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Scotch broom (*Cytisus scoparius*, Fabaceae) and the pollination and reproductive success of three Garry oak-associated plant species

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Scotch broom (*Cytisus scoparius*, Fabaceae) and the pollination and reproductive success of
three Garry oak-associated plant species

by

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A THESIS

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Abstract

A growing number of studies are observing an effect of invasive species on the pollination and reproductive success of co-flowering plants, over and above direct competition for resources. In this study, I investigate the effect of the invader Scotch broom (*Cytisus scoparius*) on the pollinator visitation, pollen deposition, and female reproductive output of three co-flowering members (two native, one exotic) of the critically endangered Garry oak grassland ecosystem on the Saanich peninsula of Vancouver Island. Higher pollinator sharing between native *Camassia leichtlinii* and Scotch broom increased pollen deposition and fruit set in invaded sites, despite a decreased visitation rate. Conversely, the invader had little detectable effect on the native *Collinsia parviflora* or the exotic *Geranium molle* where pollinator sharing was low. This study provides evidence that Scotch broom neither competes for pollination with natives, nor facilitates invasion of other exotics in Garry oak ecosystem remnants.

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To my parents, Cameron and Linda Muir, for their unfaltering support of everything I do.

I love you guys.

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List of Abbreviations

Abbreviation

ANOVA

GOE

NOI

PERMANOVA

Definition

Analysis of variance

Garry oak ecosystem

Niche overlap index (Pianka 1973)

Permutational analysis of variance (PRIMER-e)

Epigraph

They whom truth and wisdom lead, can gather honey from a weed.

- William Cowper

Chapter One: **Introduction**

Invasive species are organisms that transverse geographic boundaries with or without human effort and colonize novel habitats, thriving and reproducing sufficiently that they persist at high population densities (Pysek *et al.* 2004). Invasives are well known to threaten biodiversity and ecosystem services around the world, and few habitats on Earth are free from their influence (Mack *et al.* 2000). In Canada, 12% of exotic species are known to be weedy or invasive, and billions of dollars are spent annually control them (Government of Canada 2004).

Scotch broom (*Cytisus scoparius*, Fabaceae, hereafter *Cytisus*), is one such invasive plant established in North America. It is notorious for forming dense stands and subsequently displacing native species through direct resource competition and allelopathic effects on surrounding vegetation via root exudates and changes in soil chemistry (Ussery and Krannitz 1998, Shaben and Myers 2010). As a result it is widely regarded as a troublesome weed.

In Canada, this danger is especially salient in remnant patches of the critically imperilled Garry oak (*Quercus garryana*) savannah community, where swaths of showy yellow *Cytisus* flowers often replace the diverse and colourful array of flowers characteristic of a Garry oak meadow in bloom (Fuchs 2001).

Interestingly, the interactions between *Cytisus* and co-flowering species of the Garry oak community may be more complex than has been previously thought. In general, the negative effects of invasive plants concern direct interactions with co-flowering species, such as competition for resources such as water, nutrients or light (Levine *et al.* 2003). However, recent attention has been brought to the potential effects of indirect interactions between invaders and their co-flowering associates, most notably the possibility of an effect of invasive plants on one

of the most important stages of life in a sexually reproducing plant: pollination and reproductive success (Bjerknes *et al.* 2007).

A large proportion of flowering plant species depend obligately or facultatively on animals for pollination and subsequent seed production (Burd 1994, Ollerton 2011). It follows, then, that if invasive plants share similar animal pollinators with natives and other co-flowering species, the potential exists for invaders to disrupt or otherwise affect plant-pollinator interactions that can be crucial to the reproduction and persistence of co-flowering populations (Bjerknes *et al.* 2007). *Cytisus* produces abundant early-season flowers that are pollinated by many of the same pollinators as many common members of the Garry oak community (J. Muir, pers. obs.). Much effort is undertaken to control the spread of *Cytisus* and impede it from displacing native plants through direct competition (Ussery and Kranitz 1998), but little is known of the effect its presence has on the pollination of native and sometimes endangered plant species of the Garry oak grassland community. In a way, competition for pollen can be even more detrimental than vegetative competition – whereas direct vegetative competition for resources occurs only when plants are very close together, the effects of pollen competition act over large areas (Brown *et al.* 2002). Thus, showy invasives may generally “prime” a community for invasion even when they are rare, depressing seed production of native species and effectively making more space for themselves. Alternatively, the potential for *Cytisus* invasions to facilitate the persistence of native plant populations through pollinator attraction has not previously been acknowledged. If this turns out to be the case, conservationists may want to redirect their efforts toward more detrimental invasives such as wind-pollinated exotic grasses.

In general, the potential reproductive effects of *Cytisus* on the pollination of resident Garry oak associated plants can be placed into two broad and nonexclusive categories: changes in the quantity of pollen deposited on stigmas, and changes in the composition and subsequent quality of pollen available to the plant for reproduction (Waser 1978). The presence of broom could directly draw away pollinator visits or have more indirect effects through changes in pollinator composition or changing pollinator behaviour. I outline the main mechanisms of change in pollination in the native community below (Figure 1).

1.1 Changes to pollinator composition and abundance

The presence of invasive plants within a community can affect the composition and abundance of visiting pollinators by increasing floral resource availability in space and time, consequently supporting larger pollinator populations (Graves and Shapiro 2003, Tepedino *et al.* 2008). Although diverse effects have been observed, most results indicate positive (Carvalhiero *et al.* 2008, McKinney and Goodell 2011) to neutral (Bartomeus *et al.* 2008a, Nienhuis *et al.* 2009) effects of invaders on pollinator populations. However, alien plants can be detrimental to pollinator populations if they contain toxic floral compounds or decrease overall plant diversity within a community (Moron *et al.* 2009).

Floral visitation rates of co-flowering species is by far the most frequently studied aspect of native-invader pollination interactions, and results seem to be evenly split between facilitative, competitive, and neutral effects (Bjerknes *et al.* 2007). Facilitation can occur if the increased floral abundance caused by the presence of a showy invader acts as a pollinator “magnet” and attracts pollinators that otherwise might not visit as often (Grabas and Laverly 1999, Totland *et al.* 2006, Lopearaiza-Mikel *et al.* 2007). Plants in small, isolated communities such as many

Garry oak habitat remnants may benefit most from this type of facilitation, as they may not otherwise receive enough pollination service to maintain themselves (Groom 1998). Conversely, flowers of the invader may be more attractive to pollinators than those of co-flowering species and consequently cause a decrease in visitation to native floral displays (a pollinator “vacuum”) (Kandori *et al.* 2009, Dietzsch *et al.* 2011). For example, Brown *et al.* (2002) observed that the native *Lythrum alatum* received significantly fewer visits in the presence of the invader *Lythrum salicaria*, and Chittka and Shurkins (2001) found decreased visitation of *Stachys palustris* in the presence of the invasive *Impatiens glandulifera*.

1.2 Influences of invasives on the quality of pollen receipt

Increased visitation caused by invader facilitation should subsequently enhance pollen receipt. However, despite studies observing increased visitation of co-flowering species in the presence of exotics (Grabas and Lavery 1999, Moragues and Traveset 2005, Lopezaraiza-Mikel *et al.* 2007, Hegland *et al.* 2009), very few have observed a corresponding increase in conspecific pollen receipt (but see McKinney and Goodell 2011). Instead, pollinator preference for invader flowers tends to change the composition of pollen received by native species, decreasing the receipt of conspecific pollen and increasing the receipt of heterospecific pollen (Grabas and Lavery 1999, Larson *et al.* 2006, Lopezaraiza-Mikel *et al.* 2007, Flanagan *et al.* 2009, Cariveau and Norton 2009, Dietzsch *et al.* 2011, Thijs *et al.* 2011).

Increased deposition of heterospecific pollen can also have negative consequences on the reproduction of co-flowering species by mechanically or chemically blocking growth of conspecific pollen tubes in the stigma or style (Brown and Mitchell 2001). Allelopathic pollen is another way in which invasive species could affect the reproduction of other community

members in their novel environment. Through exudation of chemicals onto the styles of heterospecific stigmas, invader pollen can inhibit germination of conspecific pollen and subsequent pollen tube growth, the receptivity of stigmas or styles, or even the post-fertilization development of ovules into seeds (Char 1977, Kanchan and Chandra 1980, Murphy 2000). As *Cytisus* possesses alkaloids toxic to humans, this type of chemical interference via pollen is possible (Zielke *et al.* 1992). Alternatively, heterospecific pollen could fertilize, or at least disable ovules before arrival of conspecific pollen tubes (Brown and Mitchell 2001) sometimes even producing hybrids (Ellstrand *et al.* 1999), or mechanically preventing germination through physical blockage (Thomson 1989). Invasive pollen can decrease the reproductive success of co-flowering species (Thomson *et al.* 1982, Brown and Mitchell 2001, Nielsen *et al.* 2008, Matsumoto *et al.* 2009, Montgomery 2009a, Da Silva and Sargent 2011), although this effect is not universal (Moragues and Traveset 2005, Jakobsson *et al.* 2008, Flanagan *et al.* 2009, Montgomery 2009b, Tscheulin *et al.* 2009).

The invader-induced changes in the deposition of conspecific and heterospecific pollen outlined here can have great consequences for fruit and seed production of co-flowering species. Decreased deposition of compatible conspecific pollen can cause “pollen limitation” of co-flowering species, whereby insufficient compatible pollen is received by natives to maximize seed set (Knight *et al.* 2005). Similar to the trends seen in studies of pollen deposition, the reproductive success of co-flowering species generally declines (Grabas and Lavery 1999, Chittka and Schurkens 2001, Brown *et al.* 2002, Totland *et al.* 2006, Takakura *et al.* 2008, Kandori *et al.* 2009, Flanagan *et al.* 2009, Thijs *et al.* 2012) or remains constant (Grabas and Lavery 1999, Aigner 2004, Ghazoul 2004, Munoz and Cavieres 2008, Nielsen *et al.* 2008, Kaiser-Bunbury and Muller 2009, Vanparys *et al.* 2011, Thijs *et al.* 2012) in the presence of an

invader. A decline in the reproductive output of co-flowering species can ultimately have negative effects on species abundance, population viability, and genetic diversity within a community (Kearns *et al.* 1998, Knight *et al.* 2005), if population dynamics are constrained by seed production.

1.3 Overall outcomes of invader presence on native species reproductive success

The effects of invading plants on the pollination and reproductive success of resident exotics have received much less attention. Positive associations, wherein one exotic increases the success of another, occur commonly (Simberloff and Von Holle 1999, Traveset and Richardson 2006), resulting in “invasional meltdowns” (Simberloff and Von Holle 1999). For example, invasive pollinators can associate strongly with invasive plants in disturbed habitats, causing mutual facilitation (Morales and Aizen 2002, Liu *et al.* 2006). Until now, few studies have investigated the effects of invasive species on the pollination and reproductive success of other exotic co-flowering species, but the results of similar studies on natives reveal the gamut of possible observations. Floral visitation and seed set in the invasive *Carduus pycnocephalus* increased in the presence of fellow invader *Lupinus arboreus*, lending credence to the “invasional meltdown” effect (Molina-Montenegro *et al.* 2008). On the other hand, two congeneric exotic *Carduus* species experienced reduced pollinator service when co-occurring, suggesting “invasional interference” (Yang *et al.* 2011). Finally, the invader *Impatiens glandulifera* had no effect on the pollination of naturalized exotic *Oenothera biennis* (Thijs *et al.* 2012).

1.4 Objectives

In this thesis, I aim to clarify the nature of interactions between the invasive *Cytisus scoparius* and native and exotic co-flowering plant species in the endangered Garry oak grassland on pollination and reproductive success. Two native species, *Camassia leichtlinii* and *Collinsia parviflora*, and an exotic naturalized species, *Geranium molle*, were observed during the spring 2011 at four sites where *Cytisus* was present and four sites where *Cytisus* was absent. The following hypotheses were addressed:

1. *Cytisus* affects site-level pollinator composition and abundance by increasing the abundance of *Cytisus*-associated insect species within invaded areas.
2. *Cytisus* creates a pollinator vacuum, drawing floral visitors from native species and reducing their visitation rate. In contrast, visitation rate to *Geranium molle* increases due to more generalist pollinators caused by the presence of *Cytisus* and a resulting “invasional meltdown”.
3. Decreased visitation in *Cytisus*-invaded sites reduces conspecific pollen deposition and increases the proportion of heterospecific pollen on native stigmas owing to the increased floral diversity found in invaded sites. Conspecific pollen deposition in *Geranium molle* increases in *Cytisus*-invaded sites.
4. Native focal plants realize lower reproductive success in invaded sites compared to uninvaded sites, but the exotic experiences enhanced success in sites occupied by *Cytisus*.

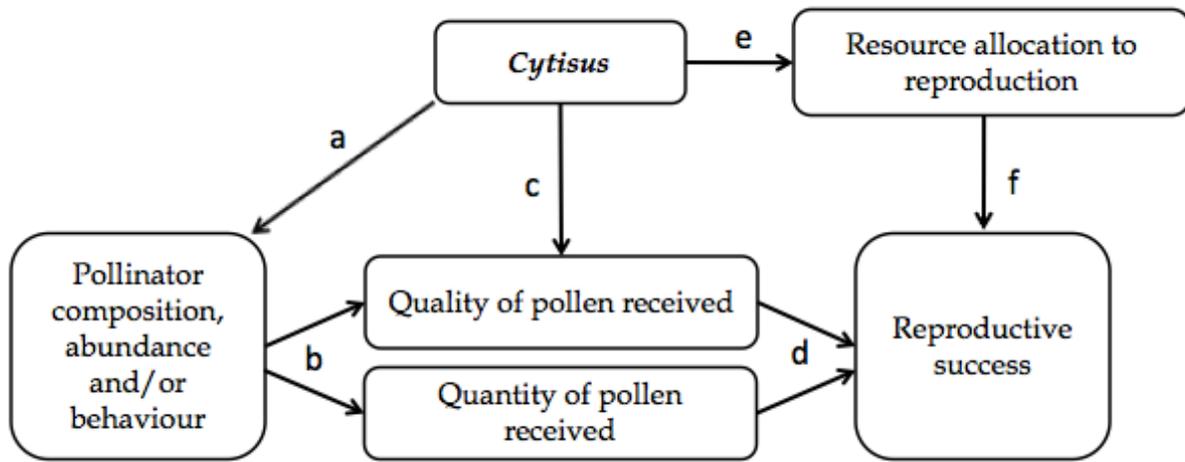


Figure 1. Possible effects of *Cytisus* on the pollination and reproductive success of co-flowering Garry oak-associated species.

The presence of Scotch broom flowers can affect the abundance, composition, or behaviour of pollinators in the community (a) by increasing available floral resources and subsequently supporting greater pollinator population sizes, attracting greater numbers of insect pollinators to the community, and/or affecting pollinator behaviour by drawing insect visits from other co-flowering species.

This change in pollinator regime may then affect both the quantity and quality of pollen received by co-flowering species (b). The quantity of pollen received may change in direct proportion to the change in pollinator visitation (i.e. increased visitation is expected to increase pollen deposition), or increased visitation may increase the receipt of heterospecific pollen, thus decreasing pollen quality. *Cytisus* pollen deposited onto co-flowering stigmas may also decrease the quality of pollen received by chemically or physically blocking the transport of compatible pollen within the style (c).

Changes in pollen quantity and quality caused by the presence of *Cytisus* may then ultimately affect the reproductive success of co-flowering plants (d). Decreased receipt of compatible pollen and/or increased receipt of poor quality pollen is expected to decrease seed set, potentially resulting in the pollen limitation of co-flowering species. Alternatively, increased conspecific pollen may increase seed set if the population is already pollen limited.

Cytisus can also affect the reproductive success of co-flowering species through soil nutrient addition with its nitrogen-fixing *Rhizobium* root nodules (e). Increased reproduction may result from increased nutrient availability within the soil, especially if co-flowering plants are resource limited (f).

Chapter Two: **Methods**

During this study, I observed the pollination and reproductive success of co-flowering species of the Garry oak ecosystem both at sites where flowering *Cytisus* was present and where it was absent (“invaded” and “uninvaded” sites, respectively) on the Saanich Peninsula of Vancouver Island during spring of 2010 and 2011. As the *Cytisus* invasion on the Saanich Peninsula is so extensive, a suitable number of “uninvaded” sites was not available; thus, all sites where flowering *Cytisus* was considered absent had been previously invaded by *Cytisus*, but most *Cytisus* plants had been removed at an unknown time prior to the study. Immediately preceding the flowering season, remaining *Cytisus* plants were removed from “uninvaded” sites. To avoid effects of *Cytisus* from adjacent areas mediated by mobile pollinators, effort was taken to remove *Cytisus* from the surrounding area. However, due to the mosaic of residential property in the landscape and the extent of *Cytisus* invasion in the area, this could not be assured.

Unless otherwise noted, all statistical analyses were carried out using SAS 9.3 (SAS Institute 2011).

