human Population Density	-0.04	0.82	-0.20	0.23	0.01	0.97	-0.19	0.24	-0.12	0.47	-0.35	0.03
Soil depth	0.39	0.01	-0.01	0.93	0.32	0.04	-0.18	0.26	-0.03	0.85	-0.07	0.67
Island Size	-0.27	0.10	-0.60	<.0001	-0.13	0.41	-0.35	0.03	-0.28	0.09	-0.59	<.0001
Neighbouring Land Area	-0.16	0.32	-0.56	0.00	-0.01	0.94	-0.07	0.67	-0.46	0.00	-0.31	0.05
Duration of European Settlement	-0.10	0.54	-0.52	0.00	-0.06	0.71	-0.29	0.07	-0.28	0.08	-0.46	0.00

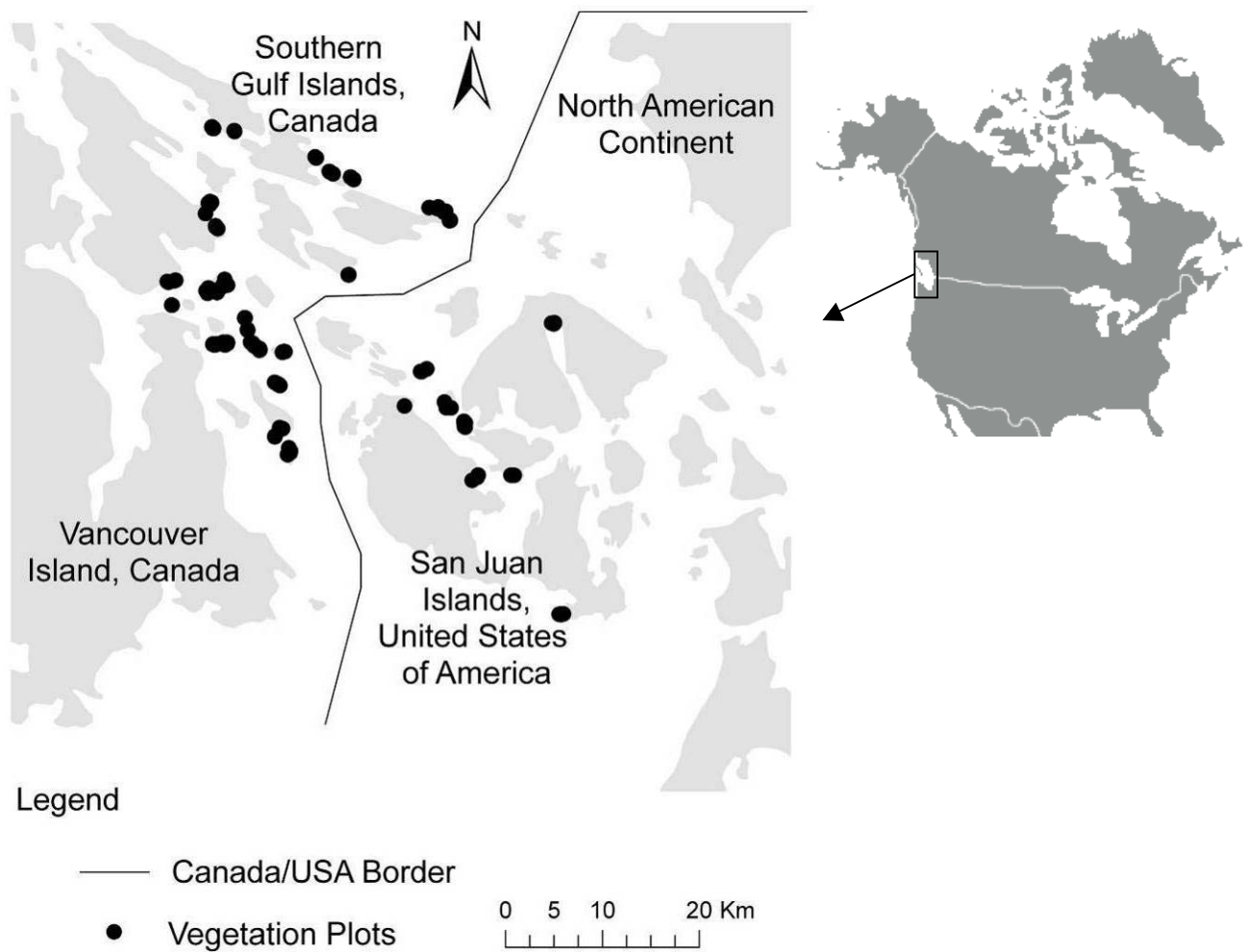
c)	<i>Bromus hordeaceus</i>		<i>Cerastium glomeratum</i>		<i>Cynosurus echinatus</i>		<i>Dactylis glomerata</i>		<i>Holcus lanatus</i>		<i>Hypochaeris radicata</i>		<i>Plantago lanceolata</i>	
	R	p	R	p	R	p	R	p	R	p	R	p	R	p
Explanatory Variables														
Herbivory	0.41	0.01	-0.19	0.23	0.08	0.63	0.24	0.14	-0.27	0.09	0.44	0.00	0.05	0.74
Human Population Density	0.34	0.03	-0.03	0.88	-0.16	0.31	0.3	0.06	0.05	0.76	0.41	0.01	0.21	0.19
Soil depth	0.05	0.77	-0.05	0.75	-0.45	0.00	0.04	0.8	0.32	0.05	-0.15	0.35	0.09	0.6
Island Size	0.44	0.00	-0.31	0.05	0.06	0.73	0.33	0.04	-0.13	0.41	0.64	<.0001	0.34	0.03
Neighbouring Land Area	0.15	0.36	-0.32	0.05	-0.06	0.73	0.1	0.55	-0.02	0.92	0.39	0.01	0.03	0.85
Duration of European Settlement	0.53	0.00	-0.17	0.29	-0.07	0.68	0.25	0.13	-0.1	0.56	0.5	0.00	0.29	0.07

continued

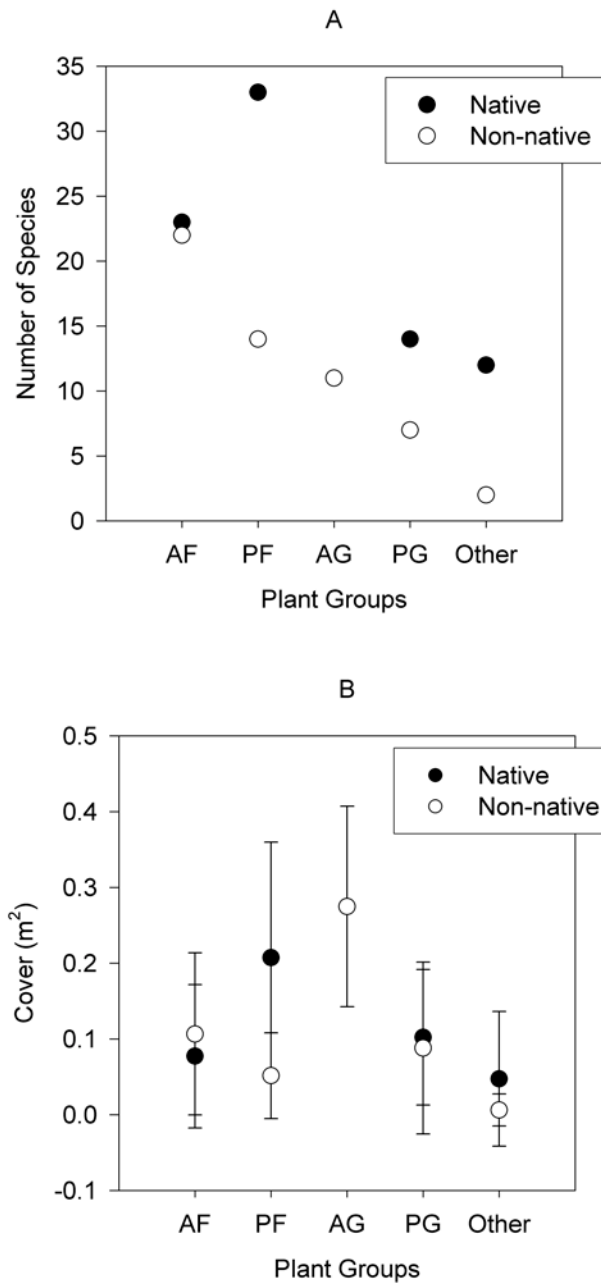
	<i>Poa pratensis</i>		<i>Trifolium dubium</i>		<i>Aira spp.</i>	
	P	p	R	p	P	p
Explanatory Variables						
Herbivory	0.13	0.43	0.41	0.01	0.59	<0.0001
Human Population Density	0.79	<.0001	0.39	0.01	-0.09	0.58
Soil depth	0.3	0.06	-0.01	0.97	-0.35	0.02
Island Size	0.38	0.02	0.58	<.0001	0.18	0.27
Neighbouring Land Area	0.28	0.08	0.36	0.02	-0.02	0.9
Duration of European Settlement	0.4	0.01	0.53	0.00	0.2	0.21



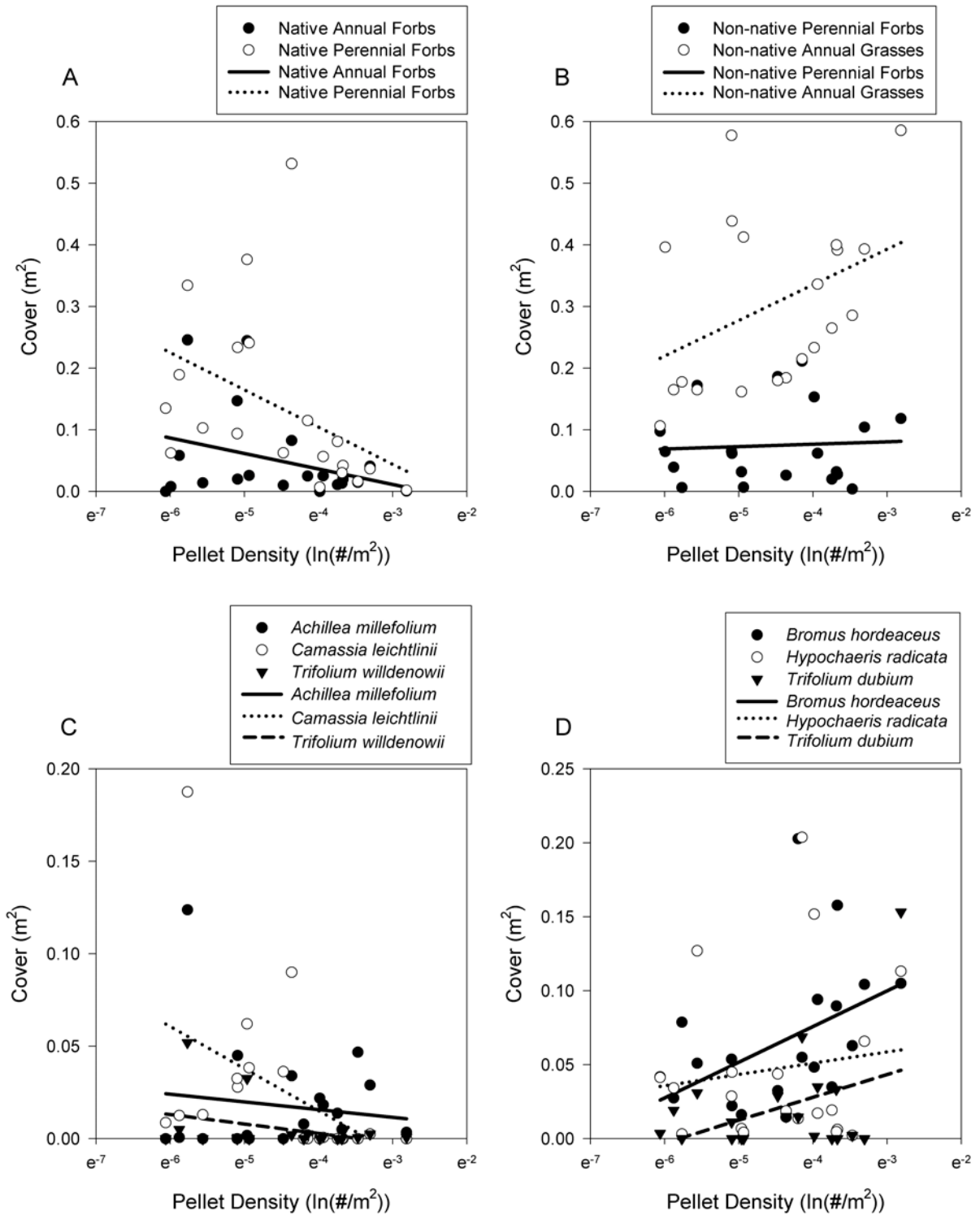
## FIGURES



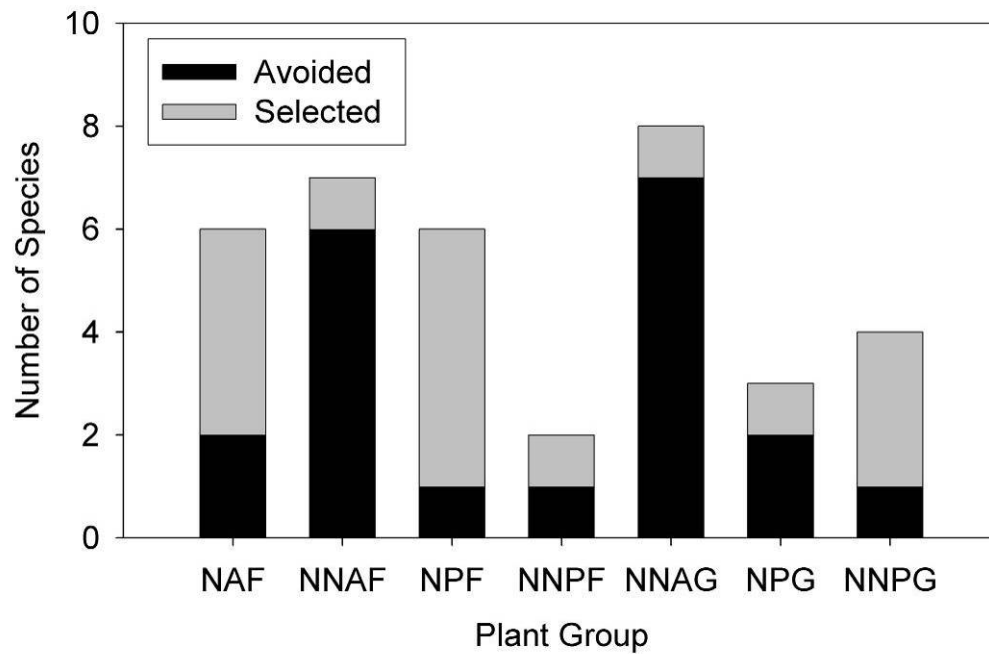
**Figure 0.1:** Vegetation plots (340) on 38 islands in the Georgia Basin. At this scale, dots representing the plots overlap.



**Figure 0.2:** Number of native and non-native species in each plant group (A) and mean cover in coastal meadows in the Georgia Basin archipelago (n=40) (B). Plant groups are categorized by origin Native (N) or Non-native (NN), life history Annual (A) or Perennial (P), and plant form Forb (F) or Grass (G). Grass includes grasses, sedges and rushes. Other (O) includes ferns and woody species that were measured by not analysed.



**Figure 0.3:** Relationships between plant groups (A and B) and focal species (C and D) with deer pellet density. Pearson (P) and Spearman (R) values are shown in Table 2.1.



**Figure 0.4:** Forage selectivity indices by plant group. The number of species in each plant group found in > 20%\* of the plots that were either avoided or selected for forage by deer. Selection was biased (Fisher's Exact,  $p=0.006$ ). \*Native annual forbs were uncommon on islands with herbivores and therefore we included the five most common native annual forbs, which occurred in 9-17% of the plots, to estimate selectivity for that plant group. Plant groups are categorized by place of origin, Native (N) or Non-native (NN), life history Annual (A) or Perennial (P), and plant form, Forb (F) or Grass (G) which includes grasses, sedges and rushes.



**Photo 0.1:** Pellow Islet, one of the smaller islands belonging to the Gulf Island National Park Reserve.



**Photo 0.2:** Vegetation survey on an unnamed islet near D'Arcy Island (visible in the background); both islands are part of the Gulf Island National Park Reserve. The dominant plant cover is *Camassia leichtlinii*.



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## LITERATURE CITED

- Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* **14**:359-376.
- Allombert, S., A. J. Gaston, and J. L. Martin. 2005a. A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation* **126**(1):1-13.
- Allombert, S., S. Stockton, and J. L. Martin. 2005b. A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology* **19**(6):1917-1929.
- Alpert, P. 2006. The advantages and disadvantages of being introduced. *Biological Invasions* **8**(7):1523-1534.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer - edge effects in northern Wisconsin. *Conservation Biology* **2**(4):348-358.
- Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium-grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* **4**(1):104-109.
- Anderson, V. J., and D. D. Briske. 1995. Herbivore-induced species replacement in grasslands - is it driven by herbivory tolerance or avoidance. *Ecological Applications* **5**(4):1014-1024.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management* **62**(4):1165-1183.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* **11**(5):1261-1275.
- Borrvall, C., and B. Ebenman. 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. *Ecology Letters* **9**(4):435-442.
- Burbidge, A. A., M. R. Williams, and I. Abbott. 1997. Mammals of Australian islands: Factors influencing species richness. *Journal of Biogeography* **24**(6):703-715.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.
- Casler, M. D., and K. P. Vogel. 1999. Accomplishments and impact from breeding for increased forage nutritional value. *Crop Science* **39**(1):12-20.



- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* **7**(8):721-733.
- Côté, S. D. 2005. Extirpation of a large black bear population by introduced white-tailed deer. *Conservation Biology* **19**(5):1668-1671.
- Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* **35**:113-147.
- Cowan, I. M. 1945. The ecological relationships of the food of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the coast forest region of Southern Vancouver Island, British Columbia. *Ecological Monographs* **15**(2):109-139.
- Cuevas, J. G., and C. Le Quesne. 2006. Low vegetation recovery after short-term cattle exclusion on Robinson Crusoe Island. *Plant Ecology* **183**(1):105-124.
- Cullen, B. R., D. F. Chapman, and P. E. Quigley. 2006. Comparative defoliation tolerance of temperate perennial grasses. *Grass and Forage Science* **61**(4):405-412.
- Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. *Bioscience* **50**(7):593-601.
- Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. *American Naturalist* **158**(3):324-330.
- D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant-communities by the alien succulent *Carpobrotus-edulis*. *Ecology* **74**(1):83-95.
- Davis, M. A. 2003. Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience* **53**(5):481-489.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* **88**(3):528-534.
- Diaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Milchunas, C. Skarpe, G. Rusch, M. Sternberg, I. Noy-Meir, J. Landsberg, W. Zhang, H. Clark, and B. D. Campbell. 2007. Plant trait responses to grazing - a global synthesis. *Global Change Biology* **13**(2):313-341.
- Emery, S. M. 2007. Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology* **95**(5):1027-1035.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* **11**(5):1301-1310.

- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* **100**(15):8916-8920.
- Ferdinands, K., K. Beggs, and P. Whitehead. 2005. Biodiversity and invasive grass species: Multiple-use or monoculture? *Wildlife Research* **32**(5):447-457.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629-644.
- Fuchs, M. A. 2001. Towards a Recovery Strategy for Garry Oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review. Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region. GBEI/EC-00-030.
- Fuller, R. J., and R. M. A. Gill. 2001. Ecological impacts of increasing numbers of deer in British woodland. *Forestry* **74**(3):193-199.
- Gabbard, B. L., and N. L. Fowler. 2007. Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions* **9**(2):149-160.
- Gauthier, G., and J. Bedard. 1991. Experimental tests of the palatability of forage plants in greater snow geese. *Journal of Applied Ecology* **28**(2):491-500.
- Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: The positive correlation between native and exotic plant diversity. *Ecology* **86**(7):1848-1855.
- Gonzales, E. K., and D. R. Clements. in review. Community response to two types of disturbance: Lessons for Garry oak ecosystem restoration.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**(9):470-474.
- Guthery, F. S., L. A. Brennan, M. J. Peterson, and J. J. Lusk. 2005. Information theory in wildlife science: Critique and viewpoint. *Journal of Wildlife Management* **69**(2):457-465.
- Hamback, P. A., L. Oksanen, P. Ekerholm, A. Lindgren, T. Oksanen, and M. Schneider. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos* **106**(1):85-92.
- Hamilton, J. G., C. Holzapel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**(4):518-526.

- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (*Cervidae*). *Oikos* **79**(2):209-218.
- Hatter, I. W., and D. W. Janz. 1994. Apparent demographic-changes in black-tailed deer associated with wolf control on northern Vancouver-Island. *Canadian Journal of Zoology* **72**(5):878-884.
- Holmgren, M. 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biological Invasions* **4**:25-33.
- Horsley, S. B., S. L. Stout, and O. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* **13**:98-1189.
- Howe, H. F., B. Zorn -Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* **87**(12):3007-3113.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, New York.
- Huston, M. A. 2004. Management strategies for plant invasions: Manipulating productivity, disturbance, and competition. *Diversity and Distributions* **10**(3):167-178.
- Johnson, B. E., and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conservation Biology* **21**(2):515-526.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**(4):164-170.
- Kirby, K. J. 2001. The impact of deer on the ground flora of British broadleaved woodland. *Forestry* **74**(3):219-229.
- Lambrinos, J. G. 2000. The impact of the invasive alien grass *Cortaderia jubata* (lemoine) stapf on an endangered Mediterranean-type shrubland in California. *Diversity and Distributions* **6**(5):217-231.
- Lea, T. 2006. Historical Garry oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. *Davidsonia* **17**(2):34-50.
- Leslie, D. M., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. *Journal of Wildlife Management* **48**(3):762-775.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**(10):975-989.

- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* **87**(1):15-26.
- Litton, C. M., D. R. Sandquist, and S. Cordell. 2006. Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *Forest Ecology and Management* **231**(1-3):105-113.
- Lomolino, M. V., D. F. Sax, B. R. Riddle, and J. H. Brown. 2006. The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography* **33**(9):1503-1510.
- MacDougall, A. S., B. R. Beckwith, and C. Y. Maslovat. 2004. Defining conservation strategies with historical perspectives: A case study from a degraded oak grassland ecosystem. *Conservation Biology* **18**(2):455-465.
- MacDougall, A. S., J. Boucher, R. Turkington, and G. E. Bradfield. 2006. Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science* **17**(1):47-56.
- MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology* **92**(3):422-434.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**(1):42-55.
- MacDougall, A. S., and R. Turkington. 2006. Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology* **87**(7):1831-1843.
- MacDougall, A. S., and S. D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* **88**(5):1105-1111.
- Mack, M. C., C. M. D'Antonio, and R. E. Ley. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C-4 grasses in Hawaii. *Ecological Applications* **11**(5):1323-1335.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**(3):689-710.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hoofed mammals. *American Naturalist* **119**(6):757-773.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals. 2nd edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Martin, J. L., and C. Baltzinger. 2002. Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal of Forest Research* **32**(7):1254-1264.
- Mayer, P. M., S. J. Tunnell, D. M. Engle, E. E. Jorgensen, and P. Nunn. 2005. Invasive grass alters litter decomposition by influencing macrodetritivores. *Ecosystems* **8**(2):200-209.
- McCullough, D. R. 1997. Irruptive behavior in ungulates. Pages 69-98 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editor. *The Science of Overabundance, Deer Ecology and population management*. Smithsonian Institution Press, Washington D.C., USA.
- McCullough, D. R. 1982. White-tailed deer pellet-group weights. *Journal of Wildlife Management* **46**(3):829-832.
- McIntyre, S., K. M. Heard, and T. G. Martin. 2003. The relative importance of cattle grazing in subtropical grasslands: Does it reduce or enhance plant biodiversity? *Journal of Applied Ecology* **40**(3):445-457.
- McIntyre, S., S. Lavorel, J. Landsberg, and T. D. A. Forbes. 1999. Disturbance response in vegetation towards a global perspective on functional traits. *Journal of Vegetation Science* **10**(5):621-630.
- McNaughton, S. J., and J. L. Tarrant. 1983. Grass leaf silicification - natural-selection for an inducible defense against herbivores. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences* **80**(3):790-791.
- McShea, W. J., S. L. Monfort, S. Hakim, J. Kirkpatrick, I. Liu, J. W. Turner, L. Chassy, and L. Munson. 1997. The effect of immunocontraception on the behavior and reproduction of white-tailed deer. *Journal of Wildlife Management* **61**(2):560-569.
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin, and D. P. Vazquez. 2006. Biotic interactions and plant invasions. *Ecology Letters* **9**(6):726-740.
- Myers, J. H., and D. Bazely. 2003. *Ecology and control of introduced plants*. Cambridge University Press, Cambridge, United Kingdom.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**(2):240-261.
- Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* **155**(6):703-723.

- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**(1):53-65.
- Prasad, V., C. A. E. Stromberg, H. Alimohammadian, and A. Sahni. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. *Science* **310**(5751):1177-1180.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**(8):2581-2592.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**(6):1655-1661.
- Riley, S. J., D. J. Decker, J. W. Enck, P. D. Curtis, T. B. Lauber, and T. L. Brown. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. *Ecoscience* **10**(4):455-461.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* **74**(3):201-208.
- Rooney, T. P., and K. Gross. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecology* **168**(2):267-277.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**(1-2):165-176.
- Rooney, T. P., S. M. Wiegmann, D. A. Rogers, and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* **18**(3):787-798.
- Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: Alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* **9**(3):169-176.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**(4):170-176.
- Stockton, S. A., S. Allombert, A. J. Gaston, and J. L. Martin. 2005. A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biological Conservation* **126**(1):118-128.
- Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecology Letters* **9**:357-374.

- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**(5548):1923-1926.
- Towns, D. R., and W. J. Ballantine. 1993. Conservation and restoration of New-Zealand island ecosystems. *Trends in Ecology & Evolution* **8**(12):452-457.
- Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution* **21**(4):208-216.
- Valone, T. J., S. E. Nordell, and S. K. M. Ernest. 2002. Effects of fire and grazing on an arid grassland ecosystem. *Southwestern Naturalist* **47**(4):557-565.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. Dispersal of trillium seeds by deer: Implications for long-distance migration of forest herbs. *Ecology* **84**(4):1067-1072.
- Vicari, M., and D. R. Bazely. 1993. Do grasses fight back - the case for antiherbivore defenses. *Trends in Ecology & Evolution* **8**(4):137-141.
- Von Holle, B., and D. Simberloff. 2004. Testing fox's assembly rule: Does plant invasion depend on recipient community structure? *Oikos* **105**(3):551-563.
- Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: A keystone herbivore. *Wildlife Society Bulletin* **25**(2):217-226.
- Wang, Z. Y., and Y. X. Ge. 2006. Invited review: Recent advances in genetic transformation of forage and turf grasses. *In Vitro Cellular & Developmental Biology-Plant* **42**(1):1-18.
- Ward, P., G. Radcliffe, J. Kirkby, J. Illingworth, and C. Cadrin. 1998. Sensitive Ecosystems Inventory: East Vancouver Island and Gulf Islands, 1993-1997. Volume 1: Methodology, Ecological Descriptions and Results. Technical Report Series No. 320 edition. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.
- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* **16**(5):585-595.
- Weiher, E. 2003. Species richness along multiple gradients: Testing a general multivariate model in oak savannas. *Oikos* **101**(2):311-316.
- Weiher, E., S. Forbes, T. Schauwecker, and J. B. Grace. 2004. Multivariate control of plant species richness and community biomass in Blackland prairie. *Oikos* **106**(1):151-157.

- Westoby, M. 1989. Selective forces exerted by vertebrate herbivores on plants. *Trends in Ecology & Evolution* **4**(4):115-117.
- White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: A neglected concept in invasion biology. *Diversity and Distributions* **12**(4):443-455.
- Whittingham, M. J., P.A . Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* **75**(5):1182-1189.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperilled species in the United States. *Bioscience* **48**(8):607-615.
- Williams, D. G., and Z. Baruch. 2000. African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions* **2**:123-140.
- Wilson, E. F. 1906. From Barnsbury, England in 1868 to Barnsbury, Canada 1906. <http://www.saltspringarchives.com/wilson.pdf> edition.
- Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: Knowledge gaps and management needs. *Wildlife Society Bulletin* **34**(2):283-292.
- Woodroffe, R. 2000. Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation* **3**:165-173.



## **Chapter 3: Influences of herbivory and shading by introduced grasses on early and established life stages of native plants in an oak meadow\***

### INTRODUCTION

The widespread abundance of non-native species has been taken as evidence for intratrophic competitive displacement of native species (Wilcove et al., 1998) but this mechanism lacks empirical support (Sax et al., 2002; Davis, 2003; Houlahan and Findlay, 2004). In contrast, intertrophic effects of predators (e.g., Rodda and Fritts, 1992; Nogales et al., 2006) and pathogens (Tompkins et al., 2003) on native animals have resulted in numerous extinctions. For example, the replacement of native Eurasian red squirrels (*Sciurus vulgaris*) by non-native eastern grey squirrels (*Sciurus carolinensis*) has been facilitated by viral transfers to which non-native squirrels are asymptomatic (Tompkins et al., 2003). The increasing dominance of non-native plants over native plants has largely been studied in the context of competitive replacement. However, ungulate herbivory can profoundly influence plant composition (Martin and Baltzinger 2002, Rooney and Waller 2003) and the role of abundant ungulates as a “third party” that causes declines of native plants in invaded communities is unknown (White et al. 2006, Jones and Callaway 2007).

Declines in native species are often the product of multiple related factors; therefore, estimating the relative contributions of herbivory and competition is complicated by their co-occurrence. Plant introductions, for example, often occur with human-related

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\* A version of this chapter will be submitted for publication. Gonzales, E. K. and Arcese, P. Influences of herbivory and shading by introduced grasses on early and established life stages of native plants in an oak meadow.

changes to landscapes including introductions of domestic livestock, or increases in native herbivore densities as a consequence of habitat modification and carnivore eradication (Côté et al. 2004). To determine whether inter- or intratrophic interactions explain native species declines in an endangered ecosystem, we contrasted herbivory and competition for light on the performance of native plant species in an invaded oak meadow with abundant ungulates.

Here, we tested the effect of herbivory and competition for light by employing two, 2x2 factorial experiments - one with transplanted native plants and one with added native seeds. Treatments tested the effects of herbivory via ungulate access or exclusion crossed with ‘neighbour removal’, cutting to remove extant vegetation and litter or an unmanipulated control. We predicted that herbivores would reduce biomass and reproductive output in established plants added to experimental plots. In contrast, we expected that live vegetation and litter on control plots would reduce the germination of native seeds and survival of seedlings. If these predictions are supported, herbivory and competition both act to reduce native plant abundance in invaded Garry oak meadows by acting on different life stages of native plants.

## MATERIALS AND METHODS

Garry oak meadows are part of a diverse oak savanna complex stretching from central California to southwestern British Columbia. Approximately 80% of Garry oak meadows have been lost due to habitat destruction (Lea, 2006) prompting preservation and recovery efforts (Fuchs 2001). Most meadows, however, are dominated by non-native grasses (MacDougall et al. 2004) originating from farmed and urban areas. These grasses

produce live material and litter that inhibit native seed germination and survival (MacDougall 2005; MacDougall and Turkington 2005); whereas episodic biomass removal by cutting, weeding or burning increases native species cover (MacDougall and Turkington 2007). In addition to increasing abundances of non-native grasses, herbivore densities have also increased in the region. Factors that have led to overabundant deer elsewhere, including habitat fragmentation, agriculture and the eradication of grey wolves (*Canis lupus*) and other predators (Côté et al. 2004), have likely relaxed limits on population growth in native Columbian black-tailed deer (*Odocoileus hemionus columbianus*) (Photo 3.1). Domestic ungulates, including free-ranging sheep and goats, also add to overall herbivore pressure in some locations.

### **Study Sites**

Our experiments took place on two sites within the same oak meadow complex on Salt Spring Island (48°46'51" N, 123°27'23" W) in the Strait of Georgia, British Columbia (Fig. 3.1). The island's 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 limiting in Garry oak meadows (MacDougall and Turkington 2004) and 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 took place in the Andreas Vogt Nature Reserve (AVNR) in 0.4 ha of oak meadow that meets CNERA at its northwest corner. Both sites were visited by *c* 10 sheep and black-tailed deer were observed daily and browse lines on trees are evident. Estimates on predator-free

islands in the region suggest that deer densities reach 20 to >40 deer/km<sup>2</sup> where browse lines are apparent (T. Martin, N. Scheerder and P. Arcese, unpub. data).

### **Experimental Design**

**Plot selection.** Because meadows are often heterogeneous, we used small, 1 m x 1 m plots to maximize plot number (Bonham 1989). To reduce the influence of abiotic drivers on variation, we identified candidate plots as those meeting the following criteria: <1% exposed rock; <10% slope; <5% canopy closure; and >10 m to a neighbouring plot, and then selected or rejected by sequential coin toss and applied treatments randomly.

**Treatments.** Herbivory (H) treatment plots were left ‘open’ (+) or ‘fenced’ (-) (1.25 x 1.25 x 1.25-m aluminum frame, open at top, large celled net on sides to exclude ungulates but not light or small animals). Our ‘shading’ (S) treatment aimed to affect competition for light by removing (-) or leaving (+) litter and live biomass. Biomass was cut and removed twice annually during the senescent period of focal herbaceous species. Focal woody species were not cut. Plots with neighbours removed were also spaded to a depth and distance of 25 cm from plot edges to sever roots and tillers. Manipulation of below ground competition was not attempted because herbicides are prohibited in our study area and weeding may have caused soil disturbances that can increase invasion.

**Extant Conditions.** The extant plant community was sampled by clipping, drying and weighing species from 14 control 1 m x 1 m plots. Because dry biomass may underestimate the contribution of forbs to the community due to their high water content (MacDougall 2005), we also identified and counted stems in 16 control 0.5 m x 1 m plots. We also took four readings of soil depth, soil moisture, and ground light levels at each plot

on AVNR. Soil depth was taken with a steel rod hammered to bedrock. Ground light level readings (LI-COR® multi-point bar quantum sensor, LI-COR®, Lincoln, Nebraska, USA) were taken three times in summer months at 10 am and 1 pm on clear, sunny days. Soil moisture readings were taken monthly at 12 cm depth (Hydrosense® TDR meter, Campbell Scientific, Logan, Utah, USA) for a year. Ground light and soil moisture data were not collected on CNERA because the extant plant community was removed from the experimental plots in 2005 (Gonzales and Clements, in review).

### **Transplant Experiment**

Transplanted individuals (Appendix D) were from local stock and kept in a common growth media at seasonal light and temperature regimes in a glasshouse for four months until planted in the 56 experimental plots. In February 2003, we planted four common camas lily (*Camassia quamash*) bulbs, four 5x5 cm plugs of the annual, seablush (*Plectritis congesta*), (mean=60 stems/plot), one Arbutus (*Arbutus menziesii*) sapling, two Garry oak (*Quercus garryana*) saplings, and two Garry oak acorns in each plot, spaced  $\geq 15$ -20 cm from each other and the plot edges. We counted the number of individual seablush and leaves of each common camas annually in April for three years. Oak and arbutus were assessed in June but survived poorly overall. Thus we used the number of leaves on oak and arbutus saplings and the number of acorns that emerged to estimate success in these species. In 2004 and 2006, we counted the number of flowers produced by extant lilies (Appendix D) which are highly palatable (Krausman et al. 1997) and used elsewhere as an index of herbivory by deer (Anderson 1994, Balgooyen and Waller 1995). Flowers were not counted in 2005 because extant lilies and all other biomass was cut and

removed from the plots. In 2006 we counted the first flowers of transplanted common camas. Two plots with extant seablush were excluded from analyses for this species. Seven exclosures were compromised by wildlife, sometimes repeatedly; those with evidence of substantial browsing were also excluded from analysis in the year compromised.

### **Seed Addition Experiment**

The seed addition experiment ran from October 2003 to April 2007 following the above methods of plot selection and treatment application, except that we used fewer (16) plots. Seeds were collected locally in June 2003, cleaned of debris, air dried, counted, then stored. Seeds were spread onto the surface of each plot in October 2003. The number of seeds added for each species was approximately related to their relative seed output and ranged from 35 to 200 seeds per species (Appendix E). Seed viability was estimated by spreading seeds on soilless media in four 0.5 m x 0.5 m trays kept between 23-25°C in a greenhouse. After 35 days, all but two perennial forbs (both lilies) had germinated at rates of 3 to 44%. We added three annual forbs, four perennial forbs and one perennial grass; however, poor germination in some species and difficulty distinguishing others from the extant community reduced reportable species to yarrow (*Achillea millefolium*), great camas (*C. leichtlinii*), blue-eyed mary (*Collinsia parviflora*), seablush and bicoloured lupine (*Lupinus bicolor*) (Appendix E). Seedlings of each species were counted each April for four years.

## **Data Analyses**

We used mixed-effects models to account for potential correlations in our spatially or temporally grouped data (Buckley et al. 2003; e.g., Proc MIXED, Proc GLIMMIX, SAS 2003). To test for the effects of extant plants on focal plants, we compared soil moisture and ground light levels in shaded (S+) and unshaded (S-) plots with general linear mixed models (Proc MIXED, SAS 2003) with month of measurement input as a repeated factor. Differences in soil depth by treatment were assessed with analysis of variance (Proc GLM, SAS 2003). To analyse the overall experiment, shading, herbivory and their interaction were treated as fixed effects, and time was included as a fixed interval variable for longitudinal data. 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, the number of measurements was input as a categorical random (repeated) variable with a first order autoregressive error-covariance structure. Additional species-specific random effects were input into the plant addition models including the pre-experiment mass of common camas bulbs and number of stems per plot of seablush. Individual common camas and oak were categorized as subsamples and included as subjects in the random statement. 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 Documentation v.5.2, SAS Inc, Cary, NC 2002). Significance was assessed at  $\alpha \leq 0.05$ . Residuals were plotted to assess model fit and those with continuous response variables

were further assessed for normality and homoscedasticity using Shapiro-Wilk and Bartlett's tests. Goodness of fit for models with discrete response variables was assessed with the ratio of  $\chi^2$ .

## RESULTS

Non-native plant species comprised 76% of sampled biomass (mean=169  $\pm$  98 SD g), with non-native grasses being the dominant group (59% of the community by weight; mean=131g  $\pm$  57 SD). Non-native species comprised 60% of the total number of stems (mean=1712  $\pm$  673 SD stems) and non-native grasses were still the dominant plant group (43% of the community by stem count; mean=1210  $\pm$  652 SD stems). Soil depth did not vary by treatment at CNERA (mean=16.21  $\pm$  8.62 cm SD,  $F_{3,52}=1.09$ ,  $p=0.36$ ) or AVNR (mean=19.42  $\pm$  10.21 cm SD,  $F_{3,12}=2.62$ ,  $p=0.1$ ). At AVNR, the extant plant community (S+) effectively decreased available soil moisture ( $F_{1,155}=6.27$ ,  $p=0.01$ ) and ground light levels ( $F_{1,43}=7.69$ ,  $p=0.01$ ), and there were no differences in moisture ( $F_{1,155}=0.22$ ,  $p=0.64$ ) or light levels ( $F_{1,43}=1.75$ ,  $p=0.19$ , respectively) due to fencing (H-) on AVNR.

### Transplant Experiment

Herbivory (H+) reduced leaf number in common camas (Fig. 3.2A) and stems of seablush, and these differences between treatments increased with time for seablush (Fig. 3.2B, Table 3.1). In contrast, shading (S+) had no effect and no interactions between treatments were detected (Table 3.1). Arbutus and oak saplings surveyed in 2003 each had more leaves in fenced (H-) than open (H+) plots (Fig. 3.3, Table 3.1); comparisons were not possible thereafter due to drought-related mortality. Replacements planted in March



2004 suffered high mortality in an unusual April drought (17 mm precipitation vs. mean of  $69 \pm 28$  mm SD from 1978-2000; Environment Canada, 2006) and were not replaced.

More oak seedlings emerged from germinated acorns in fenced (H-) than open (H+) plots, but their survival was nevertheless low overall (Fig. 3.2C, Table 3.1), with 97% of 112 acorns dead by 2005. Of five extant species of lily that occurred in our plots, fool's onion (*Triteleia hyacinthina*), nodding onion (*Allium cernuum*), harvest brodiaea (*Brodiaea coronaria*), chocolate lily (*Fritillaria affinis*), and white fawn lily (*Erythronium oregonum*), the number that produced flowers in 2004 was significantly higher in fenced (H-) plots (Fig. 3.3).

In 2006 the number of common camas flowers in 28 fenced (H-) plots averaged  $14.7 \pm 17.3$  SD compared to  $1.9 \pm 6.0$  SD flowers in 28 open plots (shaded plots dismantled). Extant lilies also flowered in 2006 at much higher frequency in fenced (H-) (mean= $56.8 \pm 105.6$  SD) than open (H+) plots (mean= $1.4 \pm 4.2$  SD flowers), having increased dramatically since 2004 (Fig. 3.3) despite being cut in 2005.

### **Seed Addition Experiment**

Herbivory (H+) reduced the number of seedlings of great camas (Fig. 3.4B), blue-eyed mary (Fig. 3.4C), and seablush (Fig. 3.4E), and this difference between treatments increased with time for seablush (Table 3.2). Bicoloured lupine declined with time in all treatments (Fig. 3.4D, Table 3.2). Yarrow was the only species that responded positively to the absence of shading (S-) (Fig. 3.4A, Table 3.2).

## DISCUSSION

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 neighbouring plants may suppress seed germination, seedling establishment and adult reproduction, hastening declines particularly in dispersal limited species (MacDougall and Turkington 2004, 2005). The accumulation of litter of non-native grasses has also been shown to reduce germination (Xiong and Nilsson 1999) and growth of native species (Foster 1999, Lenz et al. 2003). Therefore, litter removal was expected to be particularly important for the seed addition experiment. Second, abundant herbivores may limit plant growth and reproduction. Diversity has been shown to decline on islands where herbivores increased in the absence of carnivores (Terborgh et al. 2001; Hambäck et al. 2004, Allombert et al. 2005). Third, herbivory and competition may interact. In one potential outcome, 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 (Kellogg and Bridgham 2004; McIntyre et al., 2003; Rooney and Waller 2003). We tested these hypotheses in endangered Garry oak meadows to explore whether declines in native plant species were better explained by herbivory or competition.

Herbivory was the overriding factor affecting the performance of focal plant species at established life stages and the flowering of several extant lily species. Herbivory also reduced germination and survival of native seedlings more so than did shading by live plants and litter accumulation. In contrast, above ground biomass removal only affected

yellow positively (see also MacDougall and Turkington 2006). Overall, our findings suggest strongly that intertrophic interactions had a greater influence on the performance of native species than intratrophic interactions in a Garry oak meadow. Consequently, herbivores have played a greater role in the decline of palatable native species in Garry oak meadows than shading and litter accumulation by non-native grasses (see also Gonzales and Clements, in review, Gonzales and Arcese in prep). MacDougall and Wilson (2007) also show that small mammalian herbivores limited recruitment of added seeds in degraded grasslands of central Canada; by comparison, fertility, disturbance, propagule pressure, and competition all had relatively minor impacts.

Our results also show that herbivory limited sexual reproduction in both an experimentally transplanted lily species and in several extant lily species. This suggests that high ungulate density has long term demographic effects on the abundance of these species. Higher rates of flowering by extant lilies in fenced versus open plots may also illustrate a trade-off in life history in response to high herbivory. Miller et al. (2004) found that high fruit set in sagebrush mariposa lilies (*Calochortus macrocarpus*) relative to Lyall's mariposa lilies (*C. lyallii*) was offset by deer herbivory on seeds and flowers. Both species of mariposa lily responded to external factors such as drought with relatively high levels of dormancy (Miller et al. 2004). Episodic stressors such as cutting or drought may therefore be less of a setback to these species than chronic herbivory and the increase in extant lily flowers in 2006 after cutting in 2005 supports this view.

It is possible that site conditions may have contributed to the weak effect of shading in our experiment. Because stem density within our plots was high, we anticipated

that local competition would also be high (e.g., Goldberg 1987, Stevens 2004). Moreover, mowing, weeding, and fire are all known to increase native plant cover and flowering in Garry oak meadows dominated by non-native perennial grasses (MacDougall and Turkington 2007). Huston (1994) suggested that competition is more intense in resource rich sites, whereas plant communities in resource poor sites are more often structured by processes such as disturbance, herbivory and stress. Both of our study sites are characterised by shallow soils. Whether herbivory, competition, or some other processes drive declines of native species in deep soil sites, however, is less clear.

## CONCLUSIONS

Our results suggest that restoring invaded Garry oak meadows may require reducing herbivore density to increase the growth, reproduction and survival of some native plant species. Many Garry oak meadows have been subject to high herbivory for at least 50 years (MacDougall, in review) and, compared to sites with low or no historic herbivory (e.g., Gonzales and Arcese, in prep), it appears that many palatable native species have adjusted to herbivory by foregoing sexual reproduction, become rare, or been extirpated. Our related results further demonstrate that deer prefer to forage on native forbs over most annual and perennial grasses common in invaded oak meadows (Gonzales and Arcese, in prep). We suggest that managers interested in the restoration of invaded grasslands and currently focusing on the removal of non-native plants will be more successful when herbivore density is also controlled. However, because the current dominance of non-native grasses in many sites may confer a 'weighted lottery' advantage

via propagule pressure (Lavorel and Lebreton 1992), the removal of non-native species and augmentation of native species may also hasten overall restoration goals.