2.1 Focal plant species

Scotch broom (*Cytisus scoparius* (L.) Link (Fabaceae), hereafter referred to as *Cytisus*) is a woody shrub 1-3m tall, with green stems and reduced leaves. Its multitudinous large (16-20 mm) yellow flowers have a typical papilionaceous structure, with an upper banner petal (or standard), two lateral wing petals, and one fused lower keel petal that contains the stamens and style (Stout 2000) (Plate 1). The flowers have an ‘explosive’ pollination mechanism, whereby a visit from a large pollinator ‘trips’ the flower, causing the discharge of the stamens and style from the keel petal and deposition of pollen onto both the dorsal and ventral surfaces of the

insect (Darwin 1888, Stout 2000). The flower remains open after being tripped, and nectar guides are visible only in open flowers (Stout 2000). *Cytisus* flowers do not produce nectar, though they do possess deceptive nectar guides to lure floral visitors (Stout 2000). *Cytisus* is thought to be an obligate outcrosser, with self-pollinated flowers setting orders of magnitude fewer fruits than their outcrossed counterparts (Darwin 1888, Parker and Haubensak 2002, Simpson *et al.* 2005).

An extremely successful invader in temperate “Mediterranean-type” ecosystems (Fogarty and Facelli 1999), *Cytisus* is regarded as a noxious weed as a result of its aggressive displacement of native species in the eastern and western United States (Bossard 1991, Bossard and Rejmanek 1994), coastal Canada (Isaacson 2000), Australia (Waterhouse 1988, Fogarty and Facelli 1999, Downey and Smith 2000), New Zealand (Williams 1981, Partridge 1989), in addition to its establishment in Argentina, Chile, India, Japan, and South Africa (Isaacson 2000). Native to Europe, its success in open and exposed areas can be attributed to its nitrogen fixating symbiotic *Rhizobium* nodules, deep roots, reduced leaves and photosynthetic stems (Wheeler *et al.* 1987). *Cytisus* creates a dense shrub layer that can shade out native forbs, and changes the soil chemistry by increasing nitrogen content and in some cases decreasing soil pH and increasing carbon and phosphorus (Wheeler *et al.* 1987, Fogarty and Facelli 1999, Haubensak and Parker 2004, Caldwell 2006). It is a prolific seed producer (mean = 9650 viable seeds/shrub/year, as estimated by Bossard and Rejmanek 1994), and its seeds persist in the seed bank for lengthy periods (refs). *Cytisus* can also resprout after being cut or burned (Zielke *et al.* 1992).

Within each site, I studied three focal species: great camas (native, *Camassia leichtlinii* ssp. *suksdorfii*), maiden blue-eyed Mary (native, *Collinsa parviflora*), and dovesfoot geranium

(exotic, *Geranium molle*) (Plate 1). These species were chosen because they co-flower with Scotch broom, were moderately abundant at all sites, and preliminary observations indicated that they shared similar floral visitors with *Cytisus*.

Camassia leichtlinii Baker (S. Watson) subsp. *suksdorfii* (Greenman) Gould (Liliaceae, hereafter referred to as *Camassia*) is a bulbous, perennial lily native to wet meadows of western North America. A robust plant, it has showy blue to bluish-violet actinomorphic flowers (occasionally white, though such individuals were ignored in this study) (Mathew 2004) and blooms during late-spring from May to June (Turner 1983, Ranker and Hogan 2002). *Camassia* produces 6-12 seeds per locule and 3 locules per fruit (Gould 1942, Ranker and Hogan 2002). It is distinguished from its sympatric congener *Camassia quamash* by its generally larger growth form, slightly later flowering (approx 2-3 weeks later, Gould 1942) and distinguishing floral development: *C. leichtlinii* have strongly radially symmetrical flowers whose tepals twist together above the developing fruit as they senesce, whereas the radial symmetry of *C. quamash* is much weaker, with the majority of petals curving upward, except for the lower-most petal pointing straight down and tepals that do not twist as the fruits develop (Turner 1983, Beckwith 2004).

Geranium molle L. (Geraniaceae, hereafter referred to as *Geranium*) is an herbaceous annual plant with bright pink to purple actinomorphic flowers (Aedo *et al.* 1998). Each ovary has 5 locules, with 2 superimposed ovules per locule (Aedo *et al.* 1998), although in general a maximum of 5 ovules develop into seeds per ovary (J. Muir, pers. obs.). Seeds disperse via an explosive “carpel-projection” mechanism (Aedo *et al.* 1998). Originating from Europe, North Africa and Western Asia (Aedo *et al.* 1998), it has been introduced to the Americas, Southern Africa, eastern Asia, Australia, New Zealand, and recently Taiwan (Chen and Wang 2005). It is

invasive within the Garry Oak Ecosystem, but as a forb it is not considered to be as large of a threat or as destructive as invasive grasses or shrubs (Fuchs 2001). Though its closely-related congeners *Geranium pratense* and *Geranium maculatum* are primarily outcrossing (Chang 2007, Michalski and Durka 2012), this species is one of 8.6% of Geraniaceae that primarily self-fertilize autogamously (Fiz *et al.* 2008).

Collinsia parviflora Dougl. ex Lindl. (Plantaginaceae, hereafter referred to as *Collinsia*) is a winter annual common in North America from British Columbia to California, east to Ontario and Pennsylvania (Elle and Carney 2003). Its small bluish-purple flowers are zygomorphic, with five petals (two upper banner petals, two lower wing petals and a keel petal containing the sexual structures) (Elle *et al.* 2010). On Vancouver Island, *Collinsia* blooms from March-June, and ripe capsules open and disperse 3-8 seeds passively (Elle and Carney 2003, Parachnowitsch and Elle 2004). *Collinsia*'s main pollinators include species of *Bombus*, *Osmia*, and hover flies, and visitation rate varies with population size (Elle and Carney 2003). This species is primarily outcrossing, but can also produce seeds by autonomous selfing for reproductive assurance (Elle and Carney 2003, Kennedy and Elle 2008).

2.2 Study Sites

The Garry oak ecosystem (hereafter GOE), also known in the United States as the Oregon White Oak Ecosystem, occupies coastal sites with a Mediterranean climate from southwestern British Columbia to southern California (Fuchs 2001, Lea 2006). In Canada, the GOE is limited to British Columbia: southern Vancouver Island, the Gulf Islands, and isolated patches on Savary Island and in the Fraser Valley (Figure 2, Fuchs 2001). Prior to European settlement, the ecosystem was thought to have been managed by selective burning by the

indigenous Coast Salish First Peoples (Fuchs 2001). Now, it is threatened by fire suppression, urban development and subsequent fragmentation, and the invasion of alien species. Less than 5% of the original extent of GOE remains in natural unadulterated form (Lea 2006). Not only is the ecosystem itself rare, but it is home to >100 Provincially listed species at risk, including 61 Provincially listed and 11 Federally listed (COSEWIC) plant species (Fuchs 2001).

My study considered remnant patches of GOE of the Saanich peninsula on southeastern Vancouver Island (Figure 2). Though the Saanich Peninsula has the highest human population density on the island, it also contains multiple parks where GOE remnants are maintained. Due to the extent of *Cytisus* invasion in GOEs, a representative number of sites that had not been invaded by *Cytisus* were not available to represent natural conditions. Thus, eight parks containing patches of GOE were chosen, four that included *Cytisus*, and four of which had been previously cleared of *Cytisus*. Although some *Cytisus* removal has probably occurred recently at all sites, a moderate density of *Cytisus* was present at all “invaded” sites.

2.3 Plant Community Diversity

Plant diversity within each site was quantified once during peak flowering of *Cytisus* (mid- to late-May). This was done by walking transects 10 m apart throughout the entirety of each site, and recording all observed angiosperm species, and whether they were flowering (and thus co-flowering with *Cytisus*). These data were analyzed using PERMANOVA, a component of the PRIMER-E v.6 package (Anderson 2001, Clarke and Gorley 2006). PERMANOVA uses permutational analysis to test the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design on the basis of a similarity matrix (Anderson *et al.* 2008). Each analysis involved 9999 permutations. The Bray-Curtis similarity index (reference) calculated from the presence or absence of each plant species was compared between *Cytisus*-invaded and uninvaded sites. This was done twice; once for species in flower, and once for all species.

2.4 Insect diversity

During 2010, pan traps were used to sample the overall pollinator community present at each of the eight sites. Within each site, 30 pans were set out along a transect 3 m apart (for a total transect length of 87 m). Along each transect, pan colour alternated between blue, yellow and white, and each pan was half-filled with soapy water. Each survey took place from approximately 9:00 to 17:00 h, after which the pollinators were collected from the pans and stored in 95% ethanol until they could be processed and identified. The pan traps were set out in each site twice while *Cytisus* was flowering (May 25 to June 8 and June 10 to June 25). Due to permit restrictions, one site (Summit park) was excluded from pan trap sampling.

Diversity of pan-trapped insects was compared between sites with and without *Cytisus* using PERMANOVA for three datasets: early-season samples (May 25-June 8), later-season samples (June 10-June 25), and all samples combined. Specifically, considered the Bray-Curtis similarity index calculated for the $\ln(\text{abundance} + 1)$ of insects collected by all pan at a site as the dependent variable.

2.5 Floral Visitation

Pollinators were observed two to six times for each focal plant species at each site between 09:00 and 17:00 h during clear weather with temperatures above 14°C. During observation periods, pollinator visits to each species were quantified and, when possible, the visitors were collected for identification. A “pollinator” was defined as a floral visitor observed contacting the reproductive surfaces of a flower. Observations were conducted in patches of flowers representative of each site, and the flowers of focal species was counted to determine the floral abundance in the observed patch. Most observational periods ranged from 40 to 130 min in duration, but most lasted 20 min. To account for variation in sampling effort, observation duration was included as a covariate in statistical analyses.

I compared floral visitation for each focal species between sites with and without *Cytisus* using a generalized linear mixed model (SAS Institute 2011: PROC GLIMMIX). This analysis considered site nested within invasion as a random factor, and duration of the observation period, number of flowers observed, and ambient temperature (all \ln -transformed) were included as covariates. Denominator degrees of freedom for F-tests of fixed effects were determined by the method of Kenward and Roger (1997). The number of floral visitors during each observation

period was modeled with a Poisson distribution for *Camassia* and *Collinsia* and a negative binomial distribution for *Geranium* visitors: a ln-link was used in all cases.

Mean visitation rate (visits per minute per flower) was compared among focal plants as well, using a general linear model (PROC GLM) to compare these values and invasion as a factor. Site nested within *Cytisus* invasion was used as a random factor, and significant differences among plant species were determined with the use of a Tukey HSD test.

Using PERMANOVA, part of the PRIMER-E v.6 package (Anderson 2001, Clarke and Gorley 2006), the visitor community of each focal plant was tested against the null hypothesis that there is no significant difference between *Cytisus*-invaded and uninvaded sites (as in Tonietto *et al.* 2011). A Bray-Curtis similarity index was calculated for each focal plant species in each site, and the ln(X+1)-transformed pollinator species abundances were included as dependent variables in a model including the presence of *Cytisus* as a fixed effect. In addition, Pianka's niche overlap index (hereafter NOI) was calculated to determine the degree of pollinator sharing each GOE resident focal plant had with *Cytisus*:

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{(\sum p_{ij}^2 \sum p_{ik}^2)^{1/2}}$$

where p_i is the frequency of occurrence of visitor taxon i of plant species j and k . This index incorporates information about the identity and frequency of floral visitors of each plant, and ranges from 0 for total separation to 1 for complete overlap (Pianka 1973).

2.6 Pollen deposition

To relate pollen deposition to pollinator abundance, styles were collected from 10-12 senescing flowers per focal species in all sites, and stored in 0.5- μ l microcentrifuge tubes filled with a 70% ethanol solution. In the lab, each style was removed from the ethanol and stained in an aqueous solution of basic fuchsin. Stained styles were mounted on slides with a drop of glycerine and the conspecific and heterospecific pollen grains present on the stigmatic surface(s) were counted with the use of a stereo light microscope at 1000 x magnification. Pollen-grain identity was checked against a library prepared from pollen samples collected from all co-flowering species in the community at the time of stigma collection.

Pollen deposition per stigma (number of conspecific, heterospecific, and total grains, and the proportion of conspecific pollen) was analyzed using generalized linear mixed models in PROC GLIMMIX, with site nested within invader presence as a random factor. All models were fitted with a negative binomial distribution and its associated canonical log link function, except the proportion of conspecific pollen which was fitted with a binomial distribution and logit link function.

The mean number of conspecific pollen grains and the proportion of conspecific pollen grains per site were also compared among focal plant species using PROC GLM and invasion as a factor in the model. Significant differences among plant species were determined with Tukey HSD tests.

2.7 Pollen limitation

Pollen supplementation experiments were used to determine whether seed production is subject to pollen limitation in the focal GOE species and, if so, whether it is influenced by the

presence of *Cytisus*. At each site, 50 individuals of each species were randomly assigned to pollen-supplemented and naturally-pollinated groups. Pollen-supplemented plants were hand-pollinated using pollen from at least 2-3 conspecific individuals (mixed prior to application) located 1 - 15 m from the experimental plants to increase the probability of using outcross donors while minimizing the possibility of outbreeding depression. I attempted to supplement all flowers on herbaceous plants to avoid resource reallocation within inflorescences (Zimmerman and Pyke 1988). However, due to time constraints this was often not possible, so the proportion of supplemented flowers was recorded. The influence of resource reallocation was examined based on the correlation between the proportion of supplemented flowers and reproductive success of supplemented plants for each focal plant species.

Cytisus was also pollen-supplemented at three of the four invaded sites. Because of the large number of flowers per plant, I supplemented only the flowers on one branch. As seed production by a branch of *Cytisus* seemed to be independent of the rest of the plant due to the presence of leaves and bracts on the branch, this method probably was not subject to resource reallocation (Parker 1997, Wesselingh 2007).

After flowering, fruits from pollen-supplemented and naturally-pollinated groups were collected and seeds, aborted seeds and ovules were counted for each fruit in each focal species except *Cytisus*, for which early harvest of pods allowed assessment of only fruit set. Aborted seeds were recognized by their intermediate size between ovules and seeds and/or deflated appearance compared to ripe seeds. Owing to time constraints, seed set was not measured for approximately one quarter of the collected plants, but fruit set was still calculated. Thus, the sample for fruit set was larger than for seed set for all focal plants.

Pollen limitation within a site type was inferred if pollen-supplemented plants produced more fruits or seeds than naturally-pollinated plants based on the log response ratio for each site:

$$\ln R = \ln \left(\frac{\text{mean output from supplementation}}{\text{mean output from control}} \right)$$

(Knight *et al.* 2005). A log-response ratio of 0 indicates that naturally pollinated flowers received sufficient pollen to produce full seed or fruit set, and so were not pollen limited. A positive log-response ratio indicates pollen limitation, and a negative log-response ratio indicated greater fecundity of naturally pollinated plants than pollen-supplemented plants. The log response ratio was compared among species and invaded and non-invaded sites with general linear model that included floral visitation rate (number of visits per minute per flower) as a covariate. Significant differences among plant species were determined with Tukey's HSD test.

2.8 Female Reproductive Success

For each focal plant the number seeds per plant was modeled with a negative binomial distribution and a ln-link function, and both the total number of ovules per plant (including ripe seeds, aborted seeds and unripened ovules) and the proportion of fruits per flower were included as covariates in the model. The number of fruits produced per flower was fitted with a negative binomial distribution for *Camassia* and *Cytisus*-supplemented *Camassia* (number of ripe fruits as response variable and the total number of flowers as a covariate) and a binomial distribution for *Geranium* and *Collinsia* (with total ovules as trials and ripe seeds as successes), with their respective canonical link functions (log and logit, respectively). The number of seeds produced

per flower was approximated with a negative binomial distribution and a log link function for all focal species.

Plant-level reproductive success was analyzed using generalized linear mixed models in PROC GLIMMIX. For each plant, the numbers of total seeds, fruits per flower, seeds per fruit, seeds per flower and aborted seeds per fruit were compared with respect to invader presence and/or pollen supplementation treatment. All analyses initially included site nested within site type (invader present or invader absent) and spatial block nested within site as random factors. 'Block within site' was omitted from analyses when it precluded the estimation of the variance-covariance matrix for site nested within site type, as the latter random variable was deemed of greater importance as an imposed feature of the experimental design.

To determine whether *Cytisus* pollen has negative effects on the reproductive success of *Camassia* plants, a mixture of conspecific and invader pollen was applied to a group of *Camassia* plants at one site (Layritz Park). This was done by collecting fresh *Camassia* and *Cytisus* pollen and mixing it at an approximate 50:50 ratio, then applying it to the stigmas of *Camassia* flowers on 20 *Camassia* plants. These methods were repeated every 1-2 days until all flowers on each *Camassia* plant had senesced. Fruit and seed set were quantified in the lab.

A group of *Camassia* plants was also supplemented with self pollen at one site (Bear Hill Park) during the summer of 2010. Plants were bagged with 2mm mesh to exclude pollinators, and every 1-2 days each open flower was pollinated with pollen from all other open flowers on the same plant. Mesh was subsequently replaced until all flowers had senesced. Fruit and seed set were then quantified in the lab.