TABLES

**Table 0.1:** Summary of mixed models for a two level (+/-), two factor [shading (shade) and herbivory (herb)] transplant experiment in a Garry oak meadow. Experimentally added species included a perennial lily, common camas (*Camassia quamash*), an annual forb, seablush (*Plectritis congesta*), and two shrubs, Garry oak (*Quercus garryana*) and arbutus (*Arbutus menziesii*).

Response Variable	Fixed factors	Est	SE	DF	Test	P	Random factors	Distribution
Common camas leaves	shade	-0.05	0.10	1, 422	F=0.04	0.85	Initial bulb weight	Normal
	herb	-0.17	0.10	1, 422	F=3.81	0.05	Year	
	shade*herb	0.08	0.14	1, 422	F=0.33	0.57	Subject= subsample	
	time	-0.01	0.02	1, 422	F=0.53	0.47		
Seablush individuals	shade	41.39	87.90	1, 149	F=0.15	0.70	Initial individuals	Normal
	herb	154.53	86.97	1, 149	F=4.98	0.03	planted	
	shade*herb	-35.87	122.44	1, 149	F=0.09	0.77	Year	
	time	86.78	21.01	1, 149	F=10.5	0.00		
	shade*time	-21.23	29.03	1, 149	t=0.36	0.55		
	herb*time	-96.71	28.51	1, 149	t=19.15	<.0001		
Garry oak seedlings germinated	shade*herb*time	18.38	40.00	1, 149	t=0.21	0.65		
	shade	-0.29	1.00	1, 327	F=0.4	0.53	Year	Binomial
	herb	1.69	1.03	1, 327	F=2.55	0.11		
	shade*herb	-0.54	1.78	1, 327	F=0.09	0.76		
	time	-0.98	0.33	1, 327	F=32.51	<0.0001		
	shade*time	-0.44	0.59	1, 327	F=0.43	0.51		
Extant Lily flowers	herb*time	-1.30	0.63	1, 327	F=3.98	0.05		
	shade*herb*time	0.03	1.29	1, 327	F=0.00	0.98		
	shade	0.58	1.00	1, 52	F=0.09	0.77	None	Poisson
	herb	-1.56	1.01	1, 52	F=7.32	0.01		
	shade*herb	-0.74	1.43	1, 52	F=0.27	0.61		

Response Variable	Fixed factors	Est	SE	DF	Test	P	Random factors	Distribution
Garry oak sapling leaves	shade	-0.06	0.22	1, 42	F=1.62	0.21	Subject=sample	Negative Binomial
	herb	-0.76	0.23	1, 42	F=27.8	<0.0001		
	shade*herb	-0.34	0.35	1, 42	F=0.92	0.34		
Arbutus sapling leaves	shade	0.02	0.28	1, 29	F=2.97	0.10		Negative Binomial
	herb	-1.54	0.63	1, 29	F=5.63	0.02		
	shade*herb	1.27	0.76	1, 29	F=2.78	0.11		

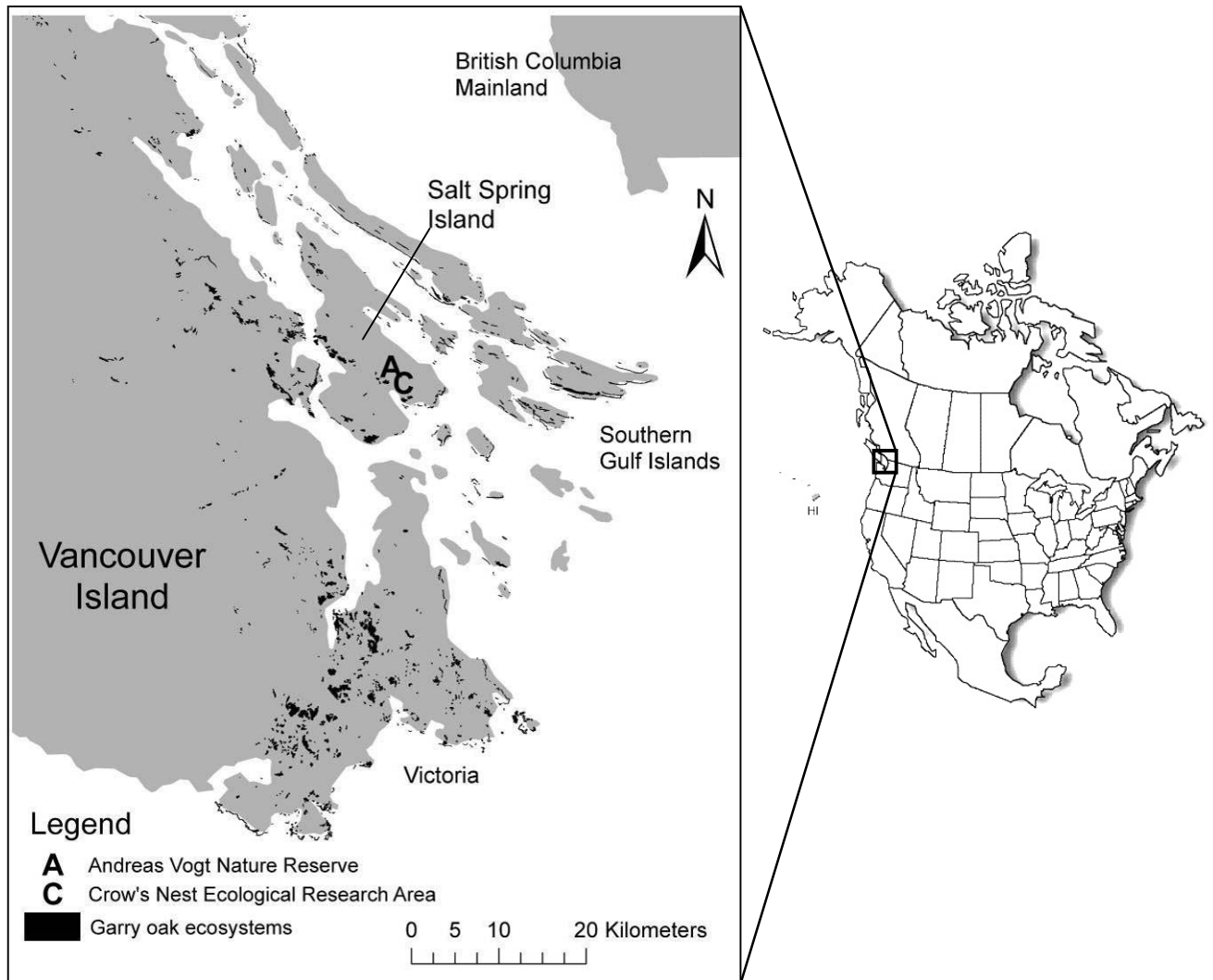
**Table 0.2:** Summary of mixed models for a two level (+/-), two factor [shading (shade) and herbivory (herb)] seed addition experiment in a Garry oak meadow. The experimentally added species were three annual forbs, blue-eyed mary (*Collinsia parviflora*), bicoloured lupine (*Lupinus bicolor*) and seablush, and two perennial forbs, yarrow (*Achillea millefolium*) and great camas (*Camassia leichtlinii*).

Response Variable	Explanatory	Est	SE	DF	Test	P	Random factors	Distribution
Yarrow	shade	-0.47	0.52	1, 57	F=4.86	0.03	Year	Negative Binomial
	herb	-0.10	0.45	1, 57	F=1.41	0.24		
	shade*herb	-0.65	0.72	1, 57	F=0.81	0.37		
	time	-0.40	0.55	1, 57	F=0.53	0.47		
Great camas	shade	-2.23	3.59	1, 57	F=0.92	0.34	Year	Normal
	herb	-4.76	3.15	1, 57	F=4.08	0.05		
	shade*herb	-0.13	4.78	1, 57	F=0.0	0.98		
	time	1.15	1.05	1, 57	F=1.2	0.28		
Blue-eyed mary	shade	0.09	0.37	1, 57	F=0.31	0.58	Year	Negative Binomial
	herb	-0.28	0.33	1, 57	F=4.21	0.04		
	shade*herb	-0.45	0.50	1, 57	F=0.82	0.37		
	time	-0.14	0.24	1, 57	F=0.35	0.56		
Bicoloured lupine	shade	0.83	0.73	1, 57	F=0.81	0.37	Year	Negative Binomial
	herb	0.88	0.65	1, 57	F=1.00	0.32		
	shade*herb	-0.82	0.93	1, 57	F=0.76	0.39		
	time	-2.00	0.58	1, 57	F=12.12	0.00		

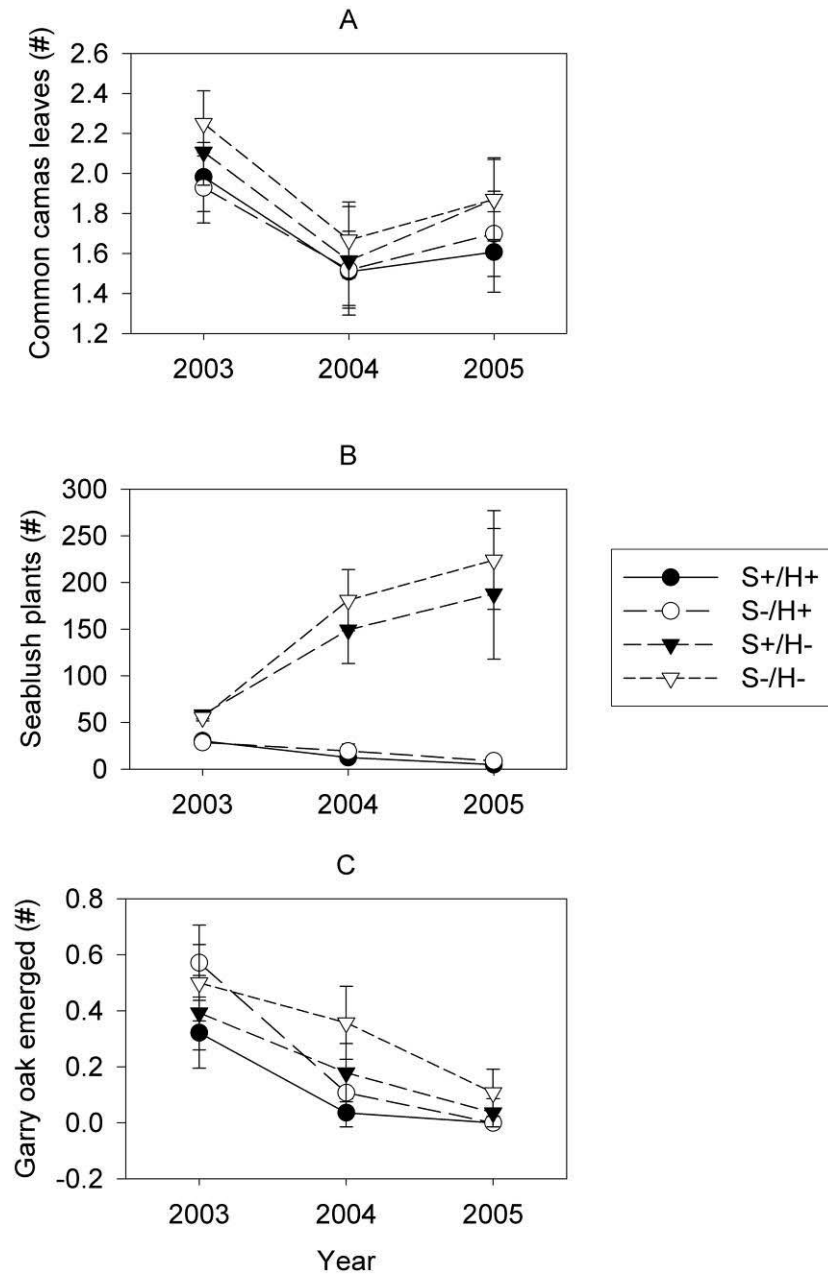


Response Variable	Explanatory	Est	SE	DF	Test	P	Random factors	Distribution
Seablush	shade	0.73	0.73	1, 54	F=3.19	0.08	Year	Negative Binomial
	herb	0.24	0.66	1, 54	F=0.62	0.43		
	shade*herb	0.30	0.99	1, 54	F=0.09	0.76		
	time	0.15	0.20	1, 54	F=3.5	0.07		
	shade*time	-0.27	0.27	1, 54	F=3.46	0.07		
	herb*time	-0.44	0.24	1, 54	F=7.83	0.01		
	shade*herb*time	-0.15	0.37	1, 54	F=0.16	0.69		

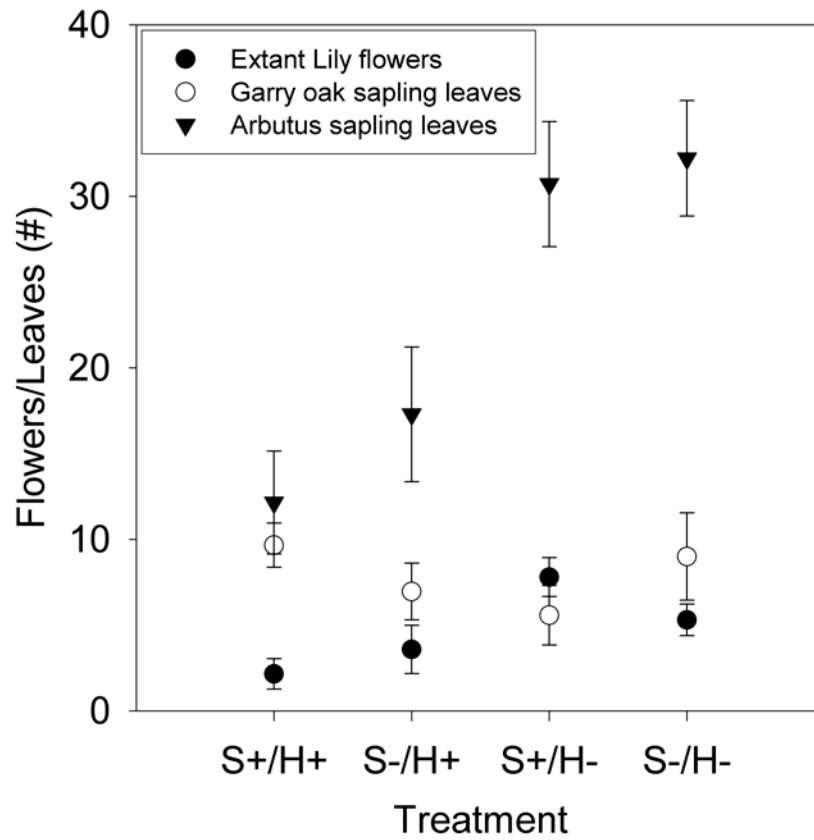
## FIGURES



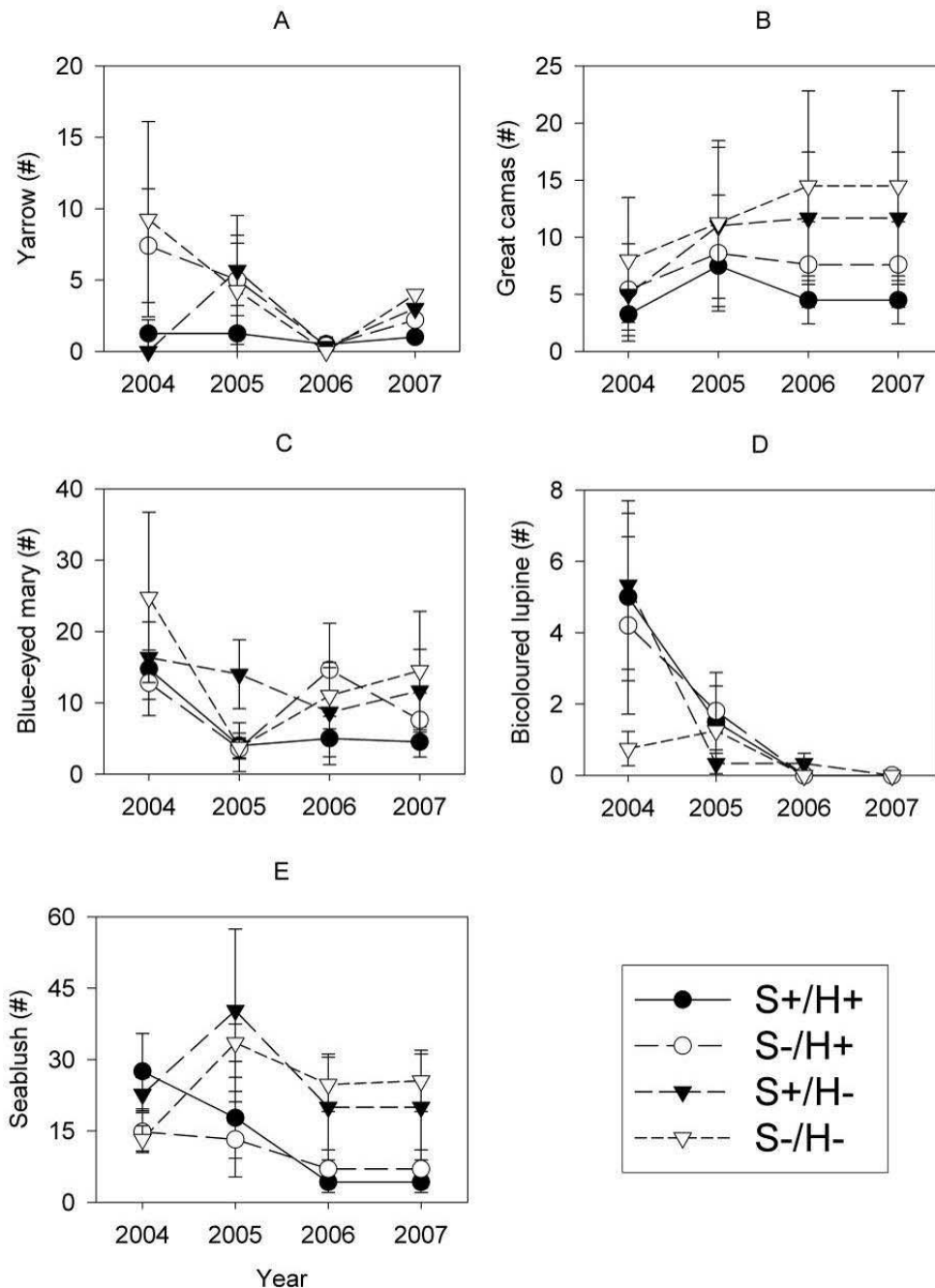
**Figure 0.1:** Crow's Nest Ecological Research Area (transplant experiment) and Andreas Vogt Nature Reserve (seed addition experiment) on Salt Spring Island on Canada's southwest coast. Garry oak meadow locations from the Sensitive Ecosystem Inventory (Ward et al. 1998).



**Figure 0.2:** The number ( $\pm 1$  SE) of common camas leaves (A), seablush stems (B), and emerging Garry oak seedlings (C) by treatment from 2003 to 2005 in a two level (+/-), two factor [shading (S) and herbivory (H)] transplant experiment.



**Figure 0.3:** The number of extant lily flowers in 2004 and the number of oak and arbutus sapling leaves by treatment in 2003 in a two level (+/-), two factor [shading (S) and herbivory (H)] transplant experiment in a Garry oak meadow (see Table 3.1 for statistical results). Error bars indicate  $\pm 1$  SE.



**Figure 0.4:** The number of yarrow (A), great camas (B), blue-eyed mary (C), bicoloured lupine (D), and seablush (E) germinating, persisting or reproducing by treatment from 2004 to 2007 in a two level (+/-), two factor [shading (S) and herbivory (H)] seed addition experiment in a Garry oak meadow. See Table 3.2 for statistical results. Error bars indicate  $\pm 1$  SE.



**Photo 0.1:** Black-tailed deer in a Garry oak meadow dominated by non-native grasses.

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#### LITERATURE CITED

- Allombert, S., S. Stockton, and J. L. Martin. 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology* **19**(6):1917-1929.
- Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium-grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* **4**(1):104-109.
- Balگوoyen, C. P., and D. M. Waller. 1995. The use of *Clintonia-borealis* and other indicators to gauge impacts of white-tailed deer on plant-communities in northern Wisconsin, USA. *Natural Areas Journal* **15**(4):308-318.
- Bonham, C. D. 1989. *Measurements for Terrestrial Vegetation*. John Wiley & Sons, New York, NY.
- Bowen, L. and Van Vuren, D. 1997. Insular endemic plants lack of defenses against herbivores. *Conservation Biology* **11**:1249-1254.
- Buckley, Y. M., S. Anderson, C. P. Catterall, R. T. Corlett, T. Engel, C. R. Gosper, R. Nathan, D. M. Richardson, M. Setter, O. Spiegel, G. Vivian-Smith, F. A. Voigt, J. E. S. Weir, and D. A. Westcott. 2006. Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology* **43**(5):848-857.
- Callaway, R. M. 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: A review and synthesis. *Ecology Letters* **5**(2):302-315.
- Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* **35**:113-147.
- Davis, M. A. 2003. Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience* **53**(5):481-489.
- Environment Canada. 2007. The Weather Office Website. . Available from [http://www.weatheroffice.ec.gc.ca/mainmenu/about\\_us\\_e.html](http://www.weatheroffice.ec.gc.ca/mainmenu/about_us_e.html) (accessed December 15 2006).
- Foster, B. L. 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. *Journal of Ecology* **87**(3):476-489.
- Fuchs, M. A. 2001. *Towards a Recovery Strategy for Garry Oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review*.



Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region.  
GBEI/EC-00-030.

- GOERT 2007. The Garry oak ecosystem recovery team website. Available from [http://www.goert.ca/about\\_species\\_at\\_risk.php](http://www.goert.ca/about_species_at_risk.php) (accessed November 2 2007).
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* **68**(5):1211-1223.
- Gonzales, E. K., and P. Arcese. in prep. Herbivores facilitate invasion of non-native grasses in endangered island Garry oak meadows.
- Gonzales, E. K., and D. R. Clements. in review. Community response to two types of disturbance: Lessons for Garry oak ecosystem restoration.
- Gonzales, E. K., Y. F. Wiersma, A. I. Maher, and T. D. Nudds. in revisions. Positive relationship between non-native and native squirrels in an urban landscape. *Canadian Journal of Zoology*.
- Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: A meta-analysis of field experiments. *American Naturalist* **155**(4):435-453.
- Hambäck, P. A., L. Oksanen, P. Ekerholm, A. Lindgren, T. Oksanen, and M. Schneider. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos* **106**(1):85-92.
- Houlahan, J. E., and C. S. Findlay. 2004. Estimating the 'critical' distance at which adjacent land-use degrades wetland water and sediment quality. *Landscape Ecology* **19**(6):677-690.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, New York.
- Jones, C. G., and R. M. Callaway. 2007. The third party. *Journal of Vegetation Science* **18**(6):771-776.
- Kellogg, C. H., and S. D. Bridgman. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. *Biological Invasions* **6**(3):319-329.
- Krausman, P. R., A. J. Kuenzi, R. C. Etchberger, H. R. Rautenstrauch, L. L. Ordway, and J. J. Hervet. 1997. Diets of desert mule deer. *Journal of Range Management* **50**(5):513-522.
- Lavorel, S., and J. D. Lebreton. 1992. Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science* **3**(1):91-100.

- Lea, T. 2006. Historical Garry oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. *Davidsonia* **17**(2):34-50.
- Lenz, T. I., J. L. Moyle-Croft, and J. M. Facelli. 2003. Direct and indirect effects of exotic annual grasses on species composition of a south Australian grassland. *Austral Ecology* **28**(1):23-32.
- MacDougall, A. S. in prep. Herbivory, hunting, and vegetation change in degraded oak savanna.
- MacDougall, A. S. 2005. Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology* **86**(12):3354-3363.
- MacDougall, A. S., B. R. Beckwith, and C. Y. Maslovat. 2004. Defining conservation strategies with historical perspectives: A case study from a degraded oak grassland ecosystem. *Conservation Biology* **18**(2):455-465.
- MacDougall, A. S., J. Boucher, R. Turkington, and G. E. Bradfield. 2006. Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science* **17**(1):47-56.
- MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology* **92**(3):422-434.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**(1):42-55.
- MacDougall, A. S., and R. Turkington. 2006. Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology* **87**(7):1831-1843.
- MacDougall, A. S., and R. Turkington. 2007. Does the type of disturbance matter when restoring disturbance-dependent grasslands? *Restoration Ecology* **15**(2):263-272.
- MacDougall, A. S., and S. D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* **88**(5):1105-1111.
- Martin, J. L., and C. Baltzinger. 2002. Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal of Forest Research* **32**(7):1254-1264.
- McIntyre, S., K. M. Heard, and T. G. Martin. 2003. The relative importance of cattle grazing in subtropical grasslands: Does it reduce or enhance plant biodiversity? *Journal of Applied Ecology* **40**(3):445-457.

- Miller, M. T., G. A. Allen, and J. A. Antos. 2004. Dormancy and flowering in two mariposa lilies (*Calochortus*) with contrasting distribution patterns. *Canadian Journal of Botany* **82**(12):1790-1799.
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin, and D. P. Vazquez. 2006. Biotic interactions and plant invasions. *Ecology Letters* **9**(6):726-740.
- Nogales, M., J. L. Rodriguez-Luengo, and P. Marrero. 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review* **36**(1):49-65.
- Rodda, G. H., and T. H. Fritts. 1992. The impact of the introduction of the colubrid snake *Boiga-irregularis* on Guam lizards. *Journal of Herpetology* **26**(2):166-174.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**(1-2):165-176.
- Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *American Naturalist* **160**(6):766-783.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**(4):170-176.
- Stevens, M. H. H., D. E. Bunker, S. A. Schnitzer, and W. P. Carson. 2004. Establishment limitation reduces species recruitment and species richness as soil resources rise. *Journal of Ecology* **92**(2):339-347.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**(5548):1923-1926.
- Tompkins, D. M., A. R. White, and M. Boots. 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters* **6**(3):189-196.
- Vourc'h G, Martin J-L, Duncan P, Escarré J, and Clausen TP. 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: A comparative study between mainland and island populations. *Oecologia* **126**:84-93.
- Vourc'h, G., M. de Garine-Wichatitsky, A. Labbe, D. Rosolowski, and J. L. Martin. 2002. Monoterpene effect on feeding choice by deer. *Journal of Chemical Ecology* **28**:2411-2427.

- Ward, P., G. Radcliffe, J. Kirkby, J. Illingworth, and C. Cadrin. 1998. Sensitive Ecosystems Inventory: East Vancouver Island and Gulf Islands, 1993-1997. Volume 1: Methodology, Ecological Descriptions and Results. Technical Report Series No. 320 edition. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.
- White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: A neglected concept in invasion biology. *Diversity and Distributions* **12**(4):443-455.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**(8):607-615.
- Xiong, S. J., and C. Nilsson. 1999. The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology* **87**(6):984-994.

## **Chapter 4: Community response to cutting and fencing for the restoration of invaded Garry oak meadows with abundant herbivores\***

### INTRODUCTION

Restoring ecological processes sometimes requires restoration techniques that simulate historical disturbances (Palmer et al. 1997). Predicting plant community response to disturbance, however, is still rudimentary (Lavorel and Garnier 2002, Hooper et al. 2005). Disturbances affect ecosystem-level processes such as production, biomass accumulation, energetics and nutrient cycling (Mooney and Godron 1983) as well as being a primary source of temporal and spatial heterogeneity in the structure and dynamics of natural communities (Sousa 1984). Disturbances have been suppressed in many natural areas, however, resulting in more homogeneous communities dominated by a few competitive, often invasive species (Wilsey and Polley 2006).

Given that present conditions and species composition differ from the historical state, re-introducing disturbance may not produce the desired restoration outcomes (Hobbs and Huenneke 1992, Keeley et al. 2003). For example, although anthropogenically driven disturbances such as resource extraction, increased herbivore pressure, eutrophication, and soil disruptions have facilitated the establishment of non-native species worldwide (Williamson 1996; Jenkins and Pimm 2003), the suppression of historical disturbances may now be maintaining their dominance in many cases (MacDougall and Turkington 2005). Many ecosystems also experience multiple types of disturbances, some episodic, such as fire, and others chronic, such as herbivory, yet field experiments investigating plant community response to multiple disturbances are rare (Wisdom

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et al. 2006). As a consequence, there is an urgent need to improve our ability to predict the effects of different types of disturbances on plant communities for the recovery of native ecosystems and natural processes (Hooper et al. 2005).

Garry oak meadows are one of Canada's most endangered ecosystems largely due to land conversion and the prevalence of non-native plant species (Fuchs 2001). Limited to southeastern Vancouver Island and the Southern Gulf islands in Canada, Garry oak meadows also extend south to central California (MacDougall et al. 2004) and restoration efforts are active on both sides of the Canada/US border (Devine et al. 2007, MacDougall and Turkington 2007). The diversity of natural Garry oak meadows was likely maintained, in part, by aboriginal fire management and fire suppression over the past 150 years is thought to be partially responsible for the loss of native plant diversity in these meadows (MacDougall et al. 2004). Under current conditions, non-native perennial graminoids dominate most Garry oak meadows. These graminoids produce clumps of living material and litter that decompose slowly, minimizing ground light levels and inhibiting germination and establishment of other species (MacDougall and Turkington 2004, MacDougall 2005). Experimental burns shift the composition, structure, and function of Garry oak meadows without eliminating small populations of native plants. This suggests that the dominance of non-native perennial graminoids is maintained by the suppression of this disturbance (MacDougall 2005).

In concert with the suppression of fire, the number of herbivores in Garry oak meadows is thought to have increased over the past 150 years. In addition to abundant native Columbian black-tailed deer (*Odocoileus hemionus columbianus*), non-native herbivores including goats (*Capra hircus*), sheep (*Ovis aries*), eastern cottontail rabbits (*Sylvilagus floridanus*), and domestic rabbits (*Oryctolagus cuniculus*) have been introduced to various Garry oak meadows

throughout the range. Herbivory has intensified in ecosystems around the world due to landscape change, predator eradication, and the introduction of domestic ungulates (Fleischner 1994). Abundant herbivores can shift plant communities to a new stable state, that is, the plant community does not revert to the historical composition once herbivory is reduced or removed (Cingolani et al. 2005). Plant communities experiencing increased herbivory have become homogenized (Rooney and Waller 2003), altered in structure (Stockton et al. 2005, Navarro et al. 2006), or dominated by less palatable species (Côté et al. 2004). If less palatable species happen also to be non-native, herbivory can be associated with an increase in the dominance of non-native plants (Kellogg and Bridgham 2004). Overall, these results suggest that herbivory may facilitate the dominance of non-native plants that are known to increase under herbivory, such as *Anthoxanthum odoratum* L. and *Rumex acetosella* L. (Crawley 1990), both of which are common in Garry oak meadows. Given the potential for complex and interacting effects of manipulating restoration techniques, we asked:

1. Does cutting (clipping and removing vegetation and litter), fencing, or both, increase native plant biomass in oak meadows?
2. How do the responses to cutting and fencing treatments vary among different plant functional groups?

We measured community response to cutting and fencing as the proportion of the biomass of a herbaceous plant community characterized by geographic origin (native/non-native), growth form (annual/perennial), and plant type (forb/graminoid). Cutting is a non-selective, episodic (pulse) biomass removal that we used as a surrogate for fire. Although fire was the historical disturbance, other non-selective methods of biomass removal such as cutting and weeding produce a similar plant community response and are, therefore, less controversial

and more broadly applicable surrogates to fire (MacDougall and Turkington 2007). Herbivory is a selective, chronic (press) biomass removal which is thought to have increased in intensity in many Garry oak meadows. In this paper, we characterized plant communities into their component plant groups because these groups influence ecosystem properties (Hooper et al. 2005), and because grouping increases the precision of predictions (Huston 1994, Lavorel et al. 1997, Loreau et al. 2001).

Our predictions for plant group responses to cutting and fencing were derived from broad characteristics of the groups, dichotomized into native/non-native, annuals/perennials, and forbs/graminoids (Table 4.1). In general, we expected native functional groups to respond positively to cutting, in contrast to non-native functional groups. The proportional biomass of annual functional groups was expected to increase with cutting while perennials declined. Traits that make subordinates poor competitors in the absence of fire or cutting (smaller size, short growing season, underground storage capacity) favour growth and reproduction following cutting (MacDougall 2005); therefore, annuals, early colonizers, and geophytes were all expected to respond positively as ground level light and space increased. If herbivory facilitates the dominance of non-native functional groups due to an ability to resist or recover from intense herbivory better than native plants (Augustine and McNaughton 1998), then native functional groups should increase with fencing. Native perennial forbs, in particular, were expected to increase with fencing due to their palatability to deer (Wiegmann and Waller 2006). Interactions between cutting and fencing were expected, given the contrasting predictions of some functional groups to the treatments. For example, cutting was expected to favour non-native annual graminoids in the presence of herbivory while fencing and cutting was expected to benefit native forbs.



## MATERIALS AND METHODS

### Study Site

Crow's Nest Ecological Research Area (CNERA) on Salt Spring Island (48°46'51" N, 123°27'23" W) is 200 m above sea level with a SE aspect. The submediterranean 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 and interspersed with exposed bedrock. The 30 ha research area is comprised of two plant communities, 1.4 ha of Garry oak meadows and the remainder is Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco] forest. To get an estimate of the present plant community composition, we took biomass measures from eight 0.5 m diameter circular plots June 16-18, 2004. Plants were cut at ground level, identified to species and dried for 3 days at 70°C prior to weighing. On average, non-native species comprised 75% (mean=25.7 g/plot) of the community biomass (mean=34.4 g/plot). Graminoids were the dominant plant group, comprising 74% (mean=25.3 g/plot) of the plant community (Fig. 4.1A). Many Garry oak meadows show signs of high levels of herbivory, such as browse lines and 'topiaried' trees. The effects of herbivory on Garry oak meadows, however, have rarely been examined, particularly in concert with other community processes. Abundant native black-tailed deer and a small flock of sheep are present at CNERA and to get an estimate of seasonal herbivore activity, we calculated the number of pellets ( $\text{m}^{-1}$ ) over five time periods from November 2005 to August 2006. Pellet counts were conducted along 10 transects varying in length ( $65.1 \pm 10.8$  m) and time ( $6.9 \pm 0.97$  min) due to variation in topography. Surveyors counted the number of pellets within approximately 1 m to each side of transects and then cleared the area of pellets. Herbivore pellet deposition peaked in March and was generally lowest during the summer (Fig. 4.1B).

## Field Methods

Fifty-six plots were distributed throughout CNERA as part of a related experiment on the effects of fencing and cutting on experimentally planted species (Gonzales and Arcese, in prep). In that experiment, two Garry oak acorns and two saplings, one *Arbutus menziesii*, four common camas bulbs (*Camassia quamash*), and four bunches of seablush (*Plectritis congesta*) were planted in each plot in February 2003. All saplings died due to drought and very few acorns emerged. Because all plots were treated equally, with minimal disturbance of the extant plant community, we assume that experimentally planted species had a limited or at least consistent influence on the extant community across treatments. Seablush, however, is an annual and generally increased in fenced plots and decreased or went extinct in the unfenced plots (Gonzales and Arcese, in prep). We therefore included the number of seablush stems counted in 2005 as a variable in our analyses to test for a response in the extant community due to the presence of seablush. Seablush also occurs naturally at CNERA and is a common species in Garry oak meadows.

Our restoration experiment examined the effects of the fencing and cutting treatments on the extant plant community. Herbivory was manipulated by creating open or fenced plots; the latter were enclosed by 1.25 m<sup>3</sup> aluminum frames and fish nets to exclude ungulates without excluding light, rodents, birds or invertebrates. The cutting treatment was manipulated by cutting and discarding litter and live plant material. Cutting occurred in the fall (October/November) and summer (July/August) each year, during the times when fires were historically set (MacDougall 2005). Herbaceous plant communities can be highly variable due to local abiotic conditions (e.g., Lortie and Cushman 2007); therefore, plot selection was designed to minimize variability due to soil moisture and soil depth. Plots were selected randomly from sites that met the following

criteria: <1% open rock, <10% slope, <5% canopy closure, >10 cm soil depth, and >10 m distance to the next plot. Plot size, 1 m x 1 m, was selected to maximize the number of replicates in the available area. Plot size and number was also limited by survey time; biomass collection took 12 to 40 person hours per plot, depending upon plot diversity and productivity. Environmental variables recorded at each plot included light (LI-COR quantum sensor, LI-COR, Lincoln, Nebraska, USA), April soil moisture (Hydrosense TDR meter, Campbell Scientific, Logan, Utah, USA), and soil depth, which was measured with a 90 cm steel rod driven into the ground to bedrock. Both soil depth and soil moisture were measured in each of the four cardinal directions adjacent to the plot edges and the average taken for each plot. The two crossed treatments [uncut(C-)/cut(C+) with fenced(F-)/unfenced(F+)] were each replicated 14 times.

We harvested plants by clipping at ground level, identifying to species, and storing in a paper bag. They were dried in a drying oven for 48 hours at 70°C and weighed to a precision of 0.01 g excluding the weight of the bag. Biomass collection began in April 2, 2005 and finished on July 19, 2005. Experimentally planted species were not collected. We also calculated resource selectivity (forage) indices by surveying additional plots to assess whether herbivores favour native plant functional groups given their availability in the plant community (Manly et al. 2002). We identified and counted all stems to species in 16 0.5 m x 0.5 m plots and noted the number of browsed and unbrowsed stems.

### **Data Analyses**

We fit total biomass with a general linear model (PROC GLM, SAS 9.1, SAS Institute 2006, Cary, NC) to the main treatment effects and their interaction to compare overall differences of biomass across treatments. Residuals were assessed with Shapiro-Wilk and Bartlett's tests to test if assumptions normality and homoscedasticity were met. We then tested

whether the discrete variable, species richness, differed with abiotic measures (soil moisture, soil depth, and light levels) and between the fencing and cutting treatments by fitting a generalized linear model (PROC GLIMMIX) with a Poisson distribution and log link function. If plot selection successfully controlled for variation due to non-target abiotic factors, we expected to see no difference in species richness, soil moisture or soil depth among plots. However, because we explicitly manipulated light levels by cutting, we expected species richness to increase with increasing light.

Mixed-effects models enable the modeling of the correlations that often exist with spatially and temporally grouped data and we fit general (Proc MIXED) and generalized (Proc GLIMMIX) linear mixed models to our data (SAS v. 9.1, SAS Inc., Cary, NC, 2003). After removing two extreme values to meet assumptions of a normal distribution, we tested whether native biomass responded to cutting, fencing, or an interaction between the two with a general linear mixed model with the day of survey input as a random factor. We used the same model to test non-native biomass against the treatments. To assess whether the proportional biomass for each plant functional group varied with fencing and/or cutting, we fit a generalized linear model (Proc GLIMMIX) with a beta distribution and logit link. The proportion of biomass was calculated for each plot to reflect the dependent nature of the response variable - the biomass of each functional group being dependent on the other functional groups in the plot. We tested the main effects of cutting and fencing, their interaction, as well as time and the number of stems of seablush. Given that biomass collection spanned more than three months, time (the day of survey) may influence the response of proportional biomass if plant functional group phenology differs. We applied an alternative model for plant functional groups that were influenced by time; we tested the interactions of time with the main factors and the three way interaction.

When no significant values were found in the higher level interactions, we report the simpler model. Significance was assessed at  $\alpha \leq 0.05$ . Goodness of fit for all generalized models was assessed with the ratio of  $X^2$  and degrees of freedom ( $\approx 1$  indicates a good fit).

Ungulates are known to favour certain plants such as lilies (Krausman et al. 1997), which are a dominant native perennial forb in our system. To test if the subordination of native plant functional groups is related to herbivory, we also tested whether black-tailed deer and sheep selected plant groups given their availability in the community using a log-linear chi-square test (Manly et al., 2002). The forage index ( $w_i$ ), is the proportion of the browsed stems ( $o_i$ ) over the proportion of the total stems ( $\mu_i$ ):

$$w_i = o_i / \mu_i \quad \text{eqn 1}$$

We identified and counted the number of browsed and unbrowsed stems in 16 0.5 m x 0.5 m plots. We calculated forage indices for each species as well as pooling species into plant functional groups. Indices greater than 1 indicate selection while indices below 1 suggest avoidance.

## RESULTS

The total biomass collected from the 56 plots was 13891 g and differed between fencing treatments ( $F_{1,52}=7.43$ ,  $P=0.01$ ) but not cutting treatments ( $F_{1,52}=1.19$ ,  $P=0.28$ ). Residuals met assumptions of normality ( $W=0.98$ ,  $P=0.34$ ) and homoscedasticity ( $X^2=3.9$ ,  $P=0.27$ ). Plot selection reduced variation in species richness due to local abiotic factors; there were no differences between species richness and April soil moisture ( $F_{1,54}=0.15$ ,  $P=0.70$ , Fig. 4.2A) or soil depth ( $F_{1,54}=0.59$ ,  $P=0.45$ , Fig. 4.2B). Species richness was influenced by ground light levels ( $F_{1,54}=7.74$ ,  $P=0.01$ , Fig. 4.2C) and differed between cut and uncut plots, although there were no

differences in richness between fencing treatments (Table 4.2, Fig. 4.2D). Time also had no influence on species richness (Table 4.2).

Overall, non-native perennial graminoids were the most abundant functional group (5018 g) while native annual forbs were the least abundant (396 g). No native annual graminoids were observed. The non-native perennial graminoid, *Anthoxanthum odoratum* L., occurred in all 56 plots and was also the most abundant by mass (3475 g). The most abundant (1707 g) native perennial graminoid, *Carex inops* Bailey, occurred in 86% of the plots. The most abundant (1669 g) and frequent (95% of the plots) non-native annual graminoid was *Bromus hordeaceus* L. The most abundant (972 g) and frequent (96% of the plots) non-native annual forb was *Vicia sativa* L. and the most abundant (355 g) and frequent (95% of the plots) native annual forb was *Lotus micranthus* Benth. The most abundant (225 g) and frequent (61% of the plots) native perennial forb was *Brodiaea coronaria* (Salisb.) Engl. and the most abundant (641 g) and frequent (82% of the plots) non-native perennial forb was *Hypochaeris radicata* L. With the exception of *Carex inops*, the eight most abundant species were not native and these eight species had a combined mass of 9050 g. The Poisson and beta distributions provided a good fit for all of the generalized linear models ( $X^2/DF = 1 \pm 0.5$ ).

### **Treatment effects**

Both cutting and fencing increased native biomass, but neither treatment affected non-native biomass (Table 4.2, Fig. 4.3). Cutting resulted in increased proportional biomass of both native and non-native annual forbs (Table 4.2, Fig. 4.4). Although neither treatment influenced the proportional biomass of native or non-native perennial forbs (Table 4.2, Fig. 4.4), the proportional biomass of native perennial forbs declined with time (Fig. 4.5). Subsequent analysis of the interaction of time with treatments found no interactions. We also found an interaction

between treatments for non-native annual graminoids: uncut, fenced plots and cut, unfenced plots both had more proportional biomass than uncut, fenced plots (Table 4.2, Fig. 4.4); the proportional biomass of native perennial graminoids increased with cutting whereas the proportional biomass of non-native perennial graminoids tended to decrease (Table 4.2, Fig. 4.4). All treatment plots differed from one another for non-native perennial graminoids, with the lowest proportional biomass in cut, fenced treatment (Table 4.2, Fig. 4.4). The number of seablush stems did not vary with plant functional group or treatments, but did approach significance for non-native annual graminoids ( $P=0.06$ ; Table 4.2).

### **Selection by Herbivores**

We counted a total of 9307 stems and 12% had been browsed. Herbivores favoured native perennial forbs given their availability in the plant community (Fig. 4.6); this trend was driven mainly by two highly preferred native lilies with species-specific forage indices of 6.48 (*Brodiaea coronaria*) and 8.15 (*Tritelaria hyacinthina*).

### **DISCUSSION**

Current conditions in the control plots (uncut/unfenced) in an invaded Garry oak meadow with abundant ungulates were dominated by non-native annual and perennial graminoids (Figs 1a, 4) but manipulations increased the biomass of native species (Table 4.2, Fig. 4.3) and the relative contribution of the functional plant groups to the community (Fig. 4.4). Non-native graminoids were proportionately reduced by the cutting treatments consistent with the hypothesis that suppression of non-selective episodic disturbance (cutting/fire) facilitates their dominance (MacDougall and Turkington 2005). Native perennial graminoids increased in proportional dominance with cutting, suggesting that either suppression by non-native graminoids and/or suppression of non-selection biomass removal (cutting/fire) were limiting factors. Although

native perennial forbs did not respond to either treatment, the other three forb functional groups benefited from cutting; non-native forbs, in particular, increased in proportional biomass (Fig. 4.4).