For both of these groups of *Camassia* plants a similar generalized linear mixed model was used during analysis to compare the effect of invader pollen and self pollen treatments with

conspecific pollen supplementation and natural pollination treatments. As these treatments were implemented at only one site, site was not a factor in the analysis. The Tukey test was used to identify significant differences between pairs of treatments.

2.9 The effect of selfing and resource allocation on reproductive success

As within-plant characteristics such as resource allocation and mating system can also affect plant reproductive success, I carried out further analyses to pinpoint pollination-related effects. To determine whether plant populations in particular sites or treatment groups allocated more resources to reproduction than others, I assessed the total numbers of ovules (defined as the sum of seeds, aborted seeds and unripened ovules) and flowers per plant. These variables were modeled a negative binomial distribution (ln-link function) and compared with a generalized linear mixed model (PROC GLIMMIX) with respect to the presence of *Cytisus*, pollen-supplementation treatment, and their interaction. Site nested within *Cytisus* presences was included as a random factor, and the flower number per plant was used as a covariate for the analysis of ovule number.

I also examined effects on seed mass for *Collinsia* based on the average seed mass for 10 plants per site. Samples of up to 20 seeds were weighed to the nearest 0.0001 g on a digital balance. These data were analyzed using a general linear mixed model (PROC MIXED) to assess the effects of *Cytisus* presence, supplementation treatment and their interaction. The number of seeds in per sample was included as a covariate, and site nested within site type was used as a random factor in the analysis.

As little was known about the mating system of *Camassia*, I carried out a self-pollination experiment in the Bear Hill Park population during 2010. In addition to naturally-pollinated and

supplementally pollinated plants, a third group of plants were self-pollinated and bagged with 1-mm fabric mesh to exclude pollinators. Plants were visited every 1-2 days, during which all open flowers were pollinated with self-pollen. This was repeated until all flowers on each plant had completed flowering, when the fabric mesh exclusion bags were removed and the plants were left to set seed. Plants were collected after fruits had developed, fruits and seeds were counted, and seeds per plant, fruit set per flower, seeds per fruit, and aborted seeds per fruit were analyzed as described above for the pollen limitation experiment.

2.10 Effects of *Cytisus scoparius* pollen

To determine whether *Cytisus* pollen had a negative effects on the post-pollination pre-zygotic stage of GOE residents, most flowers on 20 *Camassia plants* were supplemented with a mixture of outcross conspecific pollen and *Cytisus* pollen that was mixed and applied in the field (in an approximate 2:1 ratio) at Layritz Park. I recorded which flowers were supplemented and which were not.

The reproductive success of *Camassia* plants subjected to the three treatments was compared with a generalized linear mixed model (PROC GLIMMIX). Analysis of seeds per plant (distribution, link function) included proportion fruit set and total ovules per plant as covariates, whereas that of fruit set and seeds per plant included flower number per plant as a covariate. Spatial block was considered as a random effect in each model.



Figure 2. Study locations on the Saanich peninsula of Vancouver Island.

Empty circles represent sites where *Cytisus* was removed, and closed circles represent sites where *Cytisus* was present.

Plate 1. The focal plant species in the current study.

Clockwise from top-left: maiden blue-eyed Mary, *Collinsia parviflora*; Great Camas, *Camassia leichtlinii*; Scotch broom, *Cytisus scoparius* (an open “tripped” flower); and dovesfoot geranium, *Geranium molle*.



Chapter Three: **Results**

The presence of *Cytisus* had variable and species-specific effects on the pollination and reproductive success of associated species in the GOE.

3.1 Plant Community Diversity

Sites with and without *Cytisus* had equivalent numbers of total angiosperm species ($F_{1,6} = 0.71, P > 0.75$) and species in flower ($F_{1,6} = 0.34, P > 0.95$).

3.2 Floral Visitors

I observed *Cytisus* for 380 min and recorded 50 floral visitors, of which 34 were collected and identified to belong to 21 taxa (Table 2). The most common floral visitors were *Bombus melanopygus* (10), *Lasioglossum pacificum* (4), and *Lasioglossum olympiae* (4).

Table 1. Floral visitors of *Cytisus scoparius* as collected by aerial net in remnant Garry oak ecosystem fragments in 2011.

Floral Visitor	Family	BH	XH	KN	LA	Total
<i>Bombus melanopygus</i>	Hymenoptera	4	1	3	2	10
<i>Lasioglossum pacificum</i>	Hymenoptera	3	0	1	1	5
<i>Lasioglossum olympiae</i>	Hymenoptera	0	3	1	0	4
<i>Bombus mixtus</i>	Hymenoptera	0	0	3	0	3
Muscidae	Diptera	0	0	0	2	2
<i>Apis mellifera</i>	Hymenoptera	0	0	0	2	2
<i>Dasysyrphus pauxillus</i>	Diptera	0	0	0	1	1
<i>Melanostoma mellinum</i>	Diptera	0	1	0	0	1
Tachinidae	Diptera	0	0	1	0	1
<i>Andrena morphosp.</i> 8	Hymenoptera	0	0	0	1	1
<i>Andrena salicifloris</i>	Hymenoptera	1	0	0	0	1
<i>Bombus flavifrons</i>	Hymenoptera	1	0	0	0	1
<i>Bombus vosnesenskii</i>	Hymenoptera	0	0	0	1	1
<i>Evylaeus morphosp.</i> 2	Hymenoptera	0	0	0	1	1
<i>Osmia morphosp.</i> A	Hymenoptera	0	1	0	0	1

During 709 min of observation of *Collinsia*, I recorded 38 visitors, 22 of which were collected and identified to be within 12 taxa (Table 3). The most common visitors were the bee fly *Bombyllius major* (4), and the solitary bees *Ceratina acantha* (4) and *Osmia odontogaster* (4).

Table 2. Floral Visitors of *Collinsia parviflora* as collected by aerial net in remnant Garry oak ecosystem fragments in 2011.

A star (*) indicates a *Cytisus*-invaded site.

Floral Visitor	Family	BH*	XH*	GO	HO	KN*	KO	LA*	SU	Total
<i>Bombylius major</i>	Diptera	0	0	2	1	0	1	0	0	4
<i>Ceratina acantha</i>	Hymenoptera	0	1	0	0	0	0	0	3	4
<i>Osmia odontogaster</i>	Hymenoptera	0	0	0	0	0	2	2	0	4
<i>Osmia tristella</i>	Hymenoptera	0	0	0	0	0	0	2	0	2
Empididae	Diptera	1	0	0	0	0	0	0	0	1
<i>Bombus bifarius</i>	Hymenoptera	0	0	0	1	0	0	0	0	1
<i>Bombus flavifrons</i>	Hymenoptera	0	0	0	1	0	0	0	0	1
<i>Nomada</i> morphosp. A	Hymenoptera	0	0	0	1	0	0	0	0	1
<i>Lasioglossum knereri</i>	Hymenoptera	0	0	0	0	0	0	1	0	1
<i>Lasioglossum pacificum</i>	Hymenoptera	0	0	0	0	1	0	0	0	1
<i>Osmia dolerosa</i>	Hymenoptera	0	0	0	0	1	0	0	0	1
<i>Osmia</i> morphosp. 6	Hymenoptera	0	0	0	0	0	0	1	0	1

During 717 min of observation of *Geranium*, I recorded 85 visitors, 63 of which were collected and identified to be within 12 taxa (Table 4). The most common visitors were *Ceratina acantha* (25), the bee fly *Bombylius major* (5), and *Osmia pusilla* (5).

Table 3. Floral visitors of *Geranium molle* as collected by aerial net in remnant Garry oak ecosystem fragments in 2011.

A star (*) indicates a *Cytisus*-invaded site.

Floral Visitor	Family	BH*	XH*	GO	HO	KN*	KO	LA*	SU	Total
<i>Ceratina acantha</i>	Hymenoptera	1	8	4	2	2	1	7	0	25
<i>Bombylius major</i>	Diptera	0	0	0	2	2	0	0	1	5
<i>Osmia pusilla</i>	Hymenoptera	1	0	1	0	1	0	2	0	5
<i>Osmia tristella</i>	Hymenoptera	0	0	0	2	2	0	0	1	5
<i>Andrena nigrocaerulea</i>	Hymenoptera	0	1	1	0	0	0	1	0	3
<i>Bombus mixtus</i>	Hymenoptera	0	0	1	0	0	1	1	0	3
<i>Bombus bifarius</i>	Hymenoptera	1	0	1	0	0	0	0	0	2
<i>Lasioglossum knereri</i>	Hymenoptera	0	0	0	0	0	1	1	0	2
<i>Osmia morphosp. A</i>	Hymenoptera	0	0	1	0	0	0	0	1	2
<i>Osmia odontogaster</i>	Hymenoptera	0	0	0	0	1	1	0	0	2
<i>Hemipenthes sp.</i>	Diptera	0	0	0	0	1	0	0	0	1
Muscidae	Diptera	1	0	0	0	0	0	0	0	1
Scathophagidae	Diptera	0	1	0	0	0	0	0	0	1
<i>Eupeodes fumipennis</i>	Diptera	0	0	0	0	0	0	1	0	1
<i>Eupeodes lasifasciatus</i>	Diptera	0	0	1	0	0	0	0	0	1
<i>Merodon equestris</i>	Diptera	0	0	0	0	0	1	0	0	1
<i>Platycheirus sp.</i>	Diptera	0	0	1	0	0	0	0	0	1
<i>Bombus melanopygus</i>	Hymenoptera	0	0	1	0	0	0	0	0	1
<i>Evylaeus morphosp. 6</i>	Hymenoptera	0	0	0	0	0	1	0	0	1
<i>Lasioglossum olympiae</i>	Hymenoptera	0	0	1	0	0	0	0	0	1
Ichneumonidae	Hymenoptera	0	0	0	0	0	1	0	0	1
<i>Osmia cyanella</i>	Hymenoptera	0	0	0	0	0	0	1	0	1
<i>Osmia kincaidii</i>	Hymenoptera	1	0	0	0	0	0	0	0	1
<i>Osmia morphosp. 4</i>	Hymenoptera	1	0	0	0	0	0	0	0	1

BH = Bear Hill Park, XH = Christmas Hill Park, GO = Gore Park, HH = Horth Hill Park, KN = Knockan Hill Park, KO = Konukson Park, LA=Layritz Park, SU= Summit Park

During 590 min of observation of *Camassia*, I recorded 165 visitors, 123 of which were collected and identified to be within 26 taxa (Table 5). The most common visitors were *Bombus mixtus* (41), *Apis mellifera* (22), and *Lasioglossum olympiae* (19).

Sites with and without *Cytisus* did not differ significantly with respect to the composition of floral visitors for any of the focal plant species (Table 5), or of the insects collected in the pan traps for either the early set, late set, or overall (Table 6, Appendix A). According to the niche overlap index, the extent of pollinator sharing between *Cytisus* and *Collinsia*, *Geranium*, and *Camassia* in the invaded sites were 0.06, 0.08, and 0.42, respectively.

Table 4. Floral visitors of *Camassia leichtlinii* as collected by aerial net in remnant Garry oak ecosystem fragments in 2011.

A star (*) indicates a *Cytisus*-invaded site.

Floral Visitor	Family	BH*	XH*	GO	HO	KN*	KO	LA*	SU	Total
<i>Bombus mixtus</i>	Hymenoptera	7	2	8	7	3	3	11	0	41
<i>Apis mellifera</i>	Hymenoptera	0	0	6	0	0	15	1	0	22
<i>Lasioglossum olympiae</i>	Hymenoptera	0	3	3	0	5	4	1	3	19
<i>Osmia lignaria</i>	Hymenoptera	0	0	0	0	1	10	0	0	11
<i>Andrena</i> morphosp. 8	Hymenoptera	0	0	2	0	1	0	0	1	4
<i>Bombus flavifrons</i>	Hymenoptera	1	0	0	3	0	0	0	0	4
Muscidae	Diptera	0	0	1	0	0	0	2	0	3
<i>Bombus bifarius</i>	Hymenoptera	2	0	0	0	0	0	1	0	3
<i>Lasioglossum knereri</i>	Hymenoptera	0	0	0	1	0	1	0	0	2
<i>Lasioglossum pacificum</i>	Hymenoptera	0	0	1	0	0	0	0	1	2
<i>Melanostoma mellinum</i>	Diptera	0	0	1	0	0	0	0	0	1
<i>Merodon equestris</i>	Diptera	0	0	0	0	1	0	0	0	1
<i>Toxomerus occidentalis</i>	Diptera	0	0	0	0	1	0	0	0	1
<i>Volucella fascialis</i>	Diptera	0	0	0	0	0	0	1	0	1
Tachinidae	Diptera	0	0	0	0	1	0	0	0	1
<i>Andrena salicifloris</i>	Hymenoptera	0	0	1	0	0	0	0	0	1
<i>Bombus melanopygus</i>	Hymenoptera	1	0	0	0	0	0	0	0	1
Chrysididae	Hymenoptera	0	0	0	0	1	0	0	0	1
<i>Evylaeus</i> morphosp. 6	Hymenoptera	0	0	0	1	0	0	0	0	1
<i>Lasioglossum incompletum</i>	Hymenoptera	0	0	0	0	1	0	0	0	1
<i>Lasioglossum zonulum</i>	Hymenoptera	0	0	0	0	0	1	0	0	1
<i>Osmia bucephala</i>	Hymenoptera	0	0	0	0	0	1	0	0	1
<i>Osmia dolerosa</i>	Hymenoptera	0	0	0	0	1	0	0	0	1
<i>Osmia</i> morphosp. 4	Hymenoptera	0	1	0	0	0	0	0	0	1
<i>Osmia odontogaster</i>	Hymenoptera	0	0	0	0	0	1	0	0	1
Tenthredinidae	Hymenoptera	0	0	0	1	0	0	0	0	1

Table 5. The effect of *Cytisus* invasion and associated covariates on the composition of observed floral visitors for each focal plant species.

Data was analyzed via permutational multivariate ANOVA (PERMANOVA) analysis, and the significance of each test was assessed with 9999 permutations.

	Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
			MS	Pseudo-F	Perm. P	MS	Pseudo-F	Perm. P	MS	Pseudo-F	Perm. P
Floral Visitor Similarity	Invasion	1	1807.9	0.658	0.68	2552.4	0.849	0.646	3307.5	0.771	0.6302
	Obs. Time	1	1429.5	0.520	0.83	2457.3	0.817	0.663	6036.4	1.41	0.1642
	Res	5	2747	-	-	3004.7	-	-	4288.3	-	-

Table 6. The effect of *Cytisus* presence and associated covariates on the composition of insect species collected via pan traps during 2010.

Data were analyzed via permutational multivariate ANOVA (PERMANOVA) analysis, and the significance of each test was assessed with 9999 permutations.

	Source of Variation	df	MS	Pseudo-F	Perm. P
Early Traps	Invasion	1	1743.8	1.349	0.1726
	Res	5	1292.0	-	-
Late Traps	Invasion	1	1394.0	0.881	0.5984
	Res	5	1583.0	-	-
All Traps	Invasion	1	1328.1	1.372	0.085
	Res	5	1967.8	-	-

3.3 Visitation Rate

Camassia, but not *Geranium* or *Collinsia*, tended to receive fewer insect visits in the presence of Scotch broom than at sites where the invader was absent (Table 7, Figure 3).

Visitation was observed to increase with the number of flowers observe for *Camassia* and *Collinsia*, but not for *Geranium*.

Table 7. The effect of *Cytisus* presence and associated covariates on floral visitation for each focal plant.

Generalized linear mixed model analysis of the Site nested within *Cytisus* invasion was used as a random effect within each model.

Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
		Den. df	F	P	Den. df	F	P	Den. df	F	P
Visitation Invasion	1	4.51	6.3	0.0591*	22.93	0.14	0.7147	5.446	0.02	0.8914
Observation Time	1	21	2.58	0.1230	14.49	6.33	0.0242	30	2.89	0.0922
# Flowers	1	21	11.76	0.0025	19.14	2.52	0.1288	30	14.21	0.0007
Temperature	1	21	0	0.9627	15.55	1.69	0.2123	30	0.88	0.3558

Bold type indicates P<0.05, asterisk (*) indicates a trend.