We found only weak support for the hypothesis that non-native plants, as a group, are better adapted to herbivory than native plants. The proportional biomass of non-native annual graminoids declined in the uncut plots when fenced, suggesting that their dominance was, in part, driven by their ability to withstand herbivory relative to other functional groups. It was non-native perennial graminoids, however, that compensated for the decline in annual graminoids, not native plants. Over time, fencing without cutting would likely exacerbate the dominance of non-native perennial graminoids with increased litter accumulation, which suppresses the germination and establishment of native species (MacDougall and Turkington 2004).

Cumulatively, there were larger differences in total biomass between fencing treatments than between cutting treatments, perhaps because herbivory is a chronic disturbance while cutting is episodic (Wisdom et al. 2006), but also because herbivory reduced the proportional biomass of dominant non-native perennial grasses. Native annual forbs and native perennial graminoids responded to fencing only if plots were also cut; therefore, cutting and fencing produced the greatest response in native functional groups, the greatest shift from current conditions. Overall, herbivory limited total native biomass (Table 4.2, Fig. 4.3), herbivores selected native perennial forbs over other plant groups (Fig. 6), and herbivory facilitated the dominance of non-native annual graminoids (Fig. 4.4).

Fencing was expected to increase the biomass of native perennial forbs because negative effects of herbivory on native forbs are well documented elsewhere (e.g., Augustine and Frelich 1998, Fletcher et al. 2001, Frankland and Nelson 2003). Deer and sheep dramatically reduced



flowering of six native perennial lilies found on CNERA (Gonzales and Arcese, in prep) and selectively browsed native perennial forbs given their availability in the community (Fig. 4.6). Two aspects of our methodology may explain the lack of response in native perennial forbs. First, the measured rarity of native forbs in the plant community may be a product of the use of biomass as the response variable, which we selected in order to directly measure the effect of biomass removing disturbances. Forbs, which have greater water content than graminoids, produce less dry weight biomass on average and may therefore represent greater component of the community if another quantity, such as cover, were used as the measure of composition. Forbs produce almost no persistent litter and a shorter canopy than graminoids; therefore, production may not be directly linked to function in oak meadows (MacDougall 2005) and restoration strategies need to account for attributes of forbs besides biomass. Second, herbivore activity peaked in March (Fig. 4.1B), when many native forbs are at peak production. The biomass of native perennial forbs declined with time (Table 4.2) and our data likely captured the response of graminoids to the treatments, but may have been too late to capture variability in the native forbs. It remains possible, therefore, that herbivores exerted greater pressure on native perennial forbs before we collected data (mainly in June).

Our results suggest that the timing of cutting or fencing treatments in ecosystem restoration could affect the response of native perennial forbs and non-native perennial graminoids. Cutting in November and August was effective in altering dominant graminoids and potentially the frequency could be reduced to once per year in either the fall or summer, as no difference was found between the timing of mowing and community response in Garry oak meadows elsewhere (MacDougall and Turkington 2005). Controlling the timing of herbivory with gated fences could also maximize reduction of non-native plants similar, conceptually, to

the temporal regulation of domestic ungulate grazing to increase heterogeneity in rangelands (Fuhlendorf and Engle 2001). Given that fencing had a greater effect on total biomass than cutting and that fencing alone increased non-native perennial graminoid biomass, manipulating seasonal herbivore access may offer a novel approach for future investigations. Our results suggest that to maximize biomass reduction of non-native perennial graminoids, meadows should be fenced fall to spring, when most native forbs are germinating and growing, then opened during summer, after native forbs have senesced.

The long-term response of Garry oak plant communities to cutting and fencing treatments is unknown because as the proportion of plant groups change, local functioning is also likely to change. For example, a shorter forb canopy and increased decomposition of plant material releases nutrients at a faster rate than graminoids (Garibaldi et al. 2007). Increasing establishment rates (Clark et al. 2005) of presently subordinate species could result in a more stable community where the frequency or intensity of cutting/fire could be reduced, particularly if species diversity increases (Hooper et al. 2005). It is also possible that there are limits on the ability of communities to revert to native dominance that depend on present species composition. For example, non-native plants in disturbed sites can form stable communities that are resistant to re-invasion by natives and resilient to losses of individual non-native species (Kulmatiski 2006). Although community structure and composition may change with time, early colonizing non-native plants are replaced by later colonizing non-native species in some communities (MacDougall and Turkington 2005, Kulmatiski 2006). MacDougall and Turkington (2006) have demonstrated that native species are recruitment limited in invaded oak meadows; thus, their subordinate status may also be due to their rarity rather than competitive inferiority (Seabloom et al. 2003a). Ultimately, augmentation of native species coupled with cutting and fencing may

provide the most rapid shifts in plant community composition from non-native to native species dominance (Seabloom et al. 2003b, MacDougall and Turkington 2005). Long-term studies that manipulate treatment levels including intensity and frequency of cutting and fencing offer the best chance to test advance understanding and increase the efficacy of restoration (Wisdom et al. 2006).

## CONCLUSIONS

Non-native species may succeed in new landscapes because they possess traits to outcompete native species, or because ecosystem processes have been altered to favour species adapted to novel conditions. We found evidence of both scenarios in Garry oak meadows. The response to cutting was similar for both native and non-native functional groups, consistent with MacDougall et al. (2006), who showed that functional characteristics of native species predicted the traits of the invaders in similar environments. However, we found that the response to herbivory differed among functional groups. Non-native annual graminoids increased under herbivory without cutting, while native annual forbs decreased in cut, unfenced plots. In contrast, non-native annual and perennial graminoids had opposite responses to fencing. These results suggest that non-native species do not, as a group, increase with herbivory. However, herbivory favours one non-native group (annual graminoids) whereas protection from herbivory favours another (perennial graminoids).

The efficacy of conservation and restoration is likely to increase when the dynamics of ecosystem function are understood at a community scale, and the life history traits of species can be used to predict responses and understand underlying mechanisms (Sinclair and Byrom 2006). The restoration of natural plant communities requires an understanding of the mechanisms that drive the dominance of particular functional groups and an ability to predict how plant

communities will respond to restoration treatments. So far, theory has outpaced field experiments, causing Hooper et al. (2005) to call for experiments to measure ecosystem response and recovery given multiple disturbances. A lack of understanding about the combined effects of herbivory and episodic disturbance currently hinders the development of effective management tactics for ungulates (Wisdom et al. 2006), even though their potential effects on trophic structure and species diversity is well-described (Rooney and Waller 2003, Côté et al. 2004). Our results suggest that although the response to herbivore removal alone was modest in most plant functional groups, interrupting current conditions by cutting and fencing is likely to provide the best overall outcome for native species in invaded oak meadows.

TABLES

**Table 0.1:** Expected and observed response of seven plant functional groups to cutting and fencing. There were no native annual graminoids observed in the plant community.

	Treatment	Native		Non-native		Native		Non-native		Native		Non-native	
		Annual	Forbs	Annual	Forbs	Perennial	Forbs	Perennial	Forbs	Perennial	Forbs	Perennial	Forbs
Expected	Cutting	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase
	Fencing	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase
Observed	Cutting	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase	Increase
	Fencing	No difference	No difference	No difference	No difference	No difference	No difference	No difference	No difference	No difference	No difference	No difference	No difference

**Table 0.2:** The response of total richness, native biomass, and non-native biomass to cutting and fencing treatments. Main effects, interactions, time (day of survey), and seablush (count of *Plectritis congesta* stems in 2005) from a two level (+/-), two factor [cutting (Cut=C) and fencing (Fence=F)] experiment in a Garry oak meadow. Seablush occurred in the plots as part of another study and were not collected. The plant community was characterized into eight plant functional groups by nativity [native (N)/non-native (NN)], growth form [annual (A)/perennial (P)], and plant type [forb (F)/graminoid (G)]. No native annual graminoids were found in the community. Parameter estimates (Est), standard errors (SE), test values (test), p-values (P), degrees of freedom (DF), -2 log likelihood value (-2LogL), and goodness of fit values ( $\chi^2/DF$ ) are given.

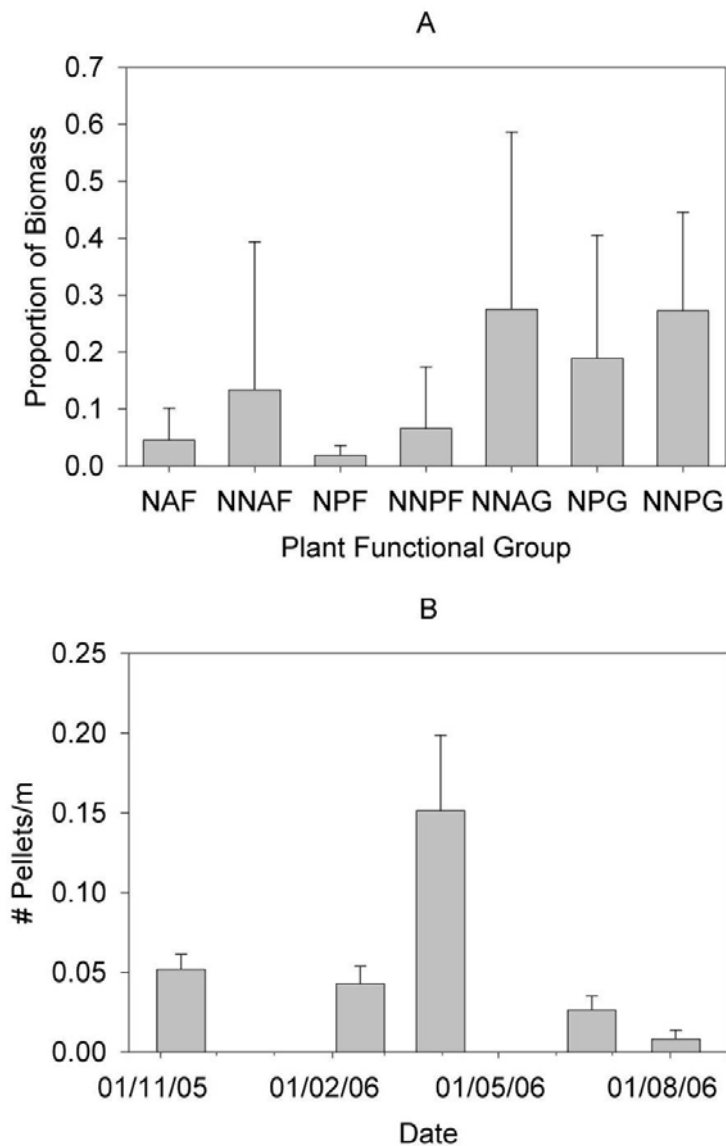
Response Variable	Effect	Cut	Fence	Cut	Fence	Est	SE	Test	P	DF	-2LogL	$\chi^2/DF$
Total Richness	Cut	C-		C+		-0.07	0.08	F=5.02	0.03	1,51	-310.85	0.65
	Fence		F-		F+	0.15	0.08	F=2.60	0.11	1,51		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	-0.12	0.11	F=0.31	0.31	1,51		
	Time					0.00	0.00	F=0.00	0.98	1,51		
Native Biomass	Cut	C-		C+		-21.02	9.88	F=4.68	0.04	1,49		
	Fence		F-		F+	-24.6	9.70	F=7.21	0.01	1,49		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	12.36	13.72	F=0.81	0.37	1,49		
	Time					0.00	0.00	F=0.00	0.98	1,51		
Non-native Biomass	Cut	C-		C+		84.71	39.08	F=3.23	0.08	1,51		
	Fence		F-		F+	-13.95	39.08	F=3.14	0.08	1,51		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	-70.04	55.27	F=1.61	0.21	1,51		
	Time					0.00	0.00	F=0.00	0.98	1,51		
Native Annual Forbs	Cut	C-		C+		-0.92	0.36	F=5.49	0.02	1,43	-278.01	1.4
	Fence		F-		F+	-0.30	0.34	F=0.02	0.88	1,43		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	0.69	0.48	F=2.08	0.16	1,43		
	Time					0.01	0.00	F=2.99	0.09	1,43		
Non-native Annual Forbs	Cut	C-		C+		-0.66	0.32	F=3.98	0.05	1,43	-115.29	1.15
	Fence		F-		F+	0.11	0.32	F=1.72	0.20	1,43		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	0.45	0.42	F=1.17	0.29	1,43		
	Time					0.00	0.00	F=0.17	0.75	1,43		
<i>Plectritis</i>	Cut	C-		C+		0.00	0.00	F=0.42	0.52	1,43		
	Fence		F-		F+	-0.30	0.34	F=0.02	0.88	1,43		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	0.69	0.48	F=2.08	0.16	1,43		
	Time					0.01	0.00	F=2.99	0.09	1,43		

Response Variable	Effect	Cut	Fence	Cut	Fence	Est	SE	Test	P	DF	-2LogL	X <sup>2</sup> /DF
Native Perennial Forbs	Cut	C-		C+		0.19	0.36	F=0.10	0.75	1,48	-191.13	1.08
	Fence		F-		F+	-0.33	0.43	F=2.13	0.15	1,48		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	-0.22	0.46	F=0.23	0.63	1,48		
	Time					-0.01	0.00	F=10.58	<0.01	1,48		
	<i>Plectritis</i>					0.00	0.00	F=0.42	0.52	1,48		
Non-native Perennial Forbs	Cut	C-		C+		-0.31	0.45	F=0.78	0.38	1,40	-180.76	0.87
	Fence		F-		F+	0.04	0.49	F=0.04	0.84	1,40		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	0.06	0.58	0.010	0.91	1,40		
	Time					0.00	0.01	0.530	0.47	1,40		
	<i>Plectritis</i>					0.00	0.00	0.450	0.51	1,40		
Non-native Annual Graminoids	Cut	C-		C+		-0.96	0.42	F=1.2	0.28	1,43	-94.57	0.99
	Fence		F-		F+	-1.07	0.50	F=1.2	0.28	1,43		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	1.32	0.56	F=5.45	0.02	1,43		
	Cut*Fence	C-	F-	C-	F+	0.25	0.44	t=0.56	0.58	1,43		
	Cut*Fence	C-	F-	C+	F-	0.35	0.37	t=0.95	0.35	1,43		
	Cut*Fence	C-	F-	C+	F+	-0.72	0.49	t=-1.47	0.15	1,43		
	Cut*Fence	C-	F+	C+	F-	0.11	0.45	t=0.24	0.81	1,43		
	Cut*Fence	C-	F+	C+	F+	-0.96	0.42	t=-2.30	0.03	1,43		
	Cut*Fence	C+	F-	C+	F+	-1.07	0.50	t=-2.16	0.04	1,43		
	Time					-0.01	0.00	F=1.49	0.23	1,43		
	<i>Plectritis</i>					0.00	0.00	F=3.87	0.06	1,43		
Native Perennial Graminoids	Cut	C-		C+		-0.58	0.36	F=4.59	0.04	1,42	-68.18	1.17
	Fence		F-		F+	0.01	0.37	F=0.01	0.90	1,42		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	0.07	0.49	F=0.02	0.89	1,42		
	Time					0.00	0.00	F=0.9	0.35	1,42		
	<i>Plectritis</i>					0.00	0.00	F=2.93	0.09	1,42		

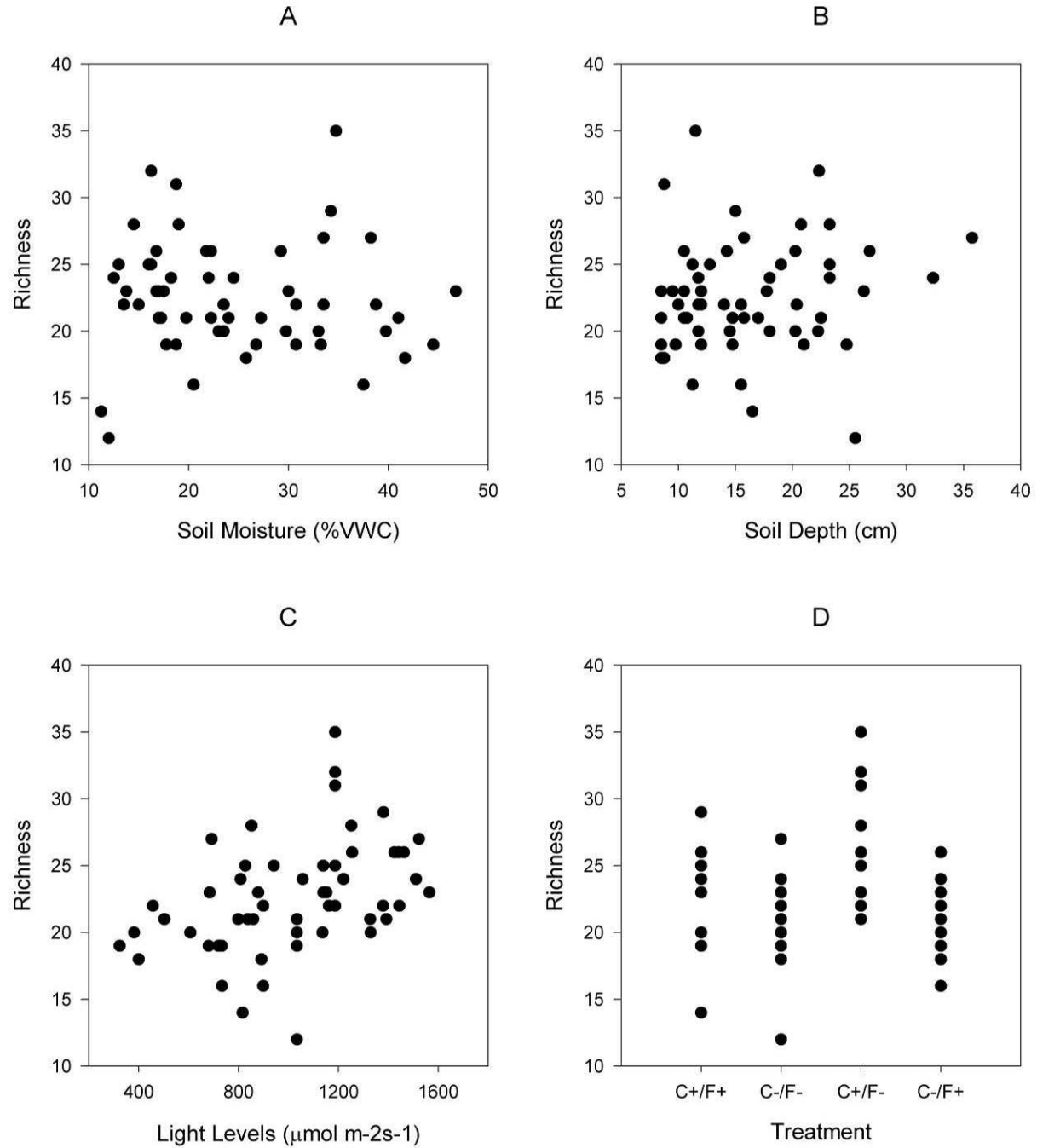
Response Variable	Effect	Cut	Fence	Cut	Fence	Est	SE	Test	P	DF	-2LogL	X <sup>2</sup> /DF
Non-native	Cut	C-		C+		1.44	0.30	F=19.31	<0.0001	1,43	-57.02	1.21
Perennial												
Graminoids	Fence		F-		F+	0.66	0.33	F=0.14	0.71	1,43		
	Cut*Fence	C+/-	F-/+	C-/+	F+/-	-1.13	0.39	F=8.48	0.01	1,43		
	Cut*Fence	C-	F-	C-	F+	-0.48	0.28	t=-1.68	0.10	1,43		
	Cut*Fence	C-	F-	C+	F-	0.30	0.26	t=1.17	0.25	1,43		
	Cut*Fence	C-	F-	C+	F+	0.96	0.33	t=2.87	0.01	1,43		
	Cut*Fence	C-	F+	C+	F-	0.78	0.28	t=2.80	0.01	1,43		
	Cut*Fence	C-	F+	C+	F+	1.44	0.30	t=4.86	<0.0001	1,43		
	Cut*Fence	C+	F-	C+	F+	0.66	0.33	t=2.02	0.05	1,43		
Time						0.01	0.00	F=3.17	0.08	1,43		
<i>Plectritis</i>						0.00	0.00	F=1.25	0.27	1,43		