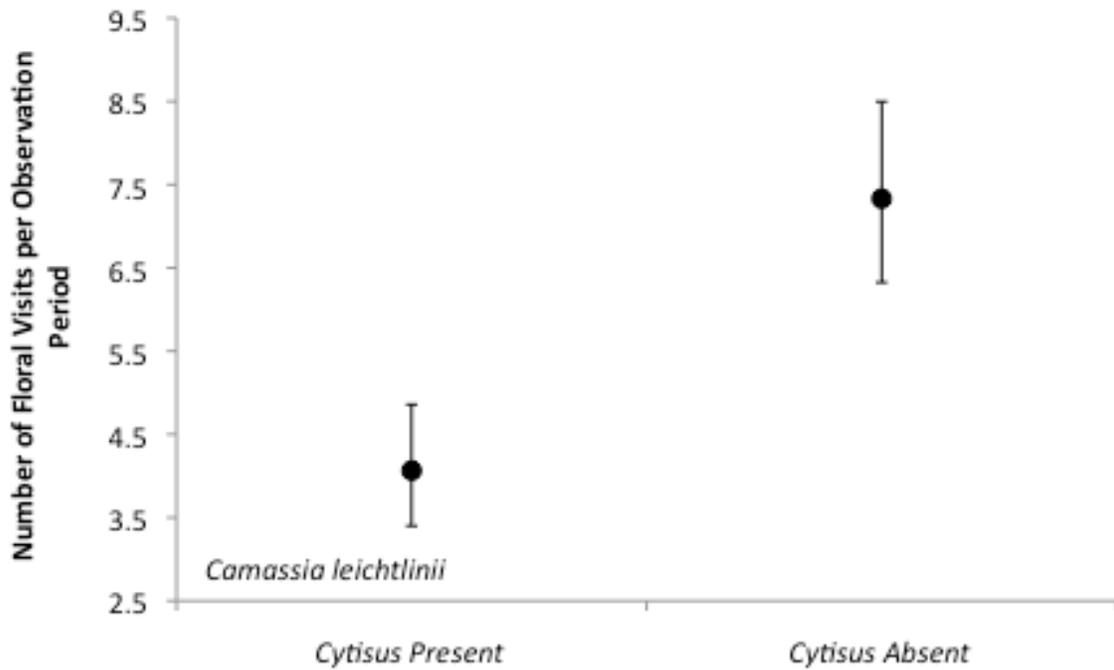


Figure 3. The effect of invader presence on the floral visitation of *Camassia leichtlinii*.

Values are back-transformed from log values estimated from generalized linear mixed models (PROC GLIMMIX) \pm one standard error. Length of observation period, total number of flowers observed, and ambient temperature are fixed covariates in the model, and site nested within *Cytisus* presence is a random effect.

Focal plant species differed significantly in floral visitation (Table 8, Figure 4), with *Camassia* receiving visits faster than *Cytisus*, *Collinsia*, or *Geranium*.

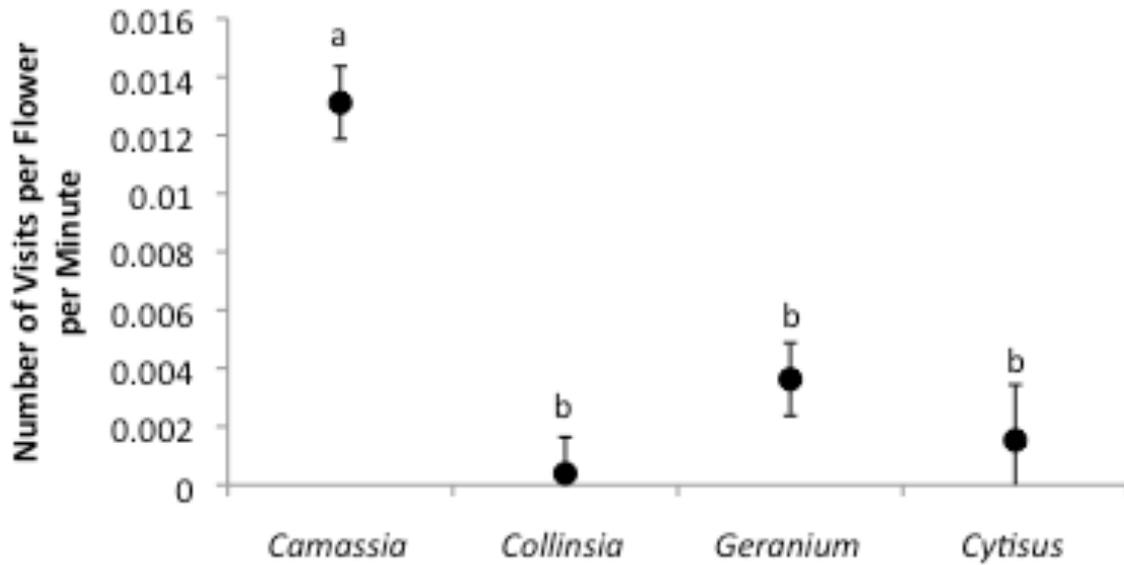


Figure 4. Relative floral visitation (number of visits per minute per flower) for each focal plant species in the study.

Least squares mean (\pm SE) insect visitation rates for the focal species.

Invader presence as a factor. Differences between focal species determined with the use of a Tukey test.

Table 8. Comparisons of floral visitation rate (visits per min per flower), pollen limitation (ln (mean output from supplementation/mean output from control)) and pollen deposition among focal plant species based on general linear model analysis and sites with and without *Cytisus*.

Seed set was not quantified in *Cytisus*. P< 0.05 is indicated in bold type, and trends are indicated with an asterisk (*).

	Source of Variation	df	MS	F	P
Visitation	Focal Species	3	0.00075	20.07	<0.0001
	Invasion	1	0.00002	1.60	0.2191
	Error	23	0.00001	-	-
Pollen Limitation (seeds)	Focal Species	2	0.04427	0.35	0.7071
	Invasion	1	0.02448	0.20	0.6635
	Error	20	0.12535	-	-
Pollen Limitation (fruits)	Focal Species	3	1.21303	5.73	0.0047
	Invasion	1	0.10019	0.47	0.4985
	Error	22	0.21158	-	-
Pollen Deposition (total heterospecific)	Focal Species	3	490.71	6.51	0.0024
	Invasion	1	27.647	0.37	0.5508
	Error	23	75.409	-	-
Pollen Deposition (proportion conspecific)	Focal Species	3	0.00199	0.22	0.8797
	Invasion	1	0.00245	0.27	0.6058
	Error	23	0.00894	-	-
Pollen Deposition (total conspecific)	Focal Species	3	8710.20	13.08	<0.0001
	Invasion	1	2507.35	3.77	0.0646
	Error	23	665.71	-	-

3.4 Pollen Deposition

Pollination outcomes varied between sites with and without *Cytisus* for *Camassia*, but not for *Geranium* or *Collinsia* (Table 10). *Camassia* stigmas received significantly more total pollen deposition and conspecific pollen in invaded sites than in non-invaded sites (Table 9, Figure 6, Figure 6). In contrast, neither the amount of heterospecific pollen on *Camassia* stigmas, nor the proportion of conspecific pollen deposited on *Camassia* stigmas differed among site types (Table 9).

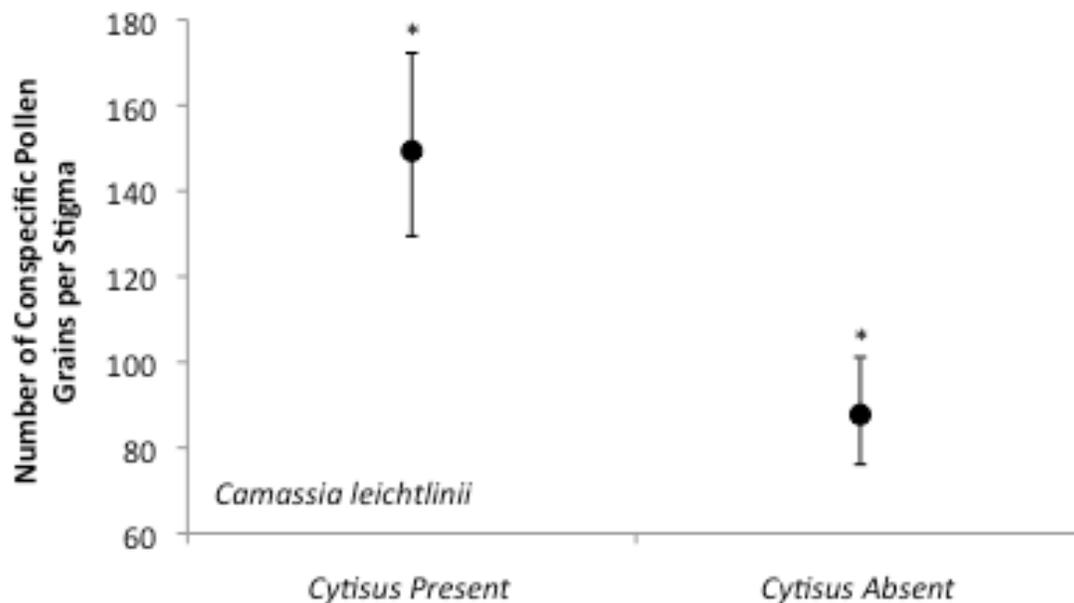


Figure 5. The effect of *Cytisus* presence on the number of conspecific pollen grains deposited on each *Camassia leichtlinii* stigma sampled.

Least squares mean (\pm SE) estimates from a generalized linear mixed model. Invader presence used as factor and site nested within *Cytisus* presence used as a random factor in the model.

Table 9. Generalized linear mixed model analysis of the effect of *Cytisus* invasion and associated covariates on the observed pollen deposition on the stigmas of each focal plant.

Site nested within *Cytisus* invasion was used as a random effect within each model. Bold values indicate significance at the 0.05 level.

	Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
			Den. df	F	P	Den. df	F	P	Den. df	F	P
# Conspecific	Invasion	1	6.047	6.95	0.0384	5.888	0.98	0.3607	6.022	0.07	0.8046
# Heterospecific	Invasion	1	6.1	0.57	0.4790	5.897	1.03	0.3503	5.977	0.97	0.3633
Total	Invasion	1	5.92	10.56	0.0178	83	2.63	0.1086	6.017	0.19	0.6814
Proportion Conspecific	Invasion	1	6.269	0.25	0.6310	6.028	0.01	0.9382	80.52	0.52	0.4744
	Total Pollen	1	73.78	279.46	<0.0001	65.91	321.69	<0.0001	70.02	357.67	<0.0001

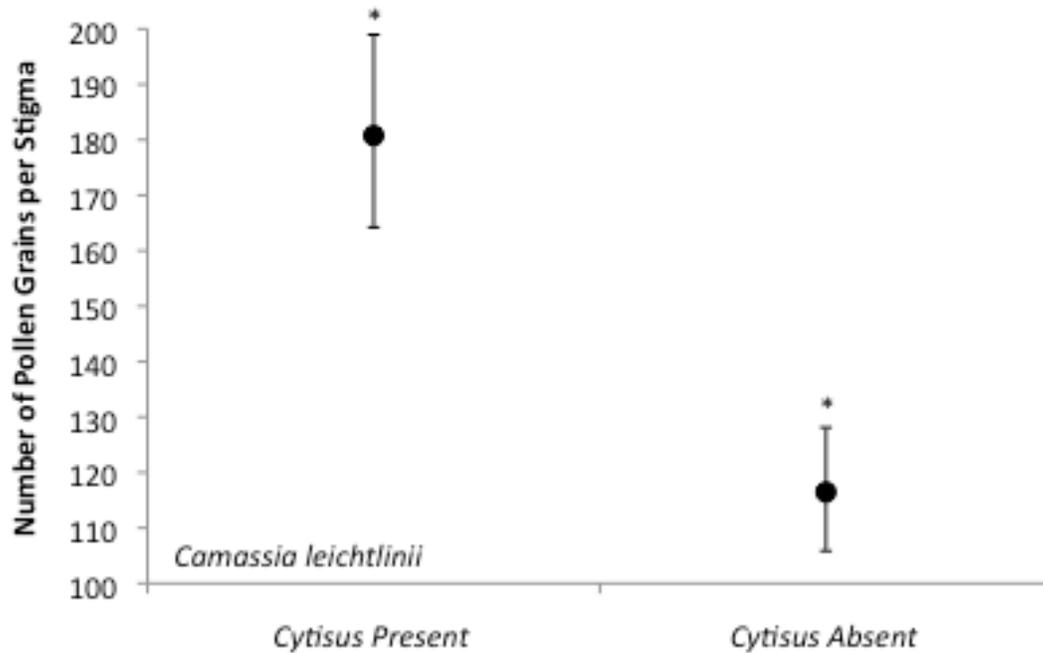


Figure 6. The effect of invader presence on the total number of pollen grains (conspecific and heterospecific) deposited on each *Camassia leichtlinii* stigma sampled.

Least squares mean (\pm SE) values from generalized linear mixed models (PROC GLIMMIX). Cytisus presence was used as a factor, and site nested within *Cytisus* invasion was used as a random effect.

The proportion of conspecific pollen deposition did not differ significantly among focal plant species (Table 8), but they differed in the number of conspecific pollen grains (Table 8, Figure 7) and heterospecific grains (Table 8, Figure 8). In particular, *Camassia* received the most conspecific and heterospecific pollen. Scotch broom had the lowest conspecific pollen deposition. These significant trends were echoed in heterospecific pollen deposition as well (Table 8, Figure 8).

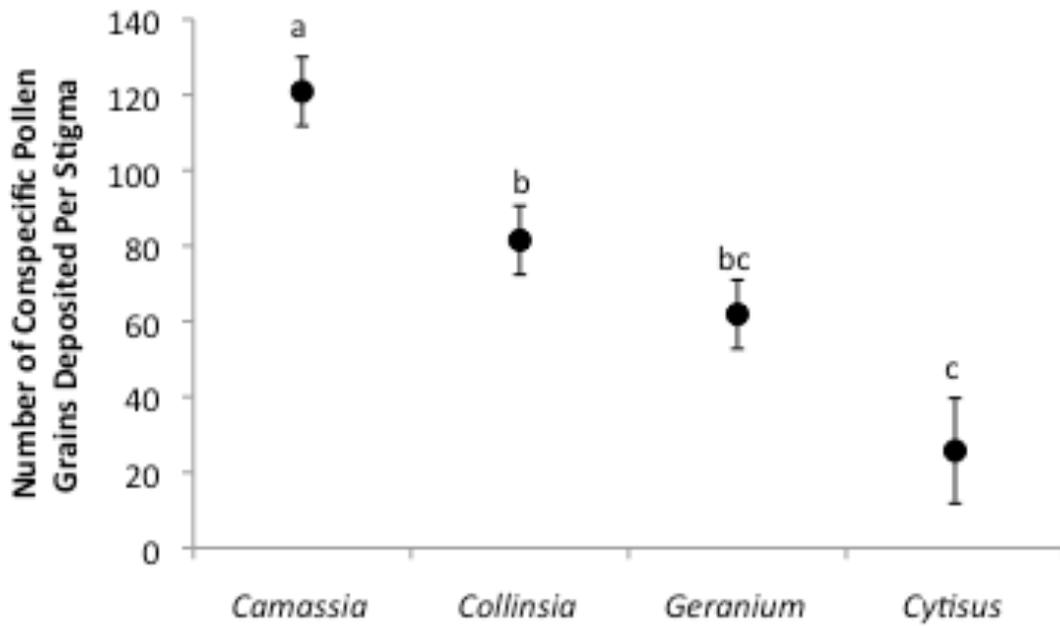


Figure 7. A comparison of conspecific pollen deposition among focal plants species in the study.

Values are estimated from general linear model (PROC GLM) \pm one standard error with invader presence as a covariate in the model and differences between plants determined with the use of a Tukey test.

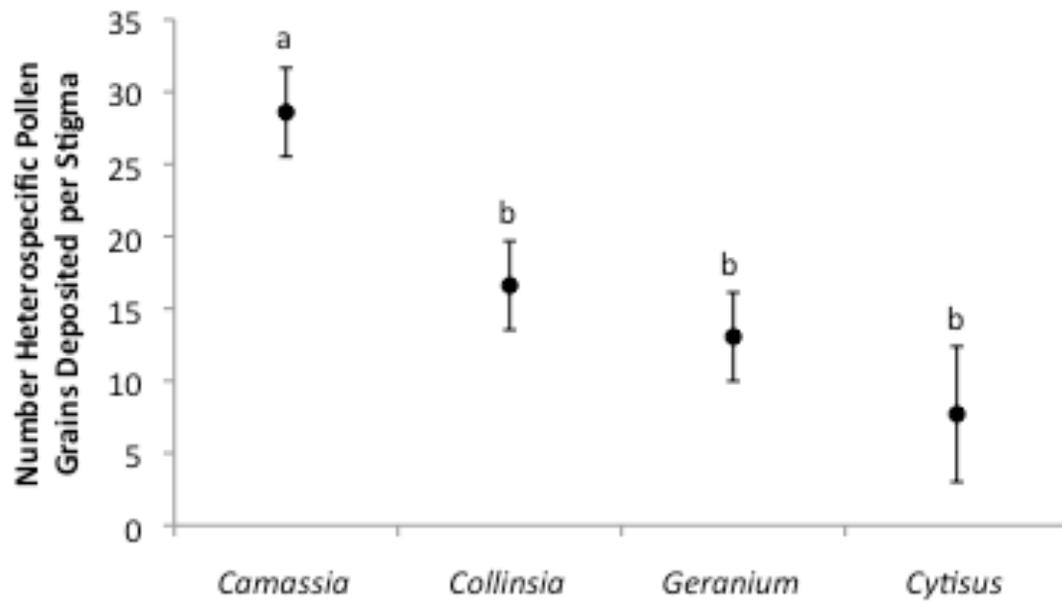


Figure 8. A comparison of heterospecific pollen deposition among focal plants species in the study.

Values are estimated from a general linear model (PROC GLM) \pm one standard error with invader presence as a covariate in the model, and differences between plants were determined via Tukey test.

Table 10. Correlations between proportion pollen-supplemented flowers and female reproductive success of the focal study species.

Bold values indicate significance at the 0.05 level.

Fitness Variable	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
	N	Pearson Coeff.	P	N	Pearson Coeff.	P	N	Pearson Coeff.	P
Prop Seeds	172	0.227	0.0027	269	-0.101	0.0967	344	-0.032	0.557
Prop Fruits	192	0.097	0.1805	542	-0.077	0.0698	441	0.138	0.0037
Seeds/Fruit	159	0.112	0.1589	266	0.104	0.0895	340	-0.059	0.2798
Aborted Seeds/Fruit	159	-0.059	0.4580	266	0.04920	0.4242	340	0.035	0.5180

3.5 Female Reproductive Success

In *Camassia*, a significant correlation was seen between the proportion of flowers supplemented and the proportion of ripe seeds produced per plant, but not in the proportion of fruits produced, seeds per fruit or aborted seeds per fruit (Table 10). *Geranium* showed no effect of supplementation, whereas a supplementation signal was only seen in the proportion fruit set in *Collinsia* (Table 10). There was no correlation between the proportion of flowers supplemented and fruit set in *Cytisus* ($r=0.1907$, $P=0.1445$, $N=60$).

No effect of invader presence, supplementation treatment, or their interaction on the number of seed production per plant or per fruit for *Camassia* was observed (Table 11). Fruit set per flower showed a significant interaction between supplementation treatment and invasion (Table 11, Figure 9). In particular, the number of fruits set in naturally pollinated *Camassia* plants was higher in sites where the invader was present than in sites where the invader was absent. Pollen-supplemented *Camassia* was also observed to have a significantly increased number of aborted seeds per fruit than its naturally-pollinated counterparts (Table 11, Figure 10).

Table 11. Generalized linear mixed model analysis of the effect of treatment (pollen supplemented or control), invasion (*Cytisus* present or absent), and associated covariates on the seeds per plant, fruits per flower and seeds per flower produced by each focal species.

Site nested within invasion and plant location nested within each site were included as random effects in each model. $P < 0.05$ is indicated in bold type, trends are indicated with a *, and NA indicates the covariate was taken into consideration within the response variable (i.e. for the binomial distribution).

	Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
			Den. df	F	P	Den. df	F	P	Den. df	F	P
Seeds/Plant	Treatment	1	316.8	0.75	0.3872	207.6	0.59	0.4448	338	1.84	0.1759
	Invasion	1	4.938	3.76	0.1109	6.138	0.29	0.615	5.613	0.05	0.8293
	Treatment x Invasion	1	315.2	0.41	0.5524	221.6	0.07	0.7852	337	2.10	0.1483
	Proportion Fruit Set	1	310.4	375.21	<0.0001	263	29.66	<0.0001	338	26.13	<0.0001
	Ovules / Plant	1	277.2	565.1	<0.0001	147.5	1083.9	<0.0001	178.5	783.99	<0.0001
Fruits/Flower	Treatment	1	378	0.02	0.8768	538	19.65	<0.0001	437	6.78	0.0095
	Invasion	1	6.418	4.57	0.0733	6.763	0.92	0.3694	6.136	1.15	0.3237
	Treatment x Invasion	1	390	5.48	0.0198	538	9.44	0.0022	437	0.01	0.9344
	Total Flowers	1	106.6	306.86	<0.0001	NA	NA	NA	NA	NA	NA
Seeds/Fruit	Treatment	1	318.4	0.89	0.3470	214.4	4.21	0.0413	338.2	1.49	0.2236
	Invasion	1	3.587	1.42	0.3063	6.292	1.03	0.3479	5.694	0.21	0.6632
	Treatment x Invasion	1	321.9	1.03	0.3113	233.8	0.01	0.9159	337	3.39	0.0666*
	Total Fruits	1	280.6	715.96	<0.0001	171.1	825.57	<0.0001	196.1	716.58	<0.0001
Aborted Seeds	Treatment	1	311.7	8.04	0.0049	218.6	1.98	0.1605	310	0.44	0.5097
	Invasion	1	3.306	0.42	0.5592	5.73	2.22	0.1889	5.782	0.06	0.8176
	Treatment x Invasion	1	316.9	0.01	0.9430	232.8	0.83	0.3619	309.3	0.12	0.7296
	Number of Fruits	1	280.5	122.91	<0.0001	179.4	127.86	<0.0001	140.9	73.15	<0.0001

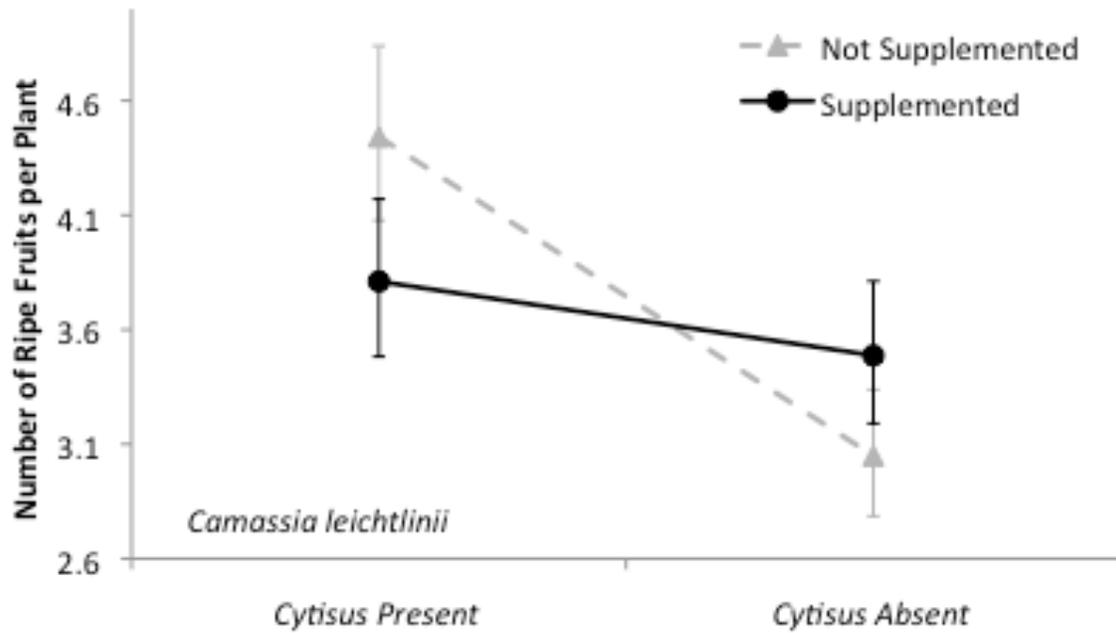


Figure 9. The effect of *Cytisus* presence and supplementation treatments on the number of fruits per plant in *Camassia leichtlinii*.

Values are back-transformed from log values estimated from generalized linear mixed models (PROC GLIMMIX) with total flowers as a covariate \pm one standard error. Site nested within *Cytisus* presence was used as a random factor in the model.

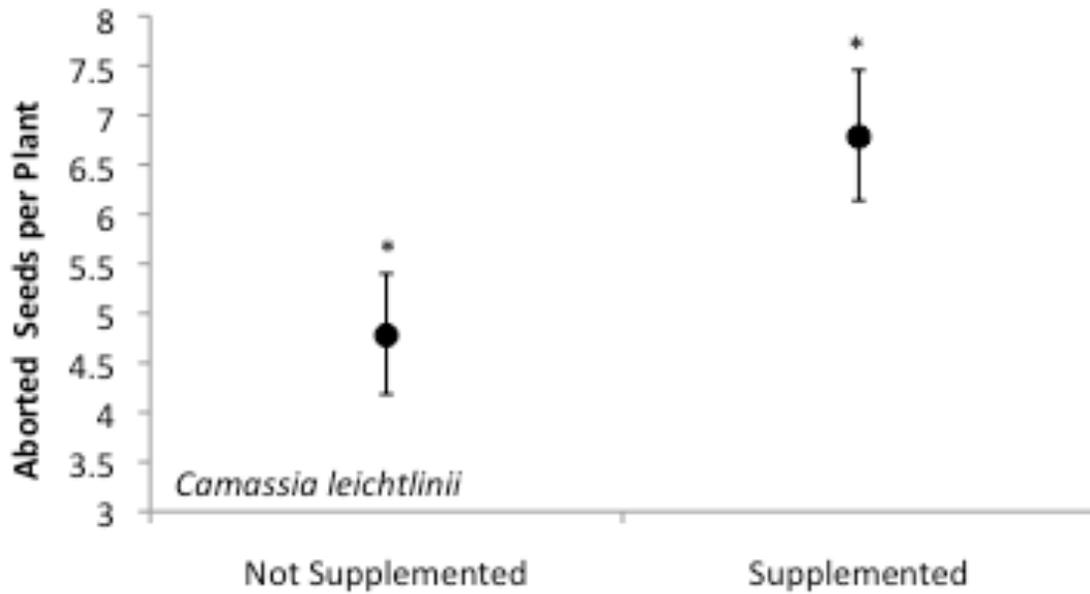


Figure 10. The effect supplementation treatment on the number of aborted seeds per plant in *Camassia leichtlinii*.

Values are back-transformed from log values estimated from generalized linear mixed models (PROC GLIMMIX) with total fruit set as a covariate \pm one standard error.

Site nested within *Cytisus* presence and plant location nested within site were used as random factors in the model.

No effect of treatment, invasion, or their interaction was observed on the number of seeds produced per plant or the number of aborted seeds per fruit for *Geranium*. While supplementation was not observed to affect the number of fruits produced per flower in *Cytisus* invaded sites, naturally pollinated flowers were more likely to set fruit in uninvaded sites than supplemented flowers, and overall this resulted in lower fruit set in supplemented flowers than in the control treatment where *Cytisus* was absent (Table 11, Figure 11). This interaction is opposite to that found in *Camassia*. A significant increase in the number of seeds per fruit in pollen-supplemented *Geranium* plants than the naturally pollinated group was also observed (Table 11, Figure 12).

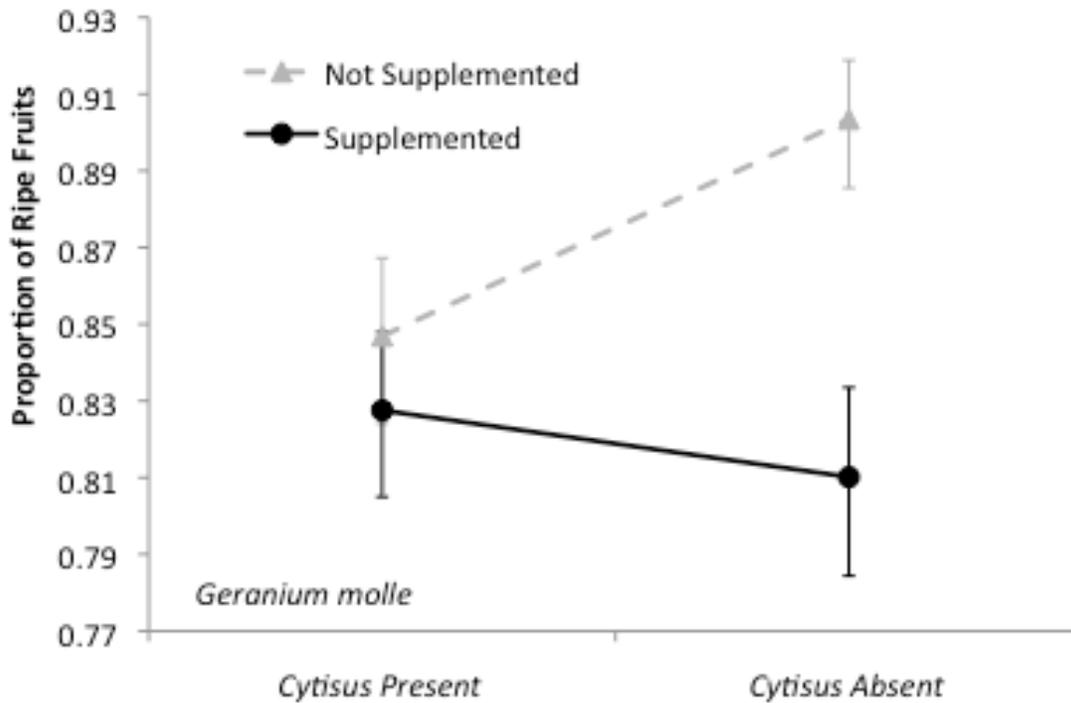


Figure 11. The effect of invader presence and pollen supplementation on the proportion of ripe fruits per flower in *Geranium molle*.

Values are back-transformed from logit values estimated from generalized linear mixed models (PROC GLIMMIX) \pm one standard error. Site nested within *Cytisus* invasion and plant location nested within site were used as random factors, and number of flowers per plant as a fixed covariate.

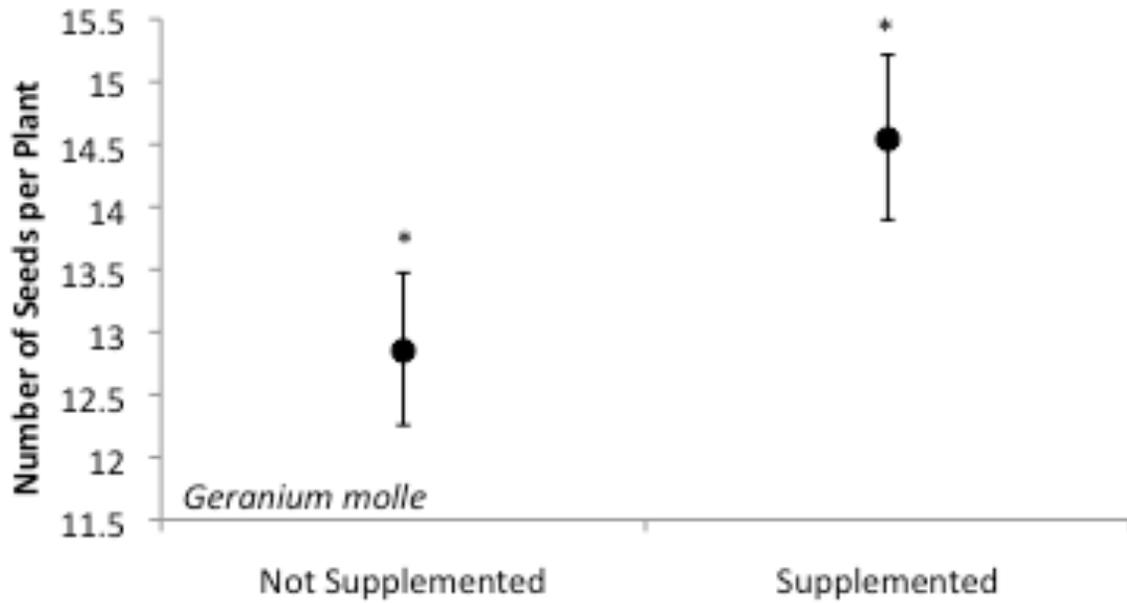


Figure 12. The effect of pollen supplementation on the proportion of seeds produced per plant in *Geranium molle*.

Values are back-transformed from log values estimated from generalized linear mixed models (PROC GLIMMIX) with number of fruits as covariate \pm one standard error. Site nested within *Cytisus* presence and plant location nested within site were used as random factors in the model.

In *Collinsia*, the number of seeds per plant and the number of aborted seeds per fruit showed no effect of invasion, supplementation, or an interaction between the two factors (Table 11). A trend toward increased seeds per fruit in control plants in invaded sites over uninvaded sites was seen, but this was not significant (Table 11, Figure 5). The fruit set per flower did indicate an increased proportion fruit set in supplemented plants than in control plants (Figure 16), but there was no effect of invasion or an interaction between invasion and supplementation (Table 11).

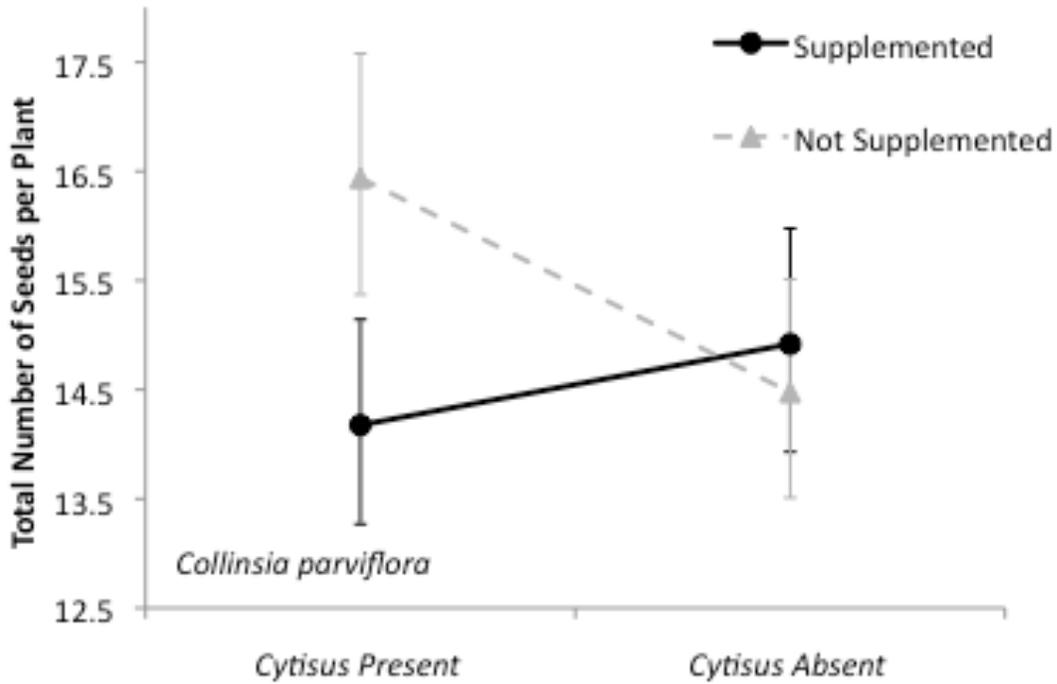


Figure 13. The effect of *Cytisus* presence and pollen supplementation on the proportion of ripe seeds per fruit in *Collinsia parviflora*.