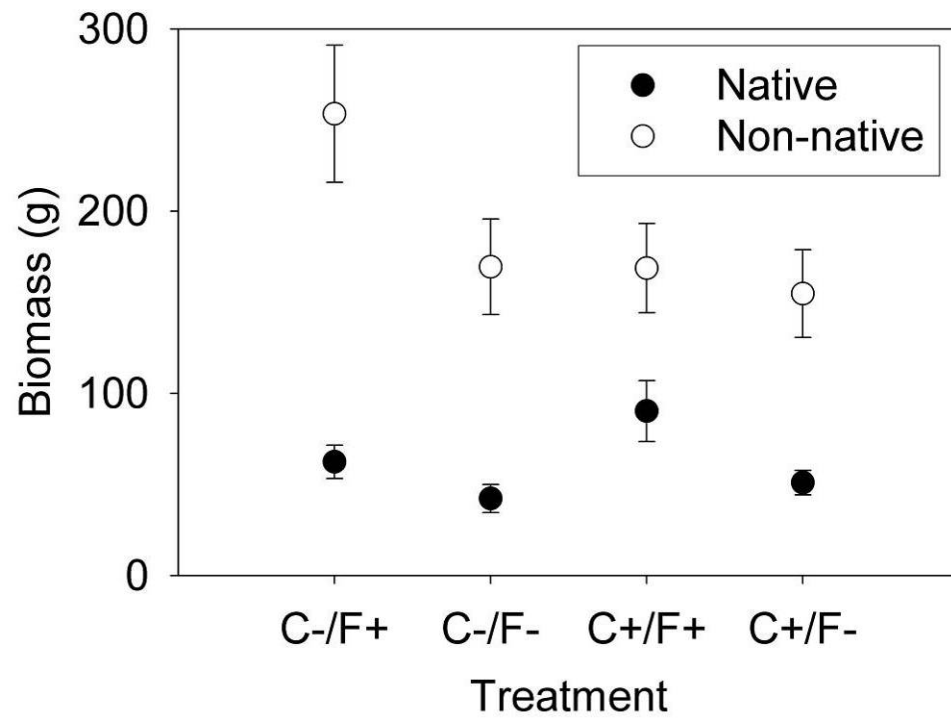
## FIGURES



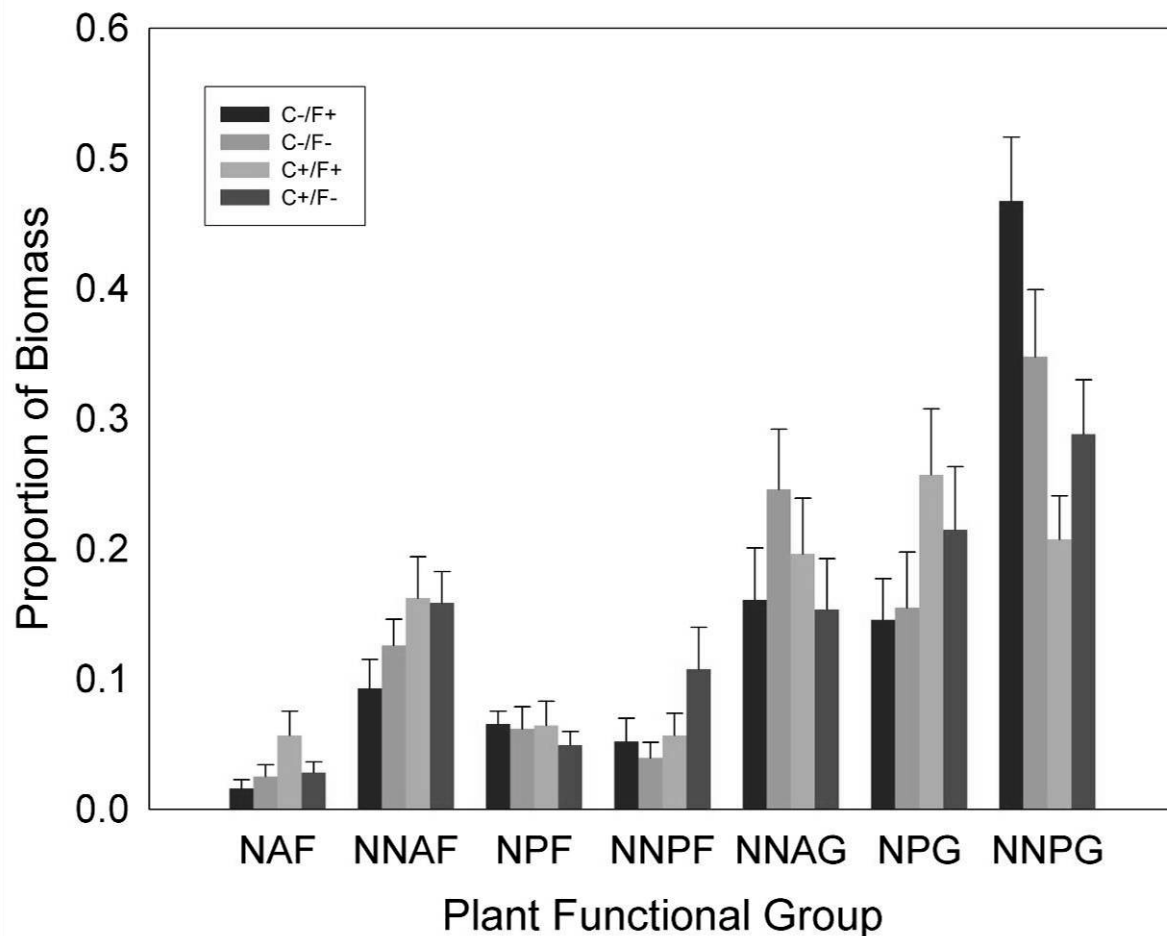
**Figure 0.1:** Extant plant community composition and seasonal herbivore deposition. A) Proportional biomass of the seven plant functional groups found at CNERA as estimated from vegetation cut at ground level on June 16-18, 2004 from eight 0.5 m diameter plots, identified to species, dried and weighed. Species were categorized into eight plant groups: native (N) or non-native (NN), annual (A) or perennial (P), and forb (F) or graminoid (G). No native annual graminoids were found. B) Summary of pellet counts along 10 transects throughout CNERA. Surveyors counted the number of pellets within approximately 1 m to each side of transects and then cleared the area of pellets. Transects varied in length ( $65.1 \pm 10.8$  m) and time ( $6.9 \pm 0.97$  min) due to topographic variability of the meadows. Error bars=+1SE.



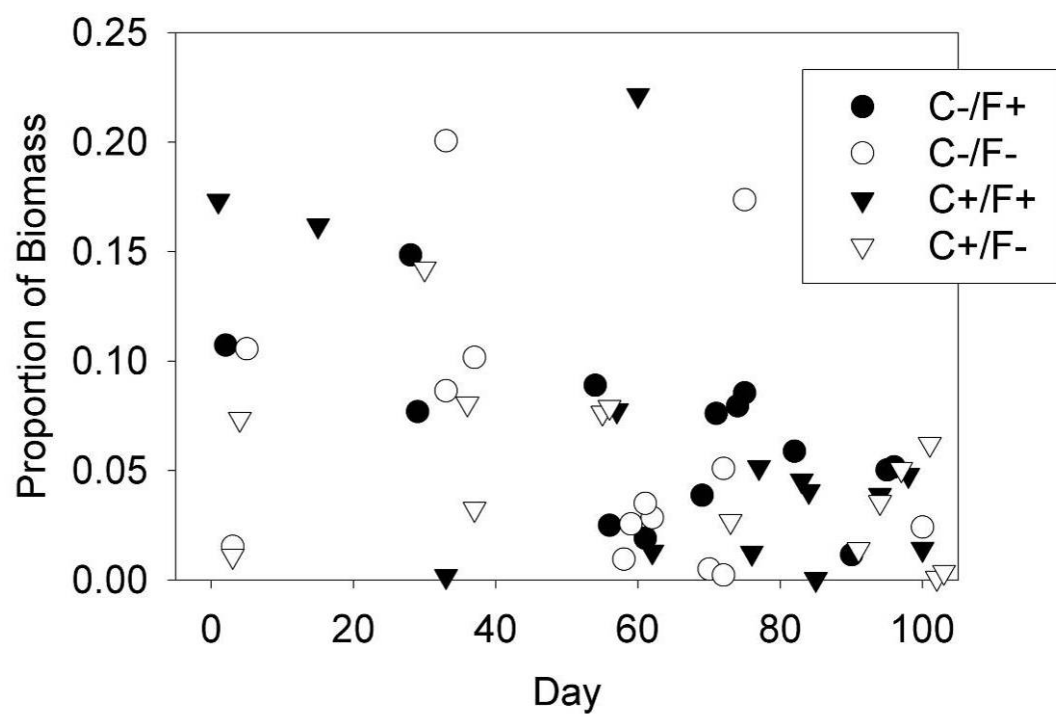
**Figure 0.2:** Relationship among species richness and soil moisture, soil depth, light levels, and experimental treatments. (A) Species richness vs. soil moisture ( $X^2/\text{DF}=0.79$ ,  $F_{1,54}=0.59$ ,  $P=0.447$ ); (B) species richness vs. soil depth ( $X^2/\text{DF}=0.8$ ,  $F_{1,54}=0.15$ ,  $P=0.698$ ); (C) species richness vs. light levels ( $X^2/\text{DF}=0.65$ ,  $F_{1,54}=7.74$ ,  $P=0.007$ ); and (D) species richness vs. treatments (Cut:  $X^2/\text{DF}=0.65$ ,  $F_{1,51}=5.02$ ,  $P=0.030$ , Fence:  $F_{1,51}=2.60$ ,  $P=0.113$ , Cut\*Fence:  $F_{1,51}=0.31$ ,  $P=0.308$ ).



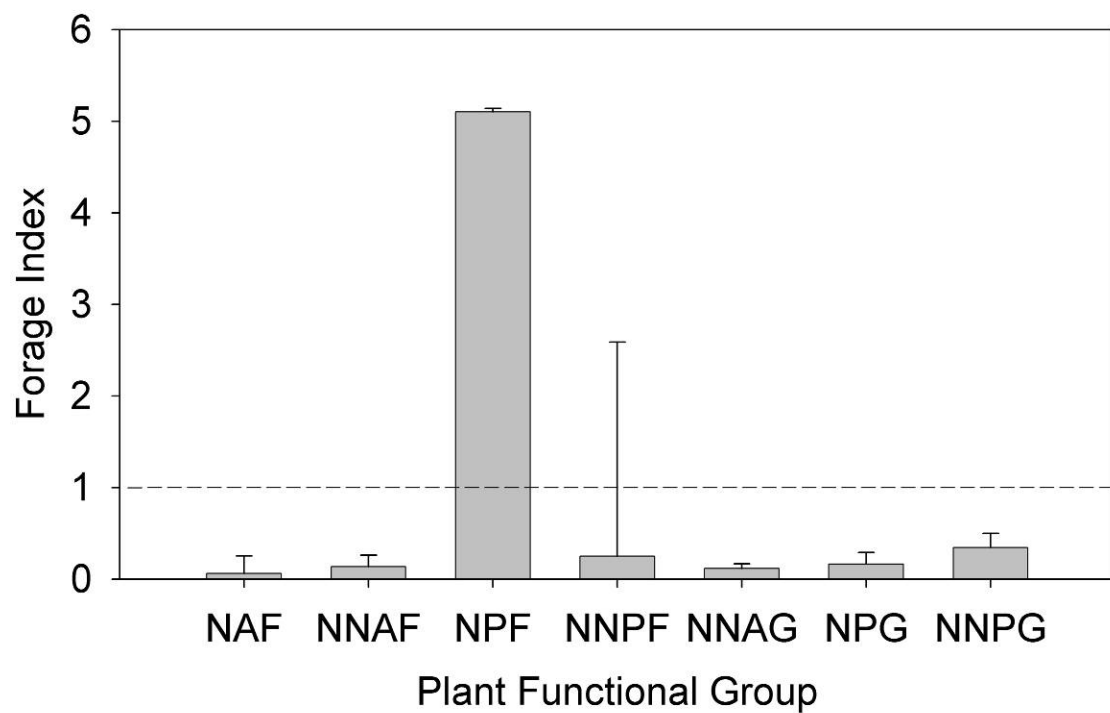
**Figure 0.3:** Native and non-native plant biomass in a two level (+/-), two factor, cutting (C) and fencing (F), experiment in a Garry oak meadow. Error bars =  $\pm 1$ SE.



**Figure 0.4:** Proportional biomass of plant functional groups characterized as native (N) or non-native (NN), annual (A) or perennial (P), and forb (F) or graminoid (G) in a two level (+/-), two factor, cutting (C) and fencing (F), experiment in a Garry oak meadow. Error bars = +1SE. There were no native annual graminoids found in the community.



**Figure 0.5.** Proportional biomass of native perennial forbs in a two level (+/-), two factor, cutting (C) and fencing (F), experiment with day of biomass collection.



**Figure 0.6.** Forage indices for plant functional groups. Values  $>1$  indicate selection in greater proportion than the availability of the plant group in the community. Error bars =  $+1SE$ .

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## LITERATURE CITED

- Augustine, D. J. and Frelich, L. E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conserv. Biol.* 12: 995-1004.
- Augustine, D. J. and McNaughton, S. J. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *J. Wildl. Manage.* 62: 1165-1183.
- Cingolani, A. M., Noy-Meir, I. and Diaz, S. 2005. Grazing effects on rangeland diversity: A synthesis of contemporary models. *Ecol. Appl.* 15: 757-773.
- Clark, B. R., Hartley, S. E., Suding, K. N. and de Mazancourt, C. 2005. The effect of recycling on plant competitive hierarchies. *Am. Nat.* 165: 609-622.
- Côté, S. D. 2005. Extirpation of a large black bear population by introduced white-tailed deer. *Conserv. Biol.* 5, 1668.
- Côté, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C. and Waller, D. M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Syst.* 35: 113-147.
- Crawley, M. J. 1990. The population dynamics of plants. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 330: 125-140.
- Devine, W. D., Harrington, C. A. and Lathrop, P. L. 2007. Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* dougl. ex hook.) seedlings. *Restor. Ecol.* 15: 212-222.
- Field, S. A., O'Connor, P. J., Tyre, A. J. and Possingham, H. P. 2007. Making monitoring meaningful. *Austral Ecol.* 32: 485-491.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conserv. Biol.* 8: 629-644.
- Fletcher, J. D., McShea, W. J., Shipley, L. A. and Shumway, D. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Nat. Areas J.* 21: 172-176.
- Frankland, F. and Nelson, T. 2003. Impacts of white-tailed deer on spring wildflowers in Illinois, USA. *Nat. Areas J.* 23: 341-348.
- Fuchs, M. A. 2001. Towards a recovery strategy for Garry oak and associated ecosystems in Canada: Ecological assessment and literature review. Rep. GBEI/EC-00-030.
- Fuhlendorf, S. D., and Engle, D. M. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625-632.



- Garibaldi, L. A., Semmartin, M. and Chaneton, E. J. 2007. Grazing-induced changes in plant composition affect litter quality and nutrient cycling in flooding Pampa grasslands. *Oecologia* 151: 650-662.
- Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, New York. 222 pp.
- Hobbs, R. J. and Huenneke, L. F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Cons. Biol.* 6: 324-337.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. and Wardle, D. A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75: 3-35.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge. 681 pp.
- Iglesias, R. M. R. and Kothmann, M. M. 1998. Best linear unbiased prediction of herbivore preferences. *J. Range Manage.* 51: 19-28.
- Jenkins, C. N. and Pimm, S. L. 2003. How big is the global weed patch? *Ann. Mo. Bot. Gard.* 90: 172-178.
- Jentsch, A. 2007. The challenge to restore processes in face of non-linear dynamics – on the crucial role of disturbance regimes. *Restor. Ecol.* 15: 334–339.
- Keeley, J. E., Lubin, D. and Fotheringham, C. J. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.* 13: 1355-1374.
- Kellogg, C. H. and Bridgham, S. D. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. *Biol. Invasions* 6: 319-329.
- Krausman, P. R., Kuenzi, A. J., Etchberger, R. C., Rautenstrauch, J. R., Ordway, L. L. and Hervet, J. J. 1997. Diets of desert mule deer. *J. Range Manage.* 50: 513–522.
- Kulmatiski, A. 2006. Exotic plants establish persistent communities. *Plant Ecol.* 187: 261-275.
- Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Funct. Ecol.* 16: 545-556.
- Lavorel, S., McIntyre, S., Landsberg, J. and Forbes, T. D. A. 1997. Plant functional classification: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12: 474-478.

- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. and Wardle, D. A. 2001. Ecology - biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294: 804-808.
- Lortie, C. J. and Cushman, J. H. 2007. Effects of a directional abiotic gradient on plant community dynamics and invasion in a coastal dune system. *J. Ecol.* 95: 468-481.
- MacDougall, A. S. 2005. Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology* 86: 3354-3363.
- MacDougall, A. S. and Turkington, R. 2007. Does the type of disturbance matter when restoring disturbance-dependent ecosystems? *Restor. Ecol.* 15: 263-272.
- MacDougall, A. S. and Turkington, R. 2006. Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology* 87: 1831-1843.
- MacDougall, A. S. and Turkington, R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86: 42-55.
- MacDougall, A. S. and Turkington, R. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *J. Ecol.* 92: 422-434.
- MacDougall, A. S., Beckwith, B. R. and Maslovat, C. Y. 2004. Defining conservation strategies with historical perspectives: A case study from a degraded oak grassland ecosystem. *Conserv. Biol.* 18: 455-465.
- MacDougall, A. S., Boucher, J., Turkington, R. and Bradfield, G. E. 2006. Patterns of plant invasion along an environmental stress gradient. *J. Veg. Sci.* 17: 47-56.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. and Erickson, W. P. 2002. *Resource selection by animals*, 2nd edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mooney, H. A. and Godron, M. (eds). 1983. *Disturbance and ecosystems*. Springer-Verlag, Berlin, 292 pp.
- Myers, J. A., Vellend, M., Gardescu, S. and Marks, P. L. 2004. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139: 35-44.
- Navarro, T., Alados, C. L. and Cabezudo, B. 2006. Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *J. Arid Environ.* 64: 298-322.
- Palmer, M. A., Ambrose, R. F. and Poff, N. L. 1997. Ecological theory and community restoration ecology. *Restor. Ecol.* 5: 291-300.

- Rooney, T. P. and Waller, D. M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* 181: 165-176.
- Seabloom, E. W., Harpole, W. S., Reichman, O. J. and Tilman, D. 2003a. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Nat. Acad. Sci. USA* 100: 13384-13389.
- Seabloom, E. W., Borer, E. T., Boucher, V. L., Burton, R. S., Cottingham, K. L., Goldwasser, L., Gram, W. K., Kendall, B. E. and Micheli, F. 2003b. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecol. Appl.* 13: 575-592.
- Sinclair, A. R. E. and Byrom, A. E. 2006. Understanding ecosystem dynamics for conservation of biota. *J. Anim. Ecol.* 75: 64-79.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15: 353-391.
- Stockton, S. A., Allombert, S., Gaston, A. J. and Martin, J. L. 2005. A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biol. Conserv.* 126: 118-128.
- Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923-1926.
- Vellend, M. 2002. A pest and an invader: White-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). *Nat. Areas J.* 22: 230-234.
- White, P. S. and Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Prog. Bot.* 62: 399-450.
- Wiegmann, S. M. and Waller, D. M. 2006. Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. *Biol. Conserv.* 129: 109-123.
- Williamson, M. H. 1996. Biological invasions. Chapman and Hall, London, UK. 244 pp.
- Wilsey, B. J. and Polley, H. W. 2006. Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia* 150: 300-309.
- Wisdom, M. J., Vavra, M., Boyd, J. M., Hemstrom, M. A., Ager, A. A. and Johnson, B. K. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: Knowledge gaps and management needs. *Wildl. Soc. Bull.* 34: 283-292.

## Chapter 5: Conclusions

*In the end, we will conserve only what we love. We will love only what we understand. —Baba Dioum (from Conservation Biology: Research Priorities for the Next Decade by Michael E. Soulé and Gordon H. Orians 2001)*

Biotic homogenization is occurring at a global scale and is characterized by increasing abundances of non-native species and declining abundances of native species (Rooney et al. 2004, McKinney and La Sorte 2007). The many processes facilitating this shift, however, are likely to interact in complex ways (White et al. 2006) and recovery may be inhibited if the mechanisms of native species decline are incorrectly identified (Didham et al. 2005). The presumption that non-native species have uniformly deleterious effects on native species has also hampered progress in invasion ecology. Specifically, a narrow focus in ecological theory (Davis et al. 2001) and the assumption that increasing abundances of non-native species explain native species decline (Gurevitch and Padilla 2004) have each limited the breadth of hypotheses considered as potential explanations of invasion success (Mitchell et al. 2006).

Management action, meanwhile, tends to take a focal species, crisis approach. In this scenario, control efforts are not typically initiated until after non-native species have become established, and often after they have become difficult and expensive to eradicate (Simberloff 2003). Non-native species eradication efforts may also focus on the symptom, but not the cause of native species decline (Didham et al. 2005), whereas effective management would be better served by an ecosystem-level approach (Hobbs and Humphries 1995). Research is starting to explore alternative hypotheses of invasion success, whereby non-native dominance is an indirect consequence of other mechanisms driving native species loss (Howe et al. 2006, MacDougall and Wilson 2007). Scientists and managers, however, are sufficiently disconnected with each

other so that advances in invasion ecology may not be implemented (Robinson 2006, Anonymous 2007). In addition to summarizing the research presented here, and considering future areas for investigation, I will address some of the issues surrounding the integration of science into management and propose solutions.

#### RESEARCH SUMMARY

*“Trouble is, just because things are obvious doesn't mean they're true.” Esmerelda (Granny) Weatherwax in The Wyrds Sisters by Terry Pratchett*

Native species are declining in Garry oak meadows and I asked whether ungulates could drive these losses and thereby facilitate indirectly the invasion of non-native grasses. Using islands as observational units in a natural experiment, I showed that increasing herbivore densities were related to declines in the abundance of native forbs, and increases in the abundance of non-native annual grasses (**Chapter 2**). I further showed that these regional patterns, the results of comparative analysis, were upheld by experiments conducted at the local scale that compared the fitness of natives species exposed to and protected from herbivory. Specifically, I showed that ungulates limited the establishment, growth, survival and reproduction of seedlings and established native forbs and shrubs (**Chapter 3**). As a result, I suggest that ungulates also reduce the abundance of native seeds in Garry oak meadows. This work supports similar studies in other habitats which showed that selective herbivory affects plant recruitment, survival and reproduction and can produce profound shifts in community composition when herbivores are abundant (Rooney and Waller 2003, Howe et al. 2006, MacDougall and Wilson 2007).

Increasing ungulate density can drive plant community transition because grasses possess avoidance and tolerance strategies to resist herbivory (Vicari and Bazely 1993, Strauss and

Agrawal 1999). Non-native annual grasses, which are phylogenetically distinct from native species in the community, appear to avoid herbivory as they were rarely browsed and increased with increasing herbivore density (**Chapter 2**). Being functionally unique has influenced successful invasion elsewhere (Strauss et al. 2006) but mechanisms underlying this success are rarely identified. Here, I showed that, in addition to competitive ability (Fargione et al. 2003), escape from herbivory is another way this can occur. Conversely, non-native perennial grasses have native analogues and were selectively browsed by ungulates (**Chapter 2**). Although herbivory reduced their biomass relative to non-native annual grasses, they remained one of the dominant plant groups (**Chapter 4**). Further, herbivore density did not affect their regional level abundances (**Chapter 2**). Conditions have changed in many Garry oak meadows to favour abundant deer (land conversion, limited or no hunting, predator eradication) and increased herbivore pressure appears to benefit the non-native grasses which possess strategies to avoid or tolerate those conditions.

That non-native annual and perennial grasses differ in their responses to herbivory has consequences for restoration. Protection from herbivores increased the biomass of non-native perennial grasses relative to non-native annual grasses (**Chapter 4**). Non-native perennial grasses suppress native forb germination and reproduction (MacDougall and Turkington 2004) and, consistent with this finding, removing live biomass and litter increased the relative biomass of native plants (**Chapter 4**). This suggests that reductions of deer alone may not result in increased abundances of native forbs; instead, non-native perennial grasses may replace non-native annual grasses. Therefore, whereas reductions to herbivory are needed for native forbs to recover, removal of non-native grasses may also be required, particularly perennial grasses protected from herbivory. Overall, however, fencing had a greater positive effect on native

biomass (**Chapter 4**) and the performance of transplanted species at both early and mature life stages relative to live biomass and litter removal (**Chapter 3**). This illustrates the strength of herbivory as a mechanism of native species decline in shallow soil Garry oak meadows.

#### FUTURE RESEARCH

Black-tailed deer (*Odocoileus hemionus*) are native to Garry oak meadows and it is likely that it is the change in their densities rather than herbivory itself that has resulted in the loss of native species. Moderate levels of herbivory can increase diversity (Connell 1978, Huston 1994) and palatable native species (*Camassia spp.*) dominated the plant community on some islands with no deer (pers. obs.). To examine the relationship between native species richness and herbivore density, I counted the number of species in each plot from the comparative analysis and calculated a mean value by island (**Chapter 2**). Using simple linear regression (Proc REG, SAS 9.1, SAS Institute 2003, Cary, NC), native richness generally declined with herbivore density ( $R^2=0.24$ ,  $F_{1,38}=12.02$ ,  $p=0.001$ , Fig. 5.1). However, deer were present on the islands with the greatest native richness. Given that reductions in deer density are needed to restore Garry oak meadows, it would be useful to experimentally quantify the density of deer that maximizes native species diversity.