Values are back-transformed from log values estimated from generalized linear mixed models (PROC GLIMMIX) with fruit set as a covariate and site nested within *Cytisus* invasion and plant location nested within site as random effects \pm one standard error.

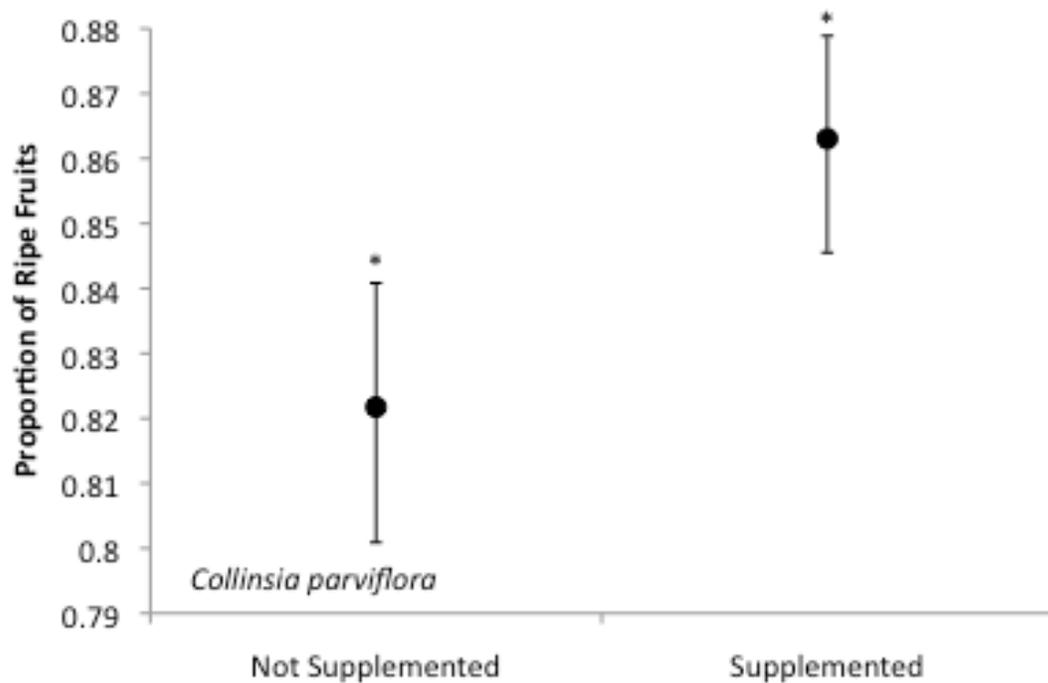


Figure 14. The effect of pollen supplementation on the proportion of ripe fruits produced in *Collinsia parviflora*.

Values are back-transformed from logit values estimated from generalized linear mixed models (PROC GLIMMIX) with number of flowers per plant as a fixed covariate and site nested within *Cytisus* invasion and plant location nested within site as random factors \pm one standard error.

Finally, *Cytisus* branches that received conspecific pollen supplementation produced more fruits than naturally-pollinated control branches ($F_{1,109,2}=4.48$, $P=0.037$, Figure 10).

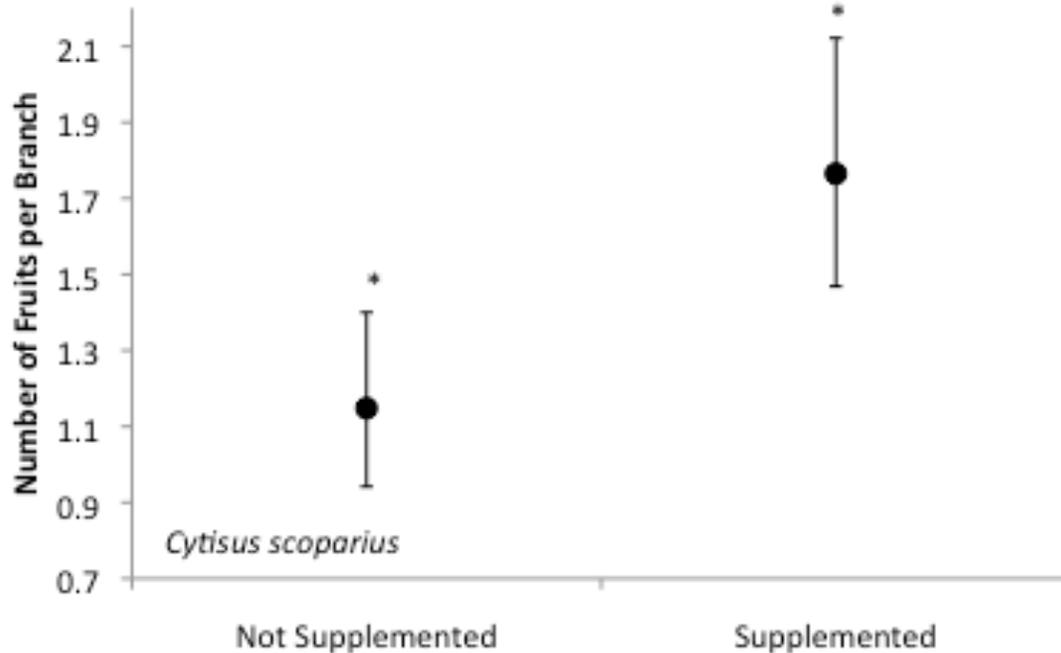


Figure 15. The effect of conspecific pollen supplementation on the fruit set of *Cytisus scoparius*.

Values are back-transformed estimates derived from generalized linear mixed models (PROC GLIMMIX) approximated with a negative binomial distribution, total flowers as a covariate in the model, and site as a random factor \pm one standard error.

3.6 The effects of selfing and resource allocation on reproductive success

Cytisus invasion did not have an effect on the resource allocation of any of the focal species, but I did see a significant difference in the number of flowers produced among treatment groups for both *Camassia* and *Geranium*. In particular, plants in the unsupplemented treatment had higher numbers of flowers per plant than their pollen-supplemented counterparts (Table 12). *Camassia* plants additionally had more ovules per plant in the pollen-supplemented group than the control group (Table 12). No difference in resource allocation patterns among *Collinsia* plants was observed between treatments (Table 12), nor an effect of pollination treatment ($F_{1,150}=0$, $P=0.9731$), *Cytisus* invasion ($F_{1,6.09}=0.31$, $P=0.6001$), or an interaction between the two ($F_{1,149}=0$, $P=0.9994$) on the mass per *Collinsia* seed.

Table 12. Generalized linear mixed model analysis of plant resource allocation to ovules and flowers for each focal plant species.

Response variables were modeled with a negative binomial distribution and its associated log link function. $P < 0.05$ is indicated in bold type.

	Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
			Den. df	F	P	Den. df	F	P	Den. df	F	P
Total Ovules per Plant	Treatment	1	343.6	4.94	0.0268	236.6	2.67	0.1035	339	0.00	0.9688
	Invasion	1	6.434	0	0.9909	6.237	0.04	0.8535	6.025	1.21	0.3128
	Treatment x Invasion	1	343.2	1.47	0.2262	254.3	0.94	0.3328	339	1.85	0.1751
	Total Flowers	1	327.6	1857.0	<0.0001	199.3	1676.01	<0.0001	217.1	1122.57	<0.0001
Total Flowers per Plant	Treatment	1	391	3.93	0.0482	515.5	6.56	0.0107	437	0.23	0.6305
	Invasion	1	5.995	0.79	0.4080	5.755	1.0	0.3574	6.026	2.14	0.1940
	Treatment x Invasion	1	391	0.12	0.7311	515.5	0.87	0.3516	437	0.31	0.5769

Table 13. Generalized linear model analysis of the effect of treatment (control, supplemented with conspecific pollen, and supplemented with self pollen), and associated covariates on the seeds per plant, fruits per flower, and seeds per flower for *Camassia leichtlinii* in Bear Hill Park during 2010.

P < 0.05 is indicated in bold type and trends are indicated with an asterisk (*).

	Source of Variation	df	Den. df	F	P
Seeds/Plant	Treatment	2	50	3.07	0.0553*
	Proportion Fruit Set	1	50	16.71	0.0002
	Total Ovules / Plant	1	50	8.83	0.0046
Fruit Set	Treatment	2	47	2.26	0.1156
Seeds/Fruit	Treatment	2	46	2.37	0.1047
	Number of Fruits	1	46	24.11	<0.0001
Aborted Seeds/Fruit	Treatment	2	28	10.37	0.0004
	Number of Fruits	1	28	3.53	0.0709

While no significant effect of self pollination on fruit set or seed set per fruit was seen, a trend of decreased seed set on a per-plant level was observed in self-pollinated *Camassia* flowers when compared to the control and conspecific supplementation treatments in 2010 (Table 13, Figure 16). More aborted seeds were observed in plants in the control treatment than those supplemented with self pollen and supplemented with outcross pollen (Table 13, Figure 17).

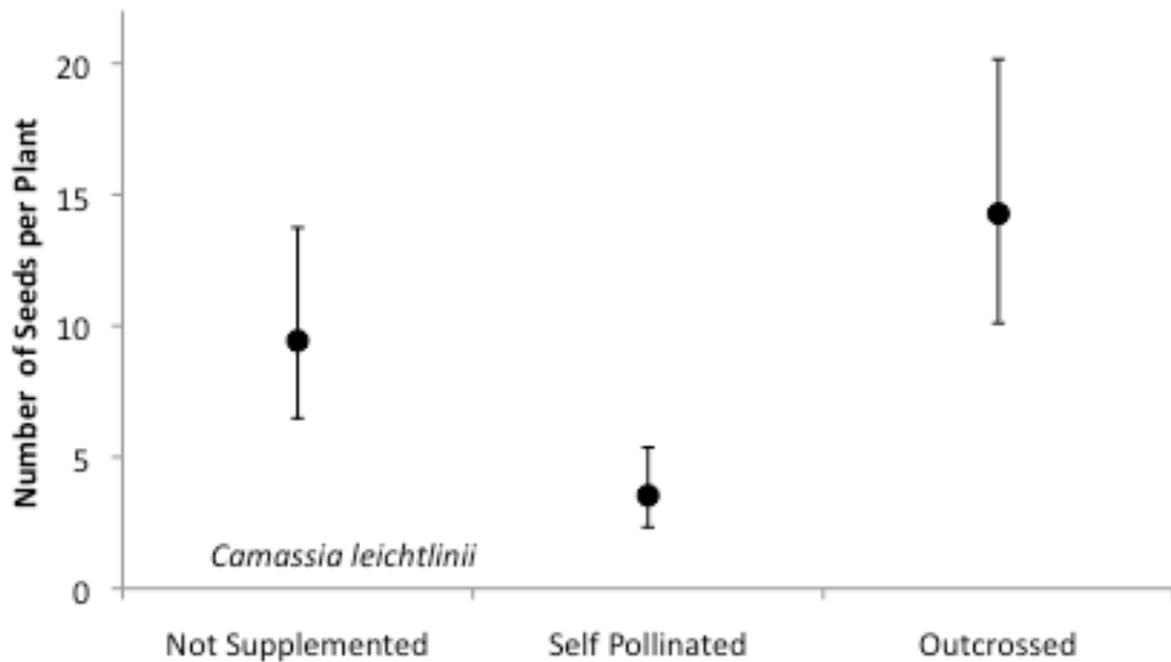


Figure 16. The effect of natural pollination (control), self pollen supplementation and outcross pollen supplementation on the reproductive success of *Camassia leichtlinii* at Bear Hill Park in the spring of 2010.

Values are back-transformed from log values estimated from generalized linear models fitted with negative binomial distribution and total ovules and proportion fruit set as covariates (PROC GLM) \pm one standard error.

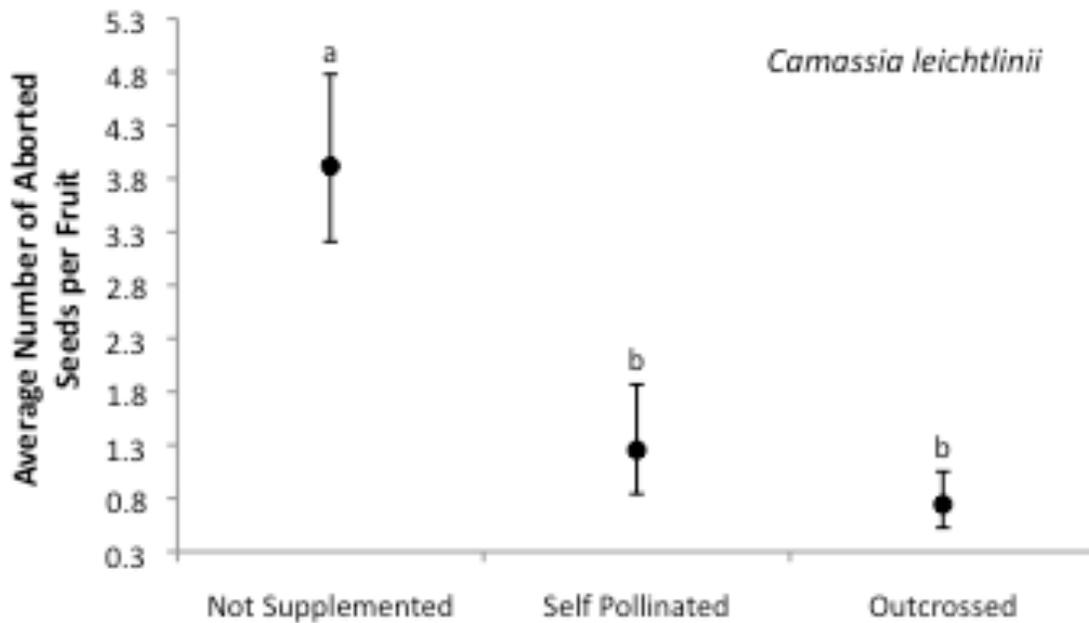


Figure 17. The effect of pollen supplementation treatment (self, outcross, or control) on the number of aborted seeds produced by *Camassia leichtlinii*.

Values are back-transformed from log values estimated from generalized linear models (PROC GLM) with number of flowers per plant as a covariate \pm one standard error.

3.7 Potential Allelopathic Effects of *Cytisus scoparius*

When *Camassia* plants were supplemented with a mixture of conspecific pollen and *Cytisus* pollen, no significant effect on the number of seeds produced per plant, fruits per flower, or seeds per fruit were observed when compared to both naturally-pollinated individuals and those supplemented with pure conspecific pollen (Table 14). However, a trend toward decreased numbers of aborted seeds per fruit in *Cytisus*-supplemented plants was seen (Table 14).

Table 14. Generalized linear mixed model analysis of the effect of pollination treatment (control, supplemented with conspecific pollen, and supplemented with a mixture of conspecific and invader pollen), and associated covariates on the seeds per plant, fruits per flower, and seeds per flower for *Camassia leichtlinii* in Layritz Park.

Plant location within site was used as a random effect within each model. $P < 0.05$ is indicated in bold type, and trends are indicated with an asterisk (*).

	Source of Variation	df	Den. df	F	P
Seeds/Plant	Treatment	2	68.47	1.9	0.1580
	Proportion Fruit Set	1	76	59.91	<0.0001
	Total Ovules / Plant	1	69.95	73.29	<0.0001
Fruit Set	Treatment	2	60.04	1.74	0.1848
	Number of Flowers	1	26.51	99.94	<0.0001
Seeds/Fruit	Treatment	2	72.59	0.22	0.8050
	Number of Fruits	1	70.56	141.64	<0.0001
Aborted Seeds/Fruit	Treatment	2	72.07	2.66	0.0765*
	Number of Fruits	1	70.48	67.55	<0.0001

3.8 Pollen Limitation

No difference in pollen limitation among species was observed based on seed production, but there was a significant difference in pollen limitation based on fruit set (Table 8, Figure 18). In particular, *Geranium* had the lowest pollen limitation *Cytisus* and *Collinsia* had the highest pollen limitation, and *Camassia* had an intermediate PL value.

No observed relationship between PL and visitation rate for *Camassia*, *Geranium*, or *Collinsia* was observed when pollen limitation was measured with either seed set or fruit set as the response variable (Table 15). In addition, no relationship seen between visitation and fruit set in *Cytisus* ($F_{1,1}=0$, $MS<0.001$, $P=0.975$).

Table 15. Regression analysis of the effect of floral visitation rate (number of visits per minute per flower) and associated covariates on the overall pollen limitation ($\ln R = \ln(\text{mean output from supplementation}/\text{mean output from control})$) of each focal species, with invasion as a covariate.

P < 0.05 is indicated in bold type, and trends are indicated with an asterisk (*).

		<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>			
	Source of Variation	df	MS	F	P	MS	F	P	MS	F	P
Pollen Limitation (seeds)	Visitation	1	0.017	0.12	0.742	0.176	2.79	0.1559	0.038	0.16	0.7057
	Invasion	1	0.040	0.29	0.611	0.001	0.02	0.8997	0.055	0.23	0.6501
	Error	5	0.138	-	-	0.063	-	-	0.239	-	-
Pollen Limitation (fruits)	Visitation	1	0.034	0.11	0.754	0.001	0	0.959	0.272	1.62	0.259
	Invasion	1	0.118	0.38	0.566	0.791	5.49	0.066*	0.055	0.33	0.593
	Error	5	0.313	-	-	0.244	-	-	0.168	-	-

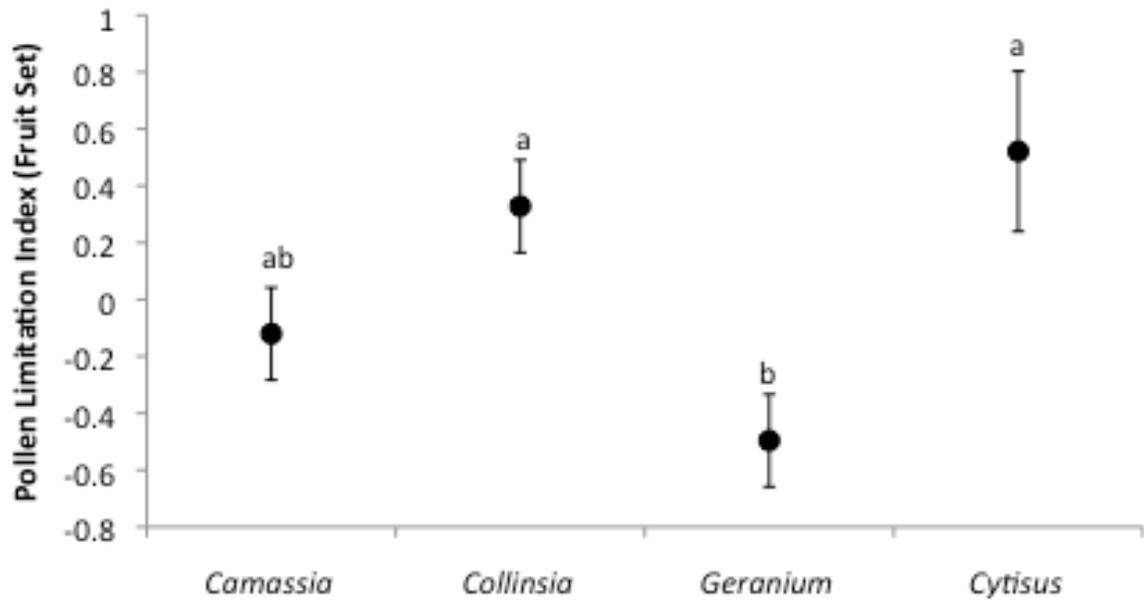


Figure 18. Relative pollen limitation effect sizes using fruit set as response variable for each focal plant species in the study.

Pollen limitation is calculated as $\ln R = \ln(\text{mean output from supplementation} / \text{mean output from control})$. Values are estimated from general linear model (PROC GLM) \pm one standard error with invader presence as a covariate in the model and differences between plants determined via Tukey test.

Chapter Four: **Discussion**

This study demonstrates highly variable effects of *Cytisus* on the pollination and reproductive success of three co-flowering GOE-associated species. *Camassia*, one of the most recognizable and iconic GOE-associated plants, displayed the highest pollinator overlap with *Cytisus* and was the only species to exhibit invader-associated effects on pollinator visitation, pollen deposition and seed set. The effects of *Cytisus* invasion were less clear cut for the native *Collinsia* or exotic *Geranium*, for which pollinator overlap was scant.

4.1 Plant Community Diversity

The presence of *Cytisus* on plant assemblage diversity did not significantly affect the presence/absence of species, for either all species or species co-flowering with *Cytisus*. This finding corroborates Shaben and Myers' (2009) finding that plant diversity and evenness in nearby GOE remnants was uncorrelated with the presence of *Cytisus*, although *Cytisus*-invaded sites tended to have a greater proportion of invasive plant species than uninvaded sites. Similarly, Parker and colleagues (1997) found no effect of *Cytisus* on assemblage composition when native and invasive species were analyzed together, but exclusion of invaders revealed decreased native species richness in the presence of *Cytisus*. Similar species richness has also been found between invaded and uninvaded sites in other ecosystems (Bartomeus *et al.* 2008a, but see Moron *et al.* 2009).

An increased proportion of invasive plant species within a *Cytisus*-invaded community is thought to be due to increased nitrogen availability caused by nitrogen-fixing bacteria in its root nodules (Maron and Connors 1996, Parker *et al.* 1997, Shaben and Myers 2009). A more

parsimonious mechanism may simply be that the increased disturbance that facilitated *Cytisus* invasion also provides suitable conditions for invasion of other alien plants and subsequent increased exotic species richness within the community (Seabloom *et al.* 2003, but see Buckley *et al.* 2007).

4.2 The Role of *Cytisus scoparius* in the GOE pollination network

The main floral visitors of *Cytisus* in the GOE remnants described here included large-bodied bees, such as *Bombus* spp., and species of *Lasioglossum* sensu stricto, such as *L. olympiae* and *L. pacificum*. Similarly, previous studies have reported that *Cytisus* flowers require large floral visitors, such as *Bombus* species, to ‘trip’ flowers, but other species visited open flowers, including the honey bee, *Apis mellifera*, and syrphid flies (Parker 1997, Stout 2000, Simpson *et al.* 2005, Suzuki 2008). These secondary visitors rarely contact stigmas, and so are unlikely pollinators (Parker 1997). Nevertheless, larger *Bombus* individuals have been observed to trip broom flowers less effectively than smaller individuals, and most *Bombus* visitors to *Cytisus* choose previously tripped flowers (Stout 2000).

Similar large-bodied insects were also major visitors of *Camassia* and *Geranium* flowers. Floral visitation of *Geranium molle* in Salamanca, Spain involved *Andrena* sp., *Halictus* sp., Syrphid, Empidid and Scathophagid flies (Fiz *et al.* 2008). *Camassia quamash* observed in another study in a GOE fragment on Vancouver Island (Parachnowisch and Elle 2007) was visited by similar species to *C. leichtlinii*, except for a *Halictus* species that I did not find.

In contrast, the most common floral visitors of *Collinsia* were smaller bees, such as *Ceratina acantha* and *Osmia odontogaster*, and the hovering bee fly *Bombyllius major*. A low niche overlap resulted (0.05), which is somewhat inconsistent with previous research on the

pollinators of *Collinsia* on Vancouver Island (Elle and Carney 2003). Although *Osmia* morphospecies visited commonly, hover flies (presumably syrphids) and several *Bombus* species were more frequently, whereas bee flies were rarely seen and apids, such as *Ceratina*, were not recorded as visitors. Still, *Bombus* species were visited *Collinsia* in this study. This difference in visitor assemblage likely reflects the low visitation recorded in this study and resulting small sample of identified visitors. The difference may also be due to differences in the surrounding floras in the two studies, as changes in the co-flowering plant community affect the types of floral visitors visiting *Collinsia* (Elle and Carney 2003).

That larger bees, such as *Bombus* and *Lasioglossum* sensu stricto, visited both *Cytisus* and the three focal plant species supports the conclusion that these plant species are linked to *Cytisus* within the GOE pollination network, but niche overlap indicates that the strengths of these interactions differ. In any case, the data did not support my hypothesis, as the presence of *Cytisus* neither affected the composition of floral visitors for any of the focal GOE associated plant species, nor affected the diversity of insects collected with pan traps at the same sites during 2010. This may translate into an absence of an effect of the presence of *Cytisus* on the composition of floral visitors, or an equal effect of *Cytisus* on all pollinators.

Pollinator overlap may be a key influence on the pollination effects of invasive species on other co-flowering species. If pollinators are not shared, invaders will not interact via differential pollinator attraction or heterospecific pollen deposition (Bjerknes *et al.* 2007). Even so, invaders can affect the pollination of specialist natives without pollinator overlap or even abiotically pollinated species by reducing native plant richness or population density through direct competition for resources (Bjerknes *et al.* 2007).

The presence of flowering plants at high densities (including invasive plants) has been

found to increase pollinator populations due to increased floral resource density (Graves and Shapiro 2003, Westphal *et al.* 2003, de Groot *et al.* 2007, Herrmann *et al.* 2007, Winfree *et al.* 2007, Tepedino *et al.* 2008). I found no evidence of more exotic pollinators where *Cytisus* was present, which has been reported for other invasive plants (Barthell *et al.* 2001, Stout *et al.* 2002, Morales and Aizen 2006, Aizen *et al.* 2008, Woods *et al.* 2011). Increased floral resources may have increased pollinator abundance in invaded sites, but this study did not detect it because insect pollinators can forage over long distances (in some cases well over 1km: Zurbuchen *et al.* 2010), and thus even in uninvaded locations they may foraged on *Cytisus* outside of site boundaries (Zurbuchen *et al.* 2010). Given the matrix of residential property surrounding GOE remnants on the Saanich peninsula, this explanation is quite reasonable.

Other studies have not observed different pollinator composition between invaded and uninvaded sites (Nielsen *et al.* 2008). For instance, the presence of invaders *Carpobrotus affine acinaciformis* or *Opuntia stricta* had no effect on pollinator species richness (Bartomeus *et al.* 2008a), and the presence of *Impatiens glandulifera* did not alter pollinator abundance or diversity (Nienhuis *et al.* 2009). However, the presence of an invasive has been observed to change in visitor diversity in other studies (Munoz and Cavieres 2008, Moron *et al.* 2009, Thijs *et al.* 2012). For example, the diversity of floral visitors to *Digitalis purpurea* was elevated in *Rhododendron ponticum*-invaded sites (Dietzsch *et al.* 2011).

Invaded pollination networks can exhibit weaker mutualistic interactions and fewer links between native plants and pollinators than uninvaded networks, if invaders usurp links shared previously among native species (Aizen *et al.* 2008). However, invasive plants can also benefit native plants by supporting more pollinator linkages within the community (Valdovinos *et al.*

2009). If this were the case in this study, floral visitors of the focal species should have differed in the presence of *Cytisus*.

4.3 *Cytisus* success in GOE remnants

When an exotic plant is introduced to a novel geographic location, the probability of its success and subsequent invasion is often unknown. One particular challenge is adapting or acclimating to a novel biotic environment. If the exotic species was entomophilous in its original habitat, it needs insect pollinators for success at the new site. If these pollinators are not readily available, then the invader may experience pollen limitation.

Some exotic plants become invasive because they are highly autogamous or have similar visitation rates to native community members (Harmon-Threatt *et al.* 2005). However, *Cytisus* outcrosses obligately and in my study had the lowest visitation of all species observed. Thus, *Cytisus* may be an outlier of sorts, possibly relying on floral numbers as a type of insurance against the unpredictable pollination conditions of novel habitats.

Although I quantified only fruit in *Cytisus* branches, the presence of increased fruit set on pollen-supplemented branches suggests that this invader is pollen limited at the GOE sites sampled. This is common for *Cytisus*, as observed in Washington prairies (Parker 1997), on the Marin Peninsula of California (Parker and Haubensak 2002), and Fukuoka, Japan (Suzuki 2008). Because *Cytisus* is obligately outcrossing, pollinator visitation may be particularly limiting at the Northern front of the invasion, as the tripping mechanism of *Cytisus* flowers requires more force at cooler temperatures (Parker and Haubensak 2002).

Many other invaders are pollen limited. Bartomeus and Vilá (2009) observed local pollen limitation in the invader *Carpobrotus* affine *acinaciformis* in north-eastern Spain. Similarly,

Goodell et al. (2010) found pollen limitation in the invasive shrub *Lonicera mackii*, both at edges and within forested habitat. However, pollen limitation is not the rule, and many invasive plants achieve full fruit and seed set. Indeed, Bartomeus and Vilà saw no pollen limitation in the invasive cactus *Opuntia stricta* in coastal Mediterranean Spain (2009).

4.4 The effect of *Cytisus scoparius* on GOE focal plants

4.4.1 Visitation

The lower visitation to *Camassia* in the presence of *Cytisus* indicates a potential for competition for pollinators. As *Cytisus* is extremely showy with hundreds of yellow flowers during peak flowering, such a competitive interaction is not unexpected, as floral visitors are known to preferentially choose more attractive floral displays (Lavery 1992).

In contrast, the presence of *Cytisus* did not affect visitation to either *Geranium* or *Collinsia*. Given the low niche overlap, this is not surprising. Many other studies have also not observed effects of exotic species on the pollination of other community members. the exotic *Carduus nutans* did not affect visitation to *Monarda fistulosa* (Cariveau and Norton 2009), and seed set and pollinator visitation to *Dithyrea maritima* did not differ between plots with and without invasive *Cakile maritima* and *Carpobrotus* species (Aigner 2004).

4.4.2 Pollen Deposition

Extensive pollinator overlap between invader and native enhances the invader's effect on conspecific pollen deposition (Thijs *et al.* 2012). This generalization holds in the current study, as the focal species with low pollinator overlap with *Cytisus* (*Geranium*, *Collinsia*) experienced similar pollen receipt in invaded and uninvaded sites. Moreover, *Camassia* had the most overlap

of floral visitors with *Cytisus*, and experienced greater total pollen receipt and conspecific pollen receipt in *Cytisus*-invaded sites. However, in contrast to previously observed decreases in conspecific pollen deposition in the face of increased visitation in the presence of an invader (Grabas and Laverty 1999, Lopezaraiza-Mikel *et al.* 2007), this study is the first observation of the opposite effect.

That heterospecific pollen deposition was not elevated in invaded sites suggests that despite reduced visitation in the presence of *Cytisus*, the remaining floral visits to *Camassia* delivered conspecific pollen more efficiently. *Cytisus* may act as a ‘magnet’ species, attracting increased numbers of floral visitors to GOE remnants, and diverting floral visitors that are less efficient at delivering conspecific pollen to *Camassia*. Small pollinator samples may have reduced the ability to detect this shift in floral visitor composition.

Although conspecific pollen counts likely include self pollen, as focal flowers were not emasculated, *Camassia* flowers in invaded sites probably did not receive more self pollen than in uninvaded sites, unless the plants themselves had somehow florally adapted to the presence of *Cytisus* within *Cytisus*-invaded sites. That all “uninvaded” sites in the current study have been recently invaded by *Cytisus* renders this hypothesis improbable. However, the observed increased conspecific pollen deposition could have resulted from changes in pollinator behaviour in the presence of broom. In particular, pollinators may have visited more flowers on the same plant, increasing geitonogamy. For instance, pollinators moved more among flowers within inflorescences between inflorescences when two invasive *Carduus* species were present in mixed arrays (Yang *et al.* 2011). Such intraplant visitation can have complex consequences on the reproductive success of self-compatible species like *Camassia* (Lloyd 1992), including the potential for inbreeding depression (Charlesworth and Charlesworth 1987).

Although *Cytisus* pollen deposition on stigmas of native species was not quantified in this study, alien pollen deposition has been found to be low in other studies (Larson *et al.* 2006, Bartomeus *et al.* 2008b, Jakobsson *et al.* 2008, Dietzsch *et al.* 2011, but see Ghazoul 2002). If so, then *Cytisus* pollen may not be detrimental to the reproduction of native species in and of itself, especially given the lack of allelopathic effect of *Cytisus* pollen on *Camassia* stigmas. However, my experimental design did not discount *Cytisus* pollen allelopathy, as all flowers were exposed to insect pollination, so that all treatments may have received some *Cytisus* pollen from insects. Allelopathy can occur with the addition of only a few pollen grains (Murphy and Aarsen 1995a,b,c,d), so it is possible that full seed set was not achieved within either treatment because pollinators were not excluded.

Plants behave differently to the addition of invader pollen. For instance, *Euphorbia esula* pollen did not affect the reproductive success of *Sisyrinchium campestre* (Montgomery 2009a), but decreased seed set by *Viola pedatifida* (Montgomery 2009b). Similarly, only one of three native plant species (*Helichrysum stoechas*, Asteraceae) suffered reduced seed set when pure pollen from the invader *Carpobrotus spp.* was applied to stigmas (Jacobsson *et al.* 2008; but see Moragues and Traveset 2005). However, “order effect” may occur wherein pure invader pollen ‘clogs’ stigmas or styles more when received first than if it is received as a mixed pollen load with conspecific pollen (as in Caruso and Alfaro 2000).