Although herbivory caused native species declines in shallow soil Garry oak meadows, herbivory can be beneficial in sites with high resource availability (Huston 1994). Whether herbivory, competition, or some other processes drive declines of native species in deep soil sites, however, is less clear. Competition is expected to be the dominant process reducing diversity in resource rich sites relative to herbivory (Huston 2004). Herbivory, therefore, may increase diversity in resource rich sites if dominant plant species are limited by browsing. The

outcome will depend on the herbivore avoidance/tolerance strategies and competitive abilities of plants in the community. Conducting the factorial experiments described in Chapters 3 and 4 at deep soil Garry oak meadows would address this hypothesis. Nevertheless, non-native perennial grasses increase with fencing and dominate deep soil sites (MacDougall and Turkington 2005), therefore, fencing and cutting is likely to produce increased native forb abundances regardless of soil depth.

Given the fragmented nature of Garry oak meadows, establishment of landscape linkages is part of the long-term recovery goals (GOERT 2007). Isolation limits opportunities for the dispersal of native seed (Tilman 1997, Levine 2000, Lord and Lee 2001), and many native plants in Garry oak meadows are dispersal limited (MacDougall 2005). However, the efficacy of patch connectivity is debated (Simberloff et al. 1992, Beier and Noss 1998) and alternative methods such as increasing patch size may be a more effective at increasing populations (Falcu and Estades 2007). Isolation has reduced the invasion of non-native species in Garry oak meadows (**Chapter 2**, Lilley and Vellend, in review). Parks Canada's decision to close the small islets in the Gulf Islands National Park Reserve to visitors coupled with non-native species removal will help preserve the native abundance of these meadows. Similarly, 'mainland' patches may benefit from a conifer buffer relative to reduce propagule pressure of non-native species (J. Bennett, pers. comm.). Landscape level studies are needed given the uncertain benefits of connectivity for Garry oak meadow recovery.

Patch connectivity is one method to increase dispersal; however, deer can also facilitate dispersal of plants (Vellend et al., 2003, Myers et al. 2004). Historically, deer were likely critical in the post-glacial colonization of the region. Presently, however, deer have contributed to the



spread of invasive species elsewhere (Vellend 2002) and research in progress suggests this could be occurring in Garry oak meadows as well (Marsico and Gonzales, unpub. data). Out of 38 plant species that germinated from deer pellets collected from Garry oak meadows, 30 were non-native and three others have both native and non-native origins (Marsico and Gonzales, unpub. data). At first this may appear incongruent with the forage selectivity analyses presented in **Chapters 2 and 4**, but selection is a function of abundance as well as preference. Herbivores forage on native forbs preferentially when available, but in invaded meadows, non-native species are typically abundant and therefore make up the bulk of the biomass consumed. Selective reduction of native plant growth and reproduction, coupled with increased dispersal of non-native plant species via endo- and ectozoochory has the potential to create a spiraling feedback effect on the abundance of native forbs. Compounded by the suppressive effects of increasing non-native grass biomass and litter, the need for conservation and restoration is clear.

## RESTORATION

*“We're supposed to meddle with things we don't understand. If we hung around waiting until we understood things, we'd never get anything done.” – Archchancellor M. Riddcully in Interesting Times by Terry Pratchett*

Herbivory is a dominant driver of native forb declines in Garry oak meadows. These declines are compounded by dispersal limitation and suppressive non-native grass biomass; therefore, restoration is likely to require a multi-tiered approach. My results suggest that it will be necessary to reduce herbivore pressure where deer are abundant, particularly on shallow soil sites. This could be achieved through fencing, culling, or increased deer alertness. For example, although hunting can reduce deer abundance, it can also benefit plants if hunted deer spend more time alert and less time feeding (Brown et al. 1999, Martin and Baltzinger 2002). Deer preferentially forage in clearings (Stewart et al. 2000), such as Garry oak meadows, but may

spend more time in forested habitats with cover if they feel threatened. Fertility control, repellents and habitat modification have also been identified as alternatives to hunting in suburban communities, although the success of these approaches remain uncertain, especially as long-term solutions (DeNicola et al. 1997, Rudolph et al. 2000, Lauber and Knuth 2004, Merrill et al. 2006). In deep soil sites, the relative importance of protection from herbivory and removal of non-native species may be reversed, but as long as biomass removal accompanies fencing, native species are expected to increase in abundance if they are present (MacDougall and Turkington 2007).

Many Garry oak meadows have been subject to strong herbivore pressure for at least 50 years (MacDougall, in review) and it is likely that many palatable native species have already declined and been extirpated or have adjusted tactics, such as shifting from sexual to vegetative reproduction. As a consequence, native species augmentation will also be required to increase the relative abundance of native species, return extirpated species, and provide sufficient population sizes as a buffer against herbivory for sites where deer cannot be reduced substantially. Sites with low densities of herbivores may provide a template for historical Garry oak meadow composition, as well as seed sources for native species augmentation. The dominance of non-native grasses also confers a long-term ‘weighted lottery’ advantage via propagule pressure (Lavorel and Lebreton 1992), suggesting that non-native removal may hasten native species recovery.

The invasion of non-native species has stimulated theoretical and applied research as well as public involvement, however, these groups are largely disconnected from each other (Davis et al. 2001, Robinson 2006). Whereas non-native species are still widely viewed in a reified

fashion in the restoration community, recent research in invasion ecology incorporates a community level perspective (Shea and Chesson 2002). The successful identification of the causal factors enhancing ecosystem invasibility should lead to more effective, integrated control programs (Hobbs and Humphries 1995). The knowledge gained from research, however, has yet to be widely incorporated into management action (Rogers 1998, Robinson 2006, Anonymous 2007). Restoration efforts remain focused on the control of established focal non-native species whereas early detection and treatment of non-native species before they become established will prevent many future problems (Simberloff 2003). Extensive funds have been dedicated to failed eradication efforts for species where deleterious ecological effects are equivocal (Hager and McCoy 1998, Sheail 1999, Gonzales et al., in press). Given that conservation funds are limited, we need to find effective, efficient solutions and this will require scientists and managers communicating more effectively so that knowledge and action are linked.

Both scientists (e.g., Rogers 1997, Walters 1997) and managers (Lewis 2007) recognize a need to improve communication and to implement science in resource management, but a cultural divide persists (Roux et al. 2006, Anonymous 2007). Some of the problems are institutional, science and managers have divergent operational philosophies and reward systems (Rogers 1997). Scientists have a propensity to seek problems of intellectual difficulty and innovation and managers have a drive to be pragmatic and serve their institutional hierarchy. For example, Walters (1997) identified the low success rates in implementing adaptive management on several institutional barriers, such as bureaucratic and political inaction fostered by fear of risk and scientific self-interest. Carpenter (1998) likened academic culture to an ecological community “where intense competition for limited resources in a stable, sheltered environment creates rigorously defended niches” and selects “against research on complex, variable

ecosystems that require long-term study and cross-disciplinary collaboration.” The cultural differences between these groups create barriers or delays of knowledge from scientific capability to implementation to achieve desired outcomes. Scientists and managers need to adopt approaches that bring success among their peers, but alternative approaches are needed to find a common process and purpose when interacting to solve ecological problems (Rogers 1998).

Fostering relationships between science and management is one of the goals of the Canon National Park Science Scholars Program. The Program was established in 1997 to develop the next generation of scientists working in the fields of national park management and conservation. The Program embodies Canon’s corporate principle of *kyosei*, living and working together for the common good. An annual retreat is integral to the Program and from October 9-14, 2007, a decade of ‘Canon scholars’ were invited to Grand Canyon National Park to interact with their peers, the Park community, and representatives from the Program’s collaborators. Each retreat includes a ‘Lessons Project’ to conceptualize key challenges of National Park conservation. The 2007 challenge was to recommend strategies that scientists can implement to increase the implementation of science into park management. Briefly, my recommended strategies included to:

1. Take part in efforts that encourage external scientific capacity. For example, the National Park Service established the “Sabbatical in the Parks” program whereby scientists are offered logistical support such as housing, computers, and lab space for field studies. Protected areas provide an opportunity for large scale research projects (Arcese and Sinclair 1997) that can benefit both researchers and protected areas;

2. Convey complex information by developing a common knowledge base and combining syntheses of key scientific results with information-rich visual elements. Scientific reports and publications can be ineffective media for managers given differences in background and terminology. New approaches, such as the attractive, conceptual models illustrated by Dennison and colleagues (2007), are more effective for diverse audiences;
3. Engage with managers at the beginning of a research program to learn Park priorities and incorporate them in project design (Roux et al. 2006). Then be creative in developing a research program that meets the scientific rigour and innovation needed for publication with the flexibility of providing information that managers deem relevant;
4. Appreciate the multiple considerations managers have in addition to ecological concerns. Scientists have the luxury of exploring an issue in depth. Managers must consider a breadth of issues and only some of these are ecological, others are political, financial, and social (Lewis 2007);
5. Develop dynamic conceptual and quantitative ecosystem process models to see the effects of management decisions (Clark et al. 2001, Landsberg 2003). Minimize complexity and speak honestly about uncertainty;
6. Create a collaborative communication environment with bi-directional communication flow. Scientists can identify problems whereas managers have the capacity and skills to address the problems (Hilborn et al. 2003). Scientists, however, rarely acknowledge the skills, experience, and perspectives of managers (Roux et al. 2006) and sharing information benefits from acknowledging the contributions of both

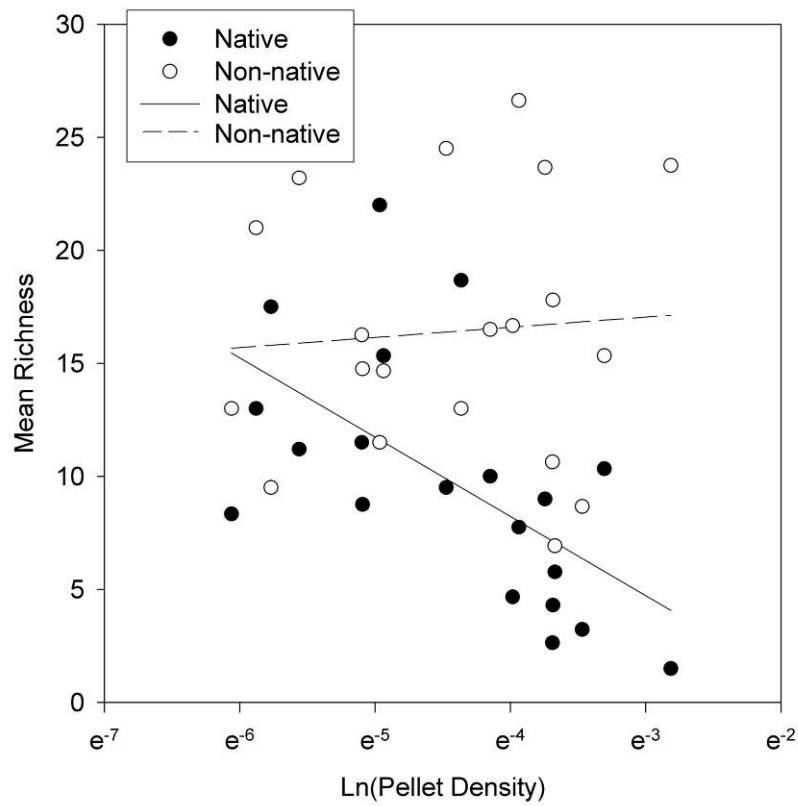
parties (Saunders et al. 2006). This requires a shift from a view of that knowledge is an entity that is transferred from scientists to managers to viewing knowledge as a “process of relating” that involves discussions among partners (Roux et al 2006:4); and

7. Begin with acknowledging the common goal. When conflict arises, examine whether there has been deviation from that goal and how to get back on track.

Implementation of biodiversity conservation actions is driven by private contributions and political decisions (Orr 2003) and social scientists have long recognized the importance of engaging people in conservation solutions (Higgs 2003). However, the human component has not always been seen as relevant to ecologists, despite the fact that human behaviour is causing the loss of biodiversity and human behavioural change will be necessary to achieve more sustainable relationships among humans and other species (Saunders et al. 2006). Increasingly, however, researchers are being urged to generate relevant science either through study of human-dominated landscapes or by improved communication with managers and the public (Rosenzweig 2003, Robinson 2006, Schwartz 2006). Information about ecological integrity needs to be communicated to the people who have a direct impact on its persistence (Norton 1998). Given the amount of Garry oak meadow in and adjacent to private hands, public outreach is going to be a critical component of conservation and restoration (e.g., Whitelaw and Eagles 2007). The proximity of Garry oak ecosystems to urban areas also increases opportunities for people to engage people in the shared personal responsibility of the maintenance of wildlands (Schwartz 2006). There is no greater way to get people to internalize a biodiversity ethic than to have them participate in ecological stewardship (Higgs 2003). The long-term persistence of

biodiversity and the conservation biologists themselves depend on increased value by the public on wildlands and those who study them (Carpenter 1998).

FIGURE



**Figure 0.1:** Mean richness of 1 m<sup>2</sup> vegetation plots on 20 island sites with herbivores in the Gulf (British Columbia, Canada) and San Juan (Washington, USA) Islands (see Chapter 2) for native ( $R^2=0.24$ ,  $F_{1,38}=12.02$ ,  $p=0.001$ ) and non-native ( $R^2=0.03$ ,  $F_{1,38}=1.14$ ,  $p=0.29$ ) species.



## LITERATURE CITED

- Anonymous 2007. The great divide: The gap between theory and practice remains surprisingly wide in conservation biology. *Nature* **450**:135-136.
- Arcese, P., and Sinclair, A. R. E. 1997. The role of protected areas as ecological baselines. *Journal of Wildlife Management* **61**:587-602.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* **12**(6):1241-1252.
- Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**(2):385-399.
- Carpenter, S. R. 1998. Keystone species and academic-agency collaboration. <http://www.consecol.org/vol2/iss1/resp2/> edition.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: An emerging imperative. *Science* **293**:657-660.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* **199**(4335):1302-1310.
- Davis, M. A., K. Thompson, and J. P. Grime. 2001. Charles S. elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* **7**:97-102.
- DeNicola, A. J., S. J. Weber, C. A. Bridges, and J. L. Stokes. 1997. Nontraditional techniques for management of overabundant deer populations. *Wildlife Society Bulletin* **25**(2):496-499.
- Dennison, W. C., T. R. Lookingbill, T. J. B. Carruthers, J. M. Hawkey, and S. L. Carter. 2007. An eye-opening approach to developing and communicating integrated environmental assessments. *Frontiers in Ecology and the Environment* **5**(6):307-314.
- Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* **20**(9):470-474.
- Falcy, M. R., and C. F. Estades. 2007. Effectiveness of corridors relative to enlargement of habitat patches. *Conservation Biology* **21**(5):1341-1346.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* **100**(15):8916-8920.
- Gauthier, G., and J. Bedard. 1991. Experimental tests of the palatability of forage plants in greater snow geese. *Journal of Applied Ecology* **28**(2):491-500.

- GOERT 2007. The Garry oak ecosystem recovery team website. Available from [http://www.goert.ca/about\\_species\\_at\\_risk.php](http://www.goert.ca/about_species_at_risk.php) (accessed November 2 2007).
- Gonzales, E. K., Y. F. Wiersma, A. I. Maher, and T. D. Nudds. in revisions. Positive relationship between non-native and native squirrels in an urban landscape. *Canadian Journal of Zoology*.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**(9):470-474.
- Hager, H. A., and K. D. McCoy. 1998. The implications of accepting untested hypotheses: A review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation* **7**(8):1069-1079.
- Higgs, E. 2003. *Nature by design*. MIT Press, Cambridge, MA.
- Hilborn, R., T. A. Branch, B. Ernst, A. Magnusson, C. V. Minte-Vera, M. D. Scheuerell, and J. L. Valero. 2003. State of the world's fisheries. *Annual Review of Environment and Resources* **28**:359-399.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* **9**(4):761-770.
- Howe, H. F., B. Zorn -Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* **87**(12):3007-3113.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, New York.
- Huston, M. A. 2004. Management strategies for plant invasions: Manipulating productivity, disturbance, and competition. *Diversity and Distributions* **10**(3):167-178.
- Landsberg, J. J. 2003. Modelling forest ecosystems: State of the art, challenges, and future directions. *Canadian Journal for Forest Research* **33**(3):385-397.
- Lauber, T. B., and B. A. Knuth. 2004. Effects of information on attitudes toward suburban deer management. *Wildlife Society Bulletin* **32**(2):322-331.
- Lavorel, S., and J. D. Lebreton. 1992. Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science* **3**(1):91-100.
- Levine, J. M. 2000. Species diversity and biological invasions: Relating local process to community pattern. *Science* **288**:852-854.
- Lewis, S. 2007. The role of science in national park service decision-making. *The George Wright Forum* **24**(2):36-40.

- Lilley, P., and M. Vellend. in review. Negative native-exotic diversity relationship among oak savannas explained by human influence and climate.
- Lord, L. A., and T. D. Lee. 2001. Interactions of local and regional processes: Species richness in tussock sedge communities. *Ecology* **82**(2):313-318.
- MacDougall, A. S. in prep. Herbivory, hunting, and vegetation change in degraded oak savanna.
- MacDougall, A. S. 2005. Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology* **86**(12):3354-3363.
- MacDougall, A. S., J. Boucher, R. Turkington, and G. E. Bradfield. 2006. Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science* **17**(1):47-56.
- MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology* **92**(3):422-434.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**(1):42-55.
- MacDougall, A. S., and R. Turkington. 2007. Does the type of disturbance matter when restoring disturbance-dependent grasslands? *Restoration Ecology* **15**(2):263-272.
- MacDougall, A. S., and S. D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* **88**(5):1105-1111.
- Martin, J. L., and C. Baltzinger. 2002. Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal of Forest Research* **32**(7):1254-1264.
- McKinney, M. L., and F. A. La Sorte. 2007. Invasiveness and homogenization: Synergism of wide dispersal and high local abundance. *Global Ecology and Biogeography* **16**(3):394-400.
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin, and D. P. Vazquez. 2006. Biotic interactions and plant invasions. *Ecology Letters* **9**(6):726-740.
- Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* **139**(1):35-44.
- Norton, B. G. 1998. Improving ecological communication: The role of ecologists in environmental policy formation. *Ecological Applications* **8**(2):350-364.

- Nuzzo, V. A. 1986. Extent and status of Midwest oak savanna: Presettlement and 1985. *Natural Areas Journal* **61**:6-36.
- Orr, D. 2003. The constitution of nature. *Conservation Biology* **17**(6):1478-1484.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**(8):2581-2592.
- Robinson, J. G. 2006. Conservation biology and real-world conservation. *Conservation Biology* **20**(3):658-669.
- Rogers, K. H. 1997. Operationalizing ecology under a new paradigm: an African perspective. in S. T. A. Pickett, R. S. Ostfeld, M. Shachak and G. E. Likens, editors. *The ecological basis of conservation*. Chapman and Hall, New York, New York.
- Rogers, K. H. 1998. Managing science/management partnerships: a challenge of adaptive management. <http://www.consecol.org/vol2/iss2/resp1/> edition.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**(1-2):165-176.
- Rooney, T. P., S. M. Wiegmann, D. A. Rogers, and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* **18**(3):787-798.
- Rosenzweig, M. L. 2003. Reconciliation ecology and the future of species diversity. *Oryx* **37**(2):194-205.
- Roux, D. J., K. H. Rogers, H. C. Biggs, P. J. Ashton, and A. Sergeant. 2006. Bridging the science–management divide: moving from unidirectional knowledge transfer to knowledge interfacing and sharing. <http://www.ecologyandsociety.org/vol11/iss1/art4/>
- Rudolph, B. A., W. F. Porter, and H. B. Underwood. 2000. Evaluating immunocontraception for managing suburban white-tailed deer in Irondequoit, New York. *Journal of Wildlife Management* **64**(2):463-473.
- Saunders, C. D., A. T. Brook, and O. E. Myers. 2006. Using psychology to save biodiversity and human well-being. *Conservation Biology* **20**(3):702-705.
- Schwartz, M. W. 2006. How conservation scientists can help develop social capital for biodiversity. *Conservation Biology* **20**(5):1550-1552.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**(4):170-176.
- Sheail, J. 1999. The grey squirrel (*Sciurus carolinensis*) - a UK historical perspective on a vertebrate pest species. *Journal of Environmental Management* **55**(3):145-156.

- Simberloff, D. 2003. Eradication-preventing invasions at the outset. *Weed Science* **51**(2):247-253.
- Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors - conservation bargains or poor investments. *Conservation Biology* **6**(4):493-504.
- Soule, M. E., and G. H. Orians. 2001. *Conservation Biology: Research Priorities For The Next Decade*. Island Press, Washington, D.C.
- Stewart, K. M., T. E. Fulbright, and D. L. Drawe. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management* **64**(3):733-741.
- Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution* **14**(5):179-185.
- Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* **103**(15):5841-5845.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**(1):81-92.
- Vellend, M. 2002. A pest and an invader: White-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). *Natural Areas Journal* **22**(3):230-234.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. Dispersal of trillium seeds by deer: Implications for long-distance migration of forest herbs. *Ecology* **84**(4):1067-1072.
- Vicari, M., and D. R. Bazely. 1993. Do grasses fight back - the case for antiherbivore defenses. *Trends in Ecology & Evolution* **8**(4):137-141.
- Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. <http://www.consecol.org/vol1/iss2/art1> edition.
- White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: A neglected concept in invasion biology. *Diversity and Distributions* **12**(4):443-455.
- Whitelaw, G. S., and P. F. J. Eagles. 2007. Planning for long, wide conservation corridors on private lands in the oak ridges moraine, Ontario, Canada. *Conservation Biology* **21**(3):675-683.

# Appendices

## APPENDIX A

Island	UTM W	UTM N
Anniversary	486585	5407867
Brackman	471601	5396177
Channel East	472037	5405421
Channel West	471764	5405249
D'Arcy	479902	5379520
Dock 1 (North)	473671	5391029
Dock 2 (South)	473639	5390925
Dock 3 (West)	473246	5391035
Flat top	494014	5388197
Galiano	472194	5413043
Georgeson	482833	5410001
Isabella East	468325	5397404
Isabella West	468231	5397379
Jones	384587	5384521
Little McConnell	498101	5382885
Lopez - Iceberg Point	508117	5363137
McConnell	498218	5382497
Mini D'Arcy (Seal Rock)	480027	5380207
Orcas	507381	5393006
Pellows	473644	5396968
Pender - Gowlland Point	486198	5397964
Portland	473263	5397038
Private 1	475949	5390796
Private 2	467532	5397251
Private 3	472483	5390812
Private 4	480154	5379813
Private 5	475256	5390518
Private 6	479260	5382216
Private 7	474410	5412737
Reay	475763	5392335
Ruckle Park (Salt Spring)	472266	5403218
Rum	479491	5390073
Sallas Rock	478590	5381366
San Juan Island - Friday Harbor Labs	499403	5377221
Saturna	496661	5403563
Shaw	503061	5377405
Tumbo	495683	5404626
Unnamed 63	484347	5408492

## APPENDIX B.

Island vegetation models for plant groups (a) and focal species (b) that had significant bivariate relationships with the explanatory variables (Table 2.1). Relative likelihoods, used to identify models best approximating the data indicated in bold, were based on Aikake weights for models with  $AIC_c$  values ( $\Delta_i$ ) that differed by  $< 2$ . Plant groups are categorized by place of origin, Native (N) or Non-native (NN), life history, Annual (A) or Perennial (P), and plant form, Forb (F) or Grass (G) which included grasses, sedges and rushes.

a)

Y	Variable 1	Variable 2	Variable 3	Variable 4	k	AIC <sub>c</sub>	$\Delta_i$	w <sub>i</sub>
NAF	Neighbour Area				2	247.52	5.36	0.02
NAF	Island size	Neighbour Area			3	244.88	2.72	0.08
<b>NAF</b>	<b>Island size</b>				<b>2</b>	<b>244.13</b>	<b>1.97</b>	<b>0.12</b>
NAF	Herbivory	Island size	Neighbour Area		4	243.83	1.67	0.14
NAF	Herbivory	Neighbour Area			3	243.55	1.39	0.16
NAF	Herbivory				2	243.44	1.28	0.17
NAF	Herbivory	Island size			3	242.16	0.00	0.32
<b>NNAF</b>	<b>Herbivory</b>	<b>Island size</b>	<b>Soil Depth</b>		<b>4</b>	<b>274.02</b>	<b>1.98</b>	<b>0.08</b>
<b>NNAF</b>	<b>Herbivory</b>	<b>Soil Depth</b>			<b>3</b>	<b>273.50</b>	<b>1.46</b>	<b>0.10</b>
<b>NNAF</b>	<b>Soil Depth</b>				<b>2</b>	<b>272.99</b>	<b>0.95</b>	<b>0.13</b>
<b>NNAF</b>	<b>Herbivory</b>	<b>Island size</b>			<b>3</b>	<b>272.71</b>	<b>0.67</b>	<b>0.15</b>
<b>NNAF</b>	<b>Island size</b>				<b>2</b>	<b>272.59</b>	<b>0.55</b>	<b>0.16</b>
<b>NNAF</b>	<b>Herbivory</b>				<b>2</b>	<b>272.23</b>	<b>0.19</b>	<b>0.19</b>
<b>NNAF</b>	<b>Island size</b>	<b>Soil Depth</b>			<b>3</b>	<b>272.04</b>	<b>0.00</b>	<b>0.21</b>
NPF	Settlement				2	316.60	34.40	0.00
NPF	Neighbour Area				2	311.60	29.40	0.00
NPF	Island size				2	309.70	27.50	0.00
NPF	Island size	Settlement			3	307.00	24.80	0.00
NPF	Herbivory				2	303.80	21.60	0.00
NPF	Island size	Neighbour Area			3	303.10	20.90	0.00
NPF	Island size	Neighbour Area	Settlement		4	300.40	18.20	0.00
NPF	Herbivory	Settlement			3	298.40	16.20	0.00
NPF	Herbivory	Island size			3	292.10	9.90	0.01
NPF	Herbivory	Neighbour Area			3	291.00	8.80	0.01
NPF	Herbivory	Neighbour Area	Settlement		4	288.70	6.50	0.03
NPF	Herbivory	Island size	Settlement		4	288.40	6.20	0.04
NPF	Herbivory	Island size	Neighbour Area		4	286.00	3.80	0.12
<b>NPF</b>	<b>Herbivory</b>	<b>Island size</b>	<b>Neighbour Area</b>	<b>Settlement</b>	<b>5</b>	<b>282.20</b>	<b>0.00</b>	<b>0.80</b>
NNPF	Neighbour Area				2	243.80	13.60	0.00
NNPF	Herbivory				2	242.90	12.70	0.00
NNPF	Herbivory	Neighbour Area			3	241.00	10.80	0.00
NNPF	Island size				2	237.80	7.60	0.01
NNPF	Island size	Neighbour Area			3	232.90	2.70	0.14
<b>NNPF</b>	<b>Herbivory</b>	<b>Island size</b>			<b>3</b>	<b>231.40</b>	<b>1.20</b>	<b>0.30</b>
<b>NNPF</b>	<b>Herbivory</b>	<b>Island size</b>	<b>Neighbour Area</b>		<b>4</b>	<b>230.20</b>	<b>0.00</b>	<b>0.54</b>
Y	Variable 1	Variable 2	Variable 3	Variable 4	k	AIC <sub>c</sub>	$\Delta_i$	w <sub>i</sub>
<b>NNAG</b>	<b>Herbivory</b>	<b>Soil Depth</b>			<b>3</b>	<b>318.59</b>	<b>1.01</b>	<b>0.29</b>
<b>NNAG</b>	<b>Herbivory</b>				<b>2</b>	<b>317.58</b>	<b>0.00</b>	<b>0.48</b>
<b>NNPG</b>	<b>Human Density</b>				<b>2</b>	<b>260.39</b>	<b>0.00</b>	



b)

Y	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	k	AIC <sub>c</sub>	$\Delta_i$	w <sub>i</sub>
<i>Camassia leichtlinii</i>	Neighbour Area					2	252.1	27.50	0.00
<i>Camassia leichtlinii</i>	Settlement					2	249.7	25.07	0.00
<i>Camassia leichtlinii</i>	Neighbour Area	Settlement				3	246	21.40	0.00
<i>Camassia leichtlinii</i>	Island Size	Settlement				3	245.9	21.31	0.00
<i>Camassia leichtlinii</i>	Island Size	Neighbour Area	Settlement			4	245.1	20.54	0.00
<i>Camassia leichtlinii</i>	Island Size					2	243.6	19.04	0.00
<i>Camassia leichtlinii</i>	Island Size	Neighbour Area				3	242.9	18.28	0.00
<i>Camassia leichtlinii</i>	Herbivory	Settlement				3	231.6	7.04	0.01
<i>Camassia leichtlinii</i>	Herbivory	Neighbour Area	Settlement			4	231.4	6.80	0.01
<i>Camassia leichtlinii</i>	Herbivory					2	229.9	5.34	0.03
<i>Camassia leichtlinii</i>	Herbivory	Neighbour Area				3	229.4	4.83	0.03
<i>Camassia leichtlinii</i>	Herbivory	Island Size	Neighbour Area	Settlement		5	227.1	2.51	0.11
<b><i>Camassia leichtlinii</i></b>	<b>Herbivory</b>	<b>Island Size</b>	<b>Neighbour Area</b>	<b>Settlement</b>		<b>4</b>	<b>225.9</b>	<b>1.28</b>	<b>0.20</b>
<b><i>Camassia leichtlinii</i></b>	<b>Herbivory</b>	<b>Island Size</b>	<b>Settlement</b>			<b>4</b>	<b>225.5</b>	<b>0.94</b>	<b>0.24</b>
<b><i>Camassia leichtlinii</i></b>	<b>Herbivory</b>	<b>Island Size</b>				<b>3</b>	<b>224.6</b>	<b>0.00</b>	<b>0.38</b>
<i>Plantago lanceolata</i>	Island Size	Settlement				3	137.5	3.06	0.15
<i>Plantago lanceolata</i>	Settlement					2	137.1	2.70	0.18
<i>Plantago lanceolata</i>	Island Size					2	134.4	0.00	0.68
<i>Poa pratensis</i>	Soil Depth					2	136.7	14.46	0.00
<i>Poa pratensis</i>	Human Density	Soil Depth				3	134.3	12.09	0.00
<i>Poa pratensis</i>	Human Density					2	132.3	10.06	0.00
<i>Poa pratensis</i>	Neighbour Area					2	131.5	9.30	0.00
<i>Poa pratensis</i>	Soil Depth	Neighbour Area				3	127.9	5.67	0.01
<i>Poa pratensis</i>	Island Size	Neighbour Area				3	127.4	5.17	0.01
<i>Poa pratensis</i>	Human Density	Soil Depth	Neighbour Area			4	126.8	4.55	0.02
<i>Poa pratensis</i>	Human Density	Island Size	Soil Depth	Settlement	Neighbour Area	6	126.8	4.51	0.02
<i>Poa pratensis</i>	Island Size	Soil Depth	Settlement	Neighbour Area		5	126.4	4.12	0.02
<i>Poa pratensis</i>	Neighbour Area	Settlement				3	126.1	3.88	0.02
<i>Poa pratensis</i>	Human Density	Island Size	Soil Depth	Neighbour Area		5	125.9	3.69	0.03
<i>Poa pratensis</i>	Island Size	Soil Depth				3	125.9	3.62	0.03
<i>Poa pratensis</i>	Island Size	Settlement				3	125.9	3.62	0.03

<b>Y</b>	<b>Variable 1</b>	<b>Variable 2</b>	<b>Variable 3</b>	<b>Variable 4</b>	<b>Variable 5</b>	<b>k</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta_i</math></b>	<b>w<sub>i</sub></b>
<i>Poa pratensis</i>	Human Density	Island Size	Soil Depth	Settlement		5	125.9	3.62	0.03
<i>Poa pratensis</i>	Island Size	Soil Depth	Neighbour Area			4	125.4	3.20	0.03
<i>Poa pratensis</i>	Island Size					2	125.4	3.13	0.03
<i>Poa pratensis</i>	Human Density	Island Size	Soil Depth			4	125.4	3.13	0.03
<i>Poa pratensis</i>	Human Density	Island Size	Neighbour Area			4	125.1	2.88	0.04
<i>Poa pratensis</i>	Island Size	Soil Depth	Settlement			4	125.1	2.85	0.04
<i>Poa pratensis</i>	Human Density	Neighbour Area				3	124.6	2.32	0.05
<i>Poa pratensis</i>	Settlement					2	124.4	2.18	0.05
<i>Poa pratensis</i>	<b>Human Density</b>	<b>Island Size</b>	<b>Settlement</b>			<b>4</b>	<b>124.2</b>	<b>1.98</b>	<b>0.06</b>
<i>Poa pratensis</i>	<b>Soil Depth</b>	<b>Settlement</b>	<b>Neighbour Area</b>			<b>4</b>	<b>123.9</b>	<b>1.63</b>	<b>0.07</b>
<i>Poa pratensis</i>	<b>Human Density</b>	<b>Soil Depth</b>	<b>Settlement</b>			<b>4</b>	<b>123.8</b>	<b>1.59</b>	<b>0.07</b>
<i>Poa pratensis</i>	<b>Human Density</b>	<b>Island Size</b>				<b>3</b>	<b>123.8</b>	<b>1.53</b>	<b>0.07</b>
<i>Poa pratensis</i>	<b>Soil Depth</b>	<b>Settlement</b>				<b>3</b>	<b>123.6</b>	<b>1.36</b>	<b>0.08</b>
<i>Poa pratensis</i>	<b>Human Density</b>	<b>Settlement</b>				<b>3</b>	<b>122.2</b>	<b>0.00</b>	<b>0.16</b>

*Hypochoeris*

<i>radicata</i>	Herbivory					2	185.6	8.75	0.00
<i>Hypochoeris</i>									
<i>radicata</i>	Herbivory	Island Size	Settlement			4	185.3	8.48	0.00
<i>Hypochoeris</i>									
<i>radicata</i>	Herbivory	Settlement				3	184.5	7.67	0.01
<i>Hypochoeris</i>									
<i>radicata</i>	Island Size	Settlement				3	184.1	7.32	0.01
<i>Hypochoeris</i>									
<i>radicata</i>	Settlement					2	182.9	6.09	0.01
<i>Hypochoeris</i>									
<i>radicata</i>	Herbivory	Island Size				3	182.7	5.87	0.02
<i>Hypochoeris</i>									
<i>radicata</i>	Herbivory	Island Size	Neighbour Area	Settlement		5	182.6	5.79	0.02
<i>Hypochoeris</i>									
<i>radicata</i>	Island Size					2	182.2	5.35	0.02
<i>Hypochoeris</i>									
<i>radicata</i>	Island Size	Neighbour Area	Settlement			4	181.3	4.53	0.03
<i>Hypochoeris</i>									
<i>radicata</i>	Herbivory	Neighbour Area	Settlement			4	180	3.19	0.06

<i>Y</i>	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	k	AIC <sub>c</sub>	$\Delta_i$	$w_i$
<i>Hypochoeris radicata</i>	Herbivory	Island Size	Neighbour Area			4	179.8	3.03	0.07
<i>Hypochoeris radicata</i>	Island Size	Neighbour Area				3	178.8	2.03	0.11
<b><i>Hypochoeris radicata</i></b>	<b>Neighbour Area</b>	<b>Settlement</b>				<b>3</b>	<b>178.8</b>	<b>1.98</b>	<b>0.11</b>
<i>Hypochoeris radicata</i>	Herbivory	Neighbour Area				3	177.4	0.61	0.22
<i>Hypochoeris radicata</i>	Neighbour Area					2	176.8	0.00	0.30
<b><i>Cerastium arvense</i></b>	<b>Soil Depth</b>					<b>2</b>	<b>109.78</b>		
<i>Cerastium glomeratum</i>	Neighbour Area					2	97.45	5.69	0.05
<i>Cerastium glomeratum</i>	Island Size	Neighbour Area				3	94.9	3.14	0.16
<b><i>Cerastium glomeratum</i></b>	<b>Island Size</b>					<b>2</b>	<b>91.76</b>	<b>0.00</b>	<b>0.79</b>
<b><i>Geranium molle</i></b>	<b>Herbivory</b>	<b>Soil Depth</b>				<b>3</b>	<b>128.3</b>	<b>1.2</b>	<b>0.22</b>
<b><i>Geranium molle</i></b>	<b>Soil Depth</b>					<b>2</b>	<b>127.2</b>	<b>0.13</b>	<b>0.38</b>
<b><i>Geranium molle</i></b>	<b>Herbivory</b>					<b>2</b>	<b>127.1</b>	<b>0</b>	<b>0.40</b>
<i>Trifolium dubium</i>	Soil Depth					2	129.6	2.66	0.16
<i>Trifolium dubium</i>	Herbivory	Soil Depth				3	129	2.06	0.22
<b><i>Trifolium dubium</i></b>	<b>Herbivory</b>					<b>2</b>	<b>126.9</b>	<b>0</b>	<b>0.62</b>
<i>Aira caryophylla</i>	Herbivory	Soil Depth				3	131.2	2.22	0.19
<b><i>Aira caryophylla</i></b>	<b>Soil Depth</b>					<b>2</b>	<b>130.8</b>	<b>1.79</b>	<b>0.24</b>
<b><i>Aira caryophylla</i></b>	<b>Herbivory</b>					<b>2</b>	<b>129</b>	<b>0</b>	<b>0.58</b>
<i>Bromus hordeaceus</i>	Herbivory	Island Size	Settlement			4	220.6	4.51	0.04
<i>Bromus hordeaceus</i>	Herbivory					2	220	3.91	0.06
<i>Bromus hordeaceus</i>	Herbivory	Island Size				3	219.1	3.03	0.09
<i>Bromus hordeaceus</i>	Island Size	Settlement				3	218.5	2.46	0.11
<b><i>Bromus hordeaceus</i></b>	<b>Herbivory</b>	<b>Settlement</b>				<b>3</b>	<b>218</b>	<b>1.91</b>	<b>0.15</b>
<b><i>Bromus hordeaceus</i></b>	<b>Island Size</b>					<b>2</b>	<b>217.9</b>	<b>1.82</b>	<b>0.16</b>
<b><i>Bromus hordeaceus</i></b>	<b>Settlement</b>					<b>2</b>	<b>216.1</b>	<b>0</b>	<b>0.39</b>
<i>Sanicula crassicaulis</i>	Island Size	Neighbour Area	Settlement			4	188.3	3.79	0.04

<i>Y</i>	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	k	AIC <sub>c</sub>	$\Delta_i$	w <sub>i</sub>
<i>Sanicula crassicaulis</i>	Island Size	Settlement				3	186.6	2.12	0.09
<b><i>Sanicula crassicaulis</i></b>	<b>Neighbour Area</b>	<b>Settlement</b>				<b>3</b>	<b>186.2</b>	<b>1.68</b>	<b>0.11</b>
<i>Sanicula crassicaulis</i>	Island Size	Neighbour Area				3	185.9	1.35	0.13
<i>Sanicula crassicaulis</i>	Settlement					2	185.4	0.93	0.16
<i>Sanicula crassicaulis</i>	Neighbour Area					2	184.8	0.34	0.22
<i>Sanicula crassicaulis</i>	Island Size					2	184.5	0	0.26
<i>Trifolium willdenowii</i>	Settlement					3	116.1	7.2	0.01
<i>Trifolium willdenowii</i>	Herbivory	Settlement				3	113.5	4.65	0.03
<i>Trifolium willdenowii</i>	Herbivory					2	111.5	2.63	0.08
<b><i>Trifolium willdenowii</i></b>	<b>Island Size</b>	<b>Settlement</b>				<b>3</b>	<b>110.7</b>	<b>1.79</b>	<b>0.11</b>
<i>Trifolium willdenowii</i>	Herbivory	Island Size	Settlement			4	109.2	0.26	0.25
<i>Trifolium willdenowii</i>	Island Size					2	109.1	0.25	0.25
<i>Trifolium willdenowii</i>	Herbivory	Island Size				3	108.9	0	0.28

# APPENDIX C.

Forage selectivity indices for common (>20% of the plots\*) focal species. \*Native annual forbs were uncommon on islands with herbivores and therefore we included the five most common native annual forbs, which occurred in 9-17% of the plots, to get an estimate of selectivity for that plant group.

Plant Group	Species	Presence	Browsed	Forage Index
Non-native annual forb	<i>Veronica arvensis</i>	44	0	0
Non-native annual grass	<i>Vulpia myuros</i>	46	0	0
Non-native annual grass	<i>Bromus sterilis</i>	52	0	0
Non-native annual forb	<i>Cerastium glomeratum</i>	52	0	0
Native annual forb	<i>Galium aparine</i>	54	0	0
Native perennial grass	<i>Festuca rubra</i>	68	0	0
Non-native annual grass	<i>Vulpia bromoides</i>	101	0	0
Non-native annual forb	<i>Geranium molle</i>	79	1	0.19
Non-native annual forb	<i>Trifolium dubium</i>	71	1	0.21
Non-native annual forb	<i>Vicia hirsuta</i>	63	1	0.24
Non-native annual grass	<i>Aira praecox</i>	55	1	0.27
Non-native annual grass	<i>Aira caryophyllea</i>	42	1	0.36
Native perennial forb	<i>Cerastium arvense</i>	59	2	0.51
Native perennial forb	<i>Hypochaeris radicata</i>	109	4	0.55
Native annual forb*	<i>Trifolium microdon</i>	25	1	0.6
Non-native annual grass	<i>Bromus hordeaceus</i>	146	7	0.72
Non-native annual forb	<i>Vicia sativa</i>	125	6	0.72
Non-native annual grass	<i>Bromus diandrus</i>	96	5	0.78
Non-native perennial grass	<i>Anthoxanthum odoratum</i>	76	4	0.79
Native perennial grass	<i>Elymus glaucus</i>	53	3	0.85
Native annual forb*	<i>Lupinus bicolor</i>	14	1	1.07
Non-native annual grass	<i>Cynosurus echinatus</i>	52	4	1.15
Native perennial grass	<i>Bromus carinatus</i>	38	3	1.18
Non-native perennial grass	<i>Holcus lanatus</i>	38	3	1.18
Native perennial forb	<i>Rumex acetosella</i>	72	6	1.25

<b>Plant Group</b>	<b>Species</b>	<b>Presence</b>	<b>Browsed</b>	<b>Forage Index</b>
Native perennial forb	<i>Achillia millefolium</i>	56	5	1.34
Native perennial forb	<i>Sanicula crassicaulis</i>	54	5	1.39
Native annual forb*	<i>Trifolium microcephalum</i>	17	2	1.76
Native annual forb*	<i>Trifolium variegatum</i>	17	2	1.76
Non-native perennial grass	<i>Dactylis glomerata</i>	59	7	1.78
Non-native perennial grass	<i>Poa pratensis</i>	90	11	1.83
Native perennial forb	<i>Vicia americana</i>	37	5	2.02
Native annual forb*	<i>Trifolium willdenowii</i>	24	5	3.12
Non-native annual forb	<i>Plantago lanceolata</i>	83	19	3.43
Native perennial forb	<i>Brodiaea coronaria</i>	55	17	4.63
Native perennial forb	<i>Camassia leichtlinii</i>	49	20	6.11

# APPENDIX D.

Characteristics and measures of the focal plant species in established plant experiment. The plant type, life stage at time of planting, growth measures, and monitoring schedule of the experimental and monitored plant species. Extant lilies are given in order of abundance.

Species	Type	Life stage	Individuals per plot	Measured	Start	Finish
Seablush	Herbaceous annual	Plants grown from seed	60 (mean)	Stems (#)	2003	2005
Common camas	Herbaceous perennial	3-year old bulbs	4	Leaves (#)	2003	2005
Arbutus	Deciduous tree	3-year old saplings	1	Leaves (#)	2003	2003
Garry oak seedlings	Deciduous tree	Germinated acorns	2	Emerged (#)	2003	2005
Garry oak saplings	Deciduous tree	4-year old saplings	2	Leaves (#)	2003	2003
Fool's onion, nodding onion, harvest brodiaea, chocolate lily and white fawn lily	Herbaceous perennials	extant	varies	Flowers (#)	2004	2004

# APPENDIX E.

Species used in the seed addition experiment, their plant type, the number of seeds per plot and activity in plot.

Species	Type	Seeds per plot	Activity in plot
Yarrow	Perennial forb	300	Germinated
Great camas	Perennial forb	200	Germinated
Blue-eyed mary	Annual forb	50	Germinated
Blue wild rye	Perennial grass	200	Did not germinate
Chocolate lily	Perennial forb	50	Germination rate too low for analyses
Bird's foot trefoil	Annual forb	200	Could not distinguish from extant species
Bicoloured lupine	Annual forb	35	Germinated
Seablush	Annual forb	200	Germinated