4.4.3 Reproductive Success

The efficacy of the pollen supplementation treatment was mixed, and depended strongly on the focal GOE plant and which metric of reproductive success was observed. Only *Collinsia* exhibited consistent pollen limitation as indicated by sensitivity to pollen supplementation through a positive correlation and in the generalized linear mixed model analysis. The role of

pollination dynamics in this relation is strengthened by the lack of evidence for differential production of reproductive structures among treatments and invasion status.

However, the magnitude of pollen limitation did not vary in the presence or absence of the invader, indicating that *Cytisus* did not affect *Collinsia* fruit set during 2011. Despite pollen limitation of fruit set, pollen supplementation did not improve *Collinsia* seed set per plant, or seed mass. These observations suggest that pollen limitation did not seem to be having an effect on the persistence of *Collinsia* populations in 2011. However, the significantly lower fruit set in the control group, but no difference in seed set when compared to supplemented plants suggests a trade off between fruit and seed set.

On the other hand, there was evidence of an effect of *Cytisus* on the pollination and reproductive success of *Camassia*. Indicative of pollen limitation, there was a positive relationship observed between seed set per plant and the proportion of flowers supplemented. However, seed set did not differ between supplementation treatments or with *Cytisus* presence. Instead, *Camassia* tended to set more fruit in *Cytisus*-invaded sites overall, and this was especially true for naturally pollinated plants. Increased fruit set in invaded sites is consistent with the increased pollen deposition in the presence of *Cytisus*, further supporting a facilitative effect of the invader on *Camassia*. In the same fashion, it makes sense that this facilitative effect would be pronounced in the control group as it is relying solely on natural pollination for reproductive success. Similarly, as naturally pollinated *Camassia* plants produced more flowers than pollen-supplemented plants, they had more opportunities to set fruit. This increased floral number may also have elicited more within-plant floral visits and subsequently increased geitonogamous self-pollination in *Cytisus*-invaded sites (Klinkhamer and De Jong 1993). However, there is no evidence of pollen limitation of fruit set in *Camassia* as evidenced by a lack

of difference between supplementation treatments in either of the site types, so I cannot conclude that this increased fruit set in control plants in invaded sites is due to an increased quantity or quality of pollen received. Furthermore, even if this change were due to differential pollen receipt, the absence of an effect on total seed production on the plant level indicates that at least in 2011 this potential facilitative pollination effect did not measurably influence the population-level reproductive success of *Camassia*.

As pollen receipt is uncertain to be the cause of this differential reproductive success in naturally pollinated *Camassia* plants, it may instead have been caused by a mechanism unrelated to pollination, such as differential resource availability. Increased reproductive success in the presence of *Cytisus* may be due to known soil chemistry changes associated with this invader. Such increased resource availability could increase the importance of pollen limitation as a restriction on plant reproductive success (Knight *et al.* 2005).

That being said, pollen-supplemented flowers exhibited more aborted seeds than naturally pollinated plants, which may point toward the countervailing force of resource limitation within each plant. The Haig-Westoby equilibrium hypothesis proposes a resource trade-off exists between pollinator attraction (and resulting ovule fertilization) and seed provisioning, and that natural selection drives flowering plants toward an equilibrium at which both pollen receipt and resource allocation to seed production are optimized (Haig and Westoby 1988, Ashman *et al.* 2004). Accordingly, even though *Camassia* flowers received sufficient pollen in the pollen supplementation treatment, intraplant resource limitations may have caused the plants to abort the maturation process part way through the process (Burd 1994). This ‘selective maturation’ is most commonly known to occur in fruit maturation, but can also occur at the seed level (Stephenson 1981, Burd 1994). The high pollen loads applied during

supplementation may have increased the possibility of selective abortion of less fit seeds.

Aborted seeds can also indicate inbreeding or outbreeding depression (Zimmerman and Aide 1989, Burd 1994, Kittelson and Maron 2000). However, as offspring parentage was not assessed in the current study, these hypotheses cannot be tested.

Geranium, the exotic focal plant in this study, behaved differently with respect to *Cytisus* invasion and pollen supplementation. no measure of reproductive success correlated with the proportion of flowers supplemented, suggesting that *Geranium* reproduction was not pollen limited. However, the significant interaction between pollen-supplementation treatment and *Cytisus* invasion showed that where *Cytisus* was absent, naturally-pollinated plants produced more fruits per flower than pollen-supplemented plants, probably because naturally-pollinated plants produced more flowers than pollen-supplemented plants. As a direct consequence, the increased fruit set is likely the result of these increased opportunities to set fruit. Alternatively, the additional flowers in naturally-pollinated plants may have attracted more pollinators, thus eliciting more visits and subsequently delivering more pollen than for the supplemented plants.

This difference in reproductive resource allocation between treatments may have been caused by a trade-off occurring within each *Geranium* plant similar to the Haig-Westoby equilibrium explained above. The production of excess flower buds can be adaptive in unpredictable pollination environments (Ehrlen 1991), and it is known that such stochastic pollination environments select for increased ovule production as a bet hedging strategy; plants that allocate resources to many ovules will gain more fitness from infrequent occurrences of high pollination than they lose through resource allocation to ovules that do not receive as much pollination (Burd *et al.* 2009). Thus, in low pollination environments (potentially such as that in the control treatment), *Geranium* plants may facultatively allocate resources to the maturation

and anthesis of more flowers at the expense of future seed provisioning to increase reproductive fitness.

It may also be that the act of pollen supplementation itself reduced reproductive success. There are several possible explanations for this failure of pollen supplementation to produce its expected outcome (ie provide sufficient pollen to induce full seed set), and all are associated with the high pollen loads applied during the act of supplementation. These include stigma or stylar “clogging” due to the overcrowding of pollen on the stigma, stigma damage caused by ensuing pollinators or pollen ‘thieves’, damage caused by the researchers during the supplementation process, low-diversity, inviable, incompatible or an insufficient amounts of pollen used during supplementation, or the inadvertent missing of peak stigma receptivity (Young and Young 1992). As this *Geranium* species is known to be primarily autogamously selfing (Fiz *et al.* 2008), it is possible that the conspecific pollen applied during supplementation may have induced outbreeding depression. Outbreeding depression occurs when pollen received from often widely separated individuals results in decreased reproductive fitness due to the disruption of local adaptation or gene co-adaptation (Waser and Price 1991). Such negative effects of outbreeding have previously been observed in exotic species. For example, the local outbreeding depression observed in the invader *Sarracenia purpurea* was thought to be caused by selection for inbreeding due to co-adaptation between genetic loci (Parisod *et al.* 2005). However, as the methods for pollen supplementation in this study used pollen harvested from individuals 30 metres away or less, such outbreeding depression is unlikely, especially as this effect was only seen in uninvasion sites.

Another, perhaps more parsimonious explanation for the observed increase in reproductive resource allocation may be experimental bias. Because plant selection was not

completely random, the possibility exists that the researchers may have inadvertently selected larger plants for the naturally pollinated treatment than they did for the supplementation treatment. This non-random attribution of plants into treatment groups would cause a similar pattern of increased flower and ovule production in the naturally-pollinated group when compared to the supplemented group.

Given that the supplementation treatment did not have its expected effect, fruit set did not correlate with proportion of flowers supplemented, and *Geranium* selfs autogamously, the increased fruit set in the control group in uninvaded sites may also be due to other environmental factors that differ between the two site types. *Cytisus* invasion affects soil nutrient and mineral composition through its nitrogen-fixing *Rhizobium* root nodules (Wheeler *et al.* 1987), so *Geranium* plants in *Cytisus*-invaded habitats may have been suppressed by soil characteristics originating from the invader. That being said, bioassays have shown conflicting results of the presence of *Cytisus* on the growth and reproduction of co-occurring species. While Haubensak and Parker (2004) observed a 30% reduction in the growth of *Achillea millefolium* in the presence of *Cytisus*, grasses *Dactylis glomerata* and *Festuca idahoensis* produced more inflorescences (Shaben and Myers 2009).

Geranium may also benefit from the absence of *Cytisus* in other ways. In this study, *Cytisus* had been previously removed from ‘uninvaded’ sites, and thus these sites may have otherwise been more disturbed than sites where *Cytisus* has been left to grow. Because *Geranium* is exotic, it may benefit more from disturbed areas (Vitousek *et al.* 1996). However, this does not explain why supplemented plants produced fewer fruits per flower than control plants where *Cytisus* was absent.

That fruits from pollen-supplemented plants produced more seeds may also be related to the Haig-Westoby mechanism. As plants in this group produced fewer flowers than the control group, they may have instead allocated their limited resources to seed production. As for *Collinsia*, the juxtaposition of more seeds per fruit and fewer fruits per flower in supplemented plants than naturally-pollinated plants may indicate a resource trade-off in *Geranium*. This “interplant compensation” has also been seen in supplementation studies of *Silene virginica* (Dudash and Fenster 1997).

4.5 Relative pollination of focal plants in the study

The efficiency of pollinators within a community depends on a number of factors, such as the floral constancy and general behaviour of each pollinator species and the floral architecture and spatial or temporal pollen/stigma presentation of plant species within the community (Bartomeus *et al.* 2008a). Although pollinator behaviour was not observed in the current study, it is worthwhile to note some of the floral characters that may explain some of the observed interspecific variation in visitation, pollen deposition, and pollen limitation.

In a previous study of the pollination of GOE associated species on Vancouver Island, *Camassia quamash*, a closely-related congener of *C. leichtlinii*, received more visits than other species in their GOE community (Parachnowisch and Elle 2007), probably because of higher nectar rewards. If floral visitation of the two species is comparable, this is consistent with the current study. *Camassia leichtlinii* had the most diverse floral visitors and the highest visitation rate per flower. This, in turn, resulted in the most conspecific and heterospecific pollen grains being deposited on *Camassia* stigmas of all focal species studied.

The high deposition of conspecific pollen on *Collinsia* stigmas is interesting, given its

low visitation rate. This may indicate that the few pollinators that were observed were more efficient, and there is evidence to suggest that zygomorphic flowers, such as those of *Collinsia* and other members of the Plantaginaceae, promotes specific pollen placement on pollinators' bodies (Neal *et al.* 1998, Fenster *et al.* 2004, Sargent 2004, but see Knight *et al.* 2005). *Cytisus* also has a zygomorphic floral shape typical of the Fabaceae family, but it had the lowest conspecific pollen deposition of all of the focal plants. This may be due to its explosive “tripping” mechanism of pollination, wherein the stamens spring forward when a pollinator first manipulates the flower (Parker 1997, Stout 2000). This could result in a diffuse pollen deposition on the body of the pollinator, which is much less targeted than the mechanism of *Collinsia*.

The trends of heterospecific pollen deposition among focal plant species are less informative. Montgomery and Rathcke (2012) found that species with “nonrestrictive” floral architecture (characterized by exerted stigmas and small corolla tube openings) received far more heterospecific pollen than those with “restrictive” floral architecture; however, such a difference was not evident in this study, except for higher deposition in *Camassia*, which can instead be explained by increased visitation rates.

Floral abundance has previously been revealed to be an important explanatory component of reproductive success within plant communities (Groom 1998). In particular, pollen limitation can vary negatively with population size (Moeller 2004, Ghazoul 2006), and small populations are visited less frequently and to receive more interspecific visits (Thomson 1981, Kevan and Baker 1983, Rathcke 1983, Sargent and Otto 2006). In the GOE remnants observed in this study, *Camassia* was common, whereas *Geranium* was less common and *Collinsia* was present in sparse patches (J. Muir pers. obs.). This may explain the observed visitation rates and subsequent deposition of conspecific pollen. *Cytisus*, on the other hand, was quite common in the four sites

where it was present (J. Muir, pers. obs.), yet it experienced low visitation and pollen deposition. Theoretically, high floral densities can have a negative effect on the per-flower visitation rate of flowers, as many flowers can saturate the pollinator availability and result in floral competition (Rathcke 1983, Essenberg 2012). Unfortunately, as floral density was not measured quantitatively in this study, this can be inferred only qualitatively from field observations.

That the invasive *Cytisus* experienced low visitation per flower is surprising, as invasive plants are thought to be successful in part because they integrate well into novel communities and take advantage of available generalist pollinators (Morales and Traveset 2009). Other invasive plants have very high floral visitation in their novel habitats (Kandori *et al.* 2009, Vanparys *et al.* 2011). For example, the invaders *Carpobrotus affine acinaciformis* and *Opuntia stricta* both received more floral visits and attracted more pollinator species than any native species with which they coflowered (Bartomeus *et al.* 2008a), and the invasive *Lespedeza cuneata* experienced higher visitation than all three native congeners (Woods *et al.* 2012). However, other studies have observed similar low visitation in *Cytisus* (Parker 1997) and other exotic and invasive plants (Hochkirch *et al.* 2012).

Previous large comparative studies found significant correlation of pollen limitation through both fruit set and seed set (Knight *et al.* 2005), suggesting that measures of fruit set are indicative of plant-level seed production. However, this association was not evident in the current study. Significant pollen limitation in fruit set, but not seed set, was similarly reported for *Silene virginiana* in forest habitats (Dudash and Fenster 1997). This result may be due to pollen supplemented plants producing fewer flowers than plants in the control treatment (Knight *et al.* 2005), and indeed that was what was found in this study for both *Camassia* and *Geranium*. As

previously stated, this may have been due to experimental bias. However, it is interesting to note that this difference in flower number among pollination treatments was not present in *Collinsia*.

Pollen limitation is well known to be linked to plant breeding system, especially self-compatibility (Knight *et al.* 2005). Frequent pollen limitation may drive the evolution of self-compatibility to ensure reproduction in environments where outcross pollen is scarce (Barrett 2002, Moeller and Gerber 2005). Thus, plant species with greater self-compatibility should be less pollen limited than self-incompatible species (Knight *et al.* 2005). *Collinsia* and *Cytisus* have been previously observed to be generally outcrossing and *Geranium* is known for autogamous selfing, but this study shows that *Camassia* is also able to reproduce when only self pollen is available. Correspondingly, the relative pollen limitation in regards to fruit set seems to reflect these mating system trends, with *Geranium* by and large exhibiting increased fruit set in the control plants when compared to the pollen supplemented group (“negative” pollen limitation). The more outcrossing species experienced greater pollen limitation, and *Camassia* was intermediate between the two. Thus, this disparity of mating systems among focal species may explain why pollen limitation did not vary significantly with visitation rates as has been previously observed in other systems (Hegland and Totland 2008).

Chapter Five: **Conclusions**

The effects of invasive plants on the pollination and reproductive success of co-flowering species is a popular research topic with important conservation implications. In this study, *Cytisus* presence had differing effects on the pollination of co-flowering GOE species, a result consistent with studies of invasive species in other systems (Moragues and Traveset 2005, Larson *et al.* 2006, Thijs *et al.* 2012, Woods *et al.* 2012). Whereas a putative facilitative effect was seen in *Camassia*, *Collinsia* and the exotic *Geranium* were relatively unaffected, despite *Collinsia*'s fruit set being pollen limited. Accordingly, this study provides evidence that *Cytisus* invasion is neither increasing the invasion success of *Geranium*, nor competing with *Camassia* or *Collinsia* for pollination within the GOE community.

Notwithstanding the trends for fruit set, there was still no effect of *Cytisus* invasion on the plant-level seed production in any of the focal species studied here, even even though the proportion of flowers supplemented with pollen did not affect seed set per plant in *Camassia*. This result may be the most important of all, as it is not fruit set, but the number of seeds produced per plant that determines plant fitness and subsequent recruitment in the next generation (Ashman *et al.* 2004). As a consequence, these results suggest that pollination dynamics are having little effect on co-flowering GOE-associated species over and above the previously acknowledged direct negative effects of competition for space and other resources.

In the context of pollination, this study suggests that *Cytisus* was not the instigator of an 'invasional meltdown' nor an 'invasional interference' for *Geranium* plants within GOE remnants in this study, as both the pollination and reproductive success of exotic *Geranium* plants were relatively unaffected by *Cytisus* presence. Rather, *Geranium* may have been more

affected by the *absence* of *Cytisus*, potentially thriving in the disturbance caused by *Cytisus* removal efforts.

The variety of results presented here showcases the diversity of plant interactions via pollinators within a community, and suggests that effects of invasive species on the pollination of native populations are species-specific. In addition, that pollinator visitation rates of focal plant species did not influence reproductive success suggests that measurement of pollinator visitation rates and plant fitness should not be mutually exclusive, and that measurement of multiple components of the plant reproductive process provides the most insight into the effects of the presence of invasives such as *Cytisus*.

However, pollinator observations, pollen supplementation experiments and quantification of reproductive success were conducted during only one growing season (spring 2011). Pollinator communities, visitation, pollen limitation, and reproductive success are all known to be temporally variable, and many studies have observed change in these variables from year to year (Moragues and Traveset 2005, Larson *et al.* 2006). For plant reproduction in particular, especially in perennial species such as *Camassia*, full understanding of plant resource allocation needs to be observed over the lifetime. Increased reproduction during one year due to supplemental pollination is often followed reduced plant growth and/or reproduction in the following season (Obeso 2002). Thus, pollination and plant reproductive success should be viewed as a series of dynamic components of fluctuating abundances, and this study is merely a snapshot in time. Spatial scale may also be important. Large-scale invader presence (hectares) significantly increases visitation to co-flowering species, whereas small-scale invader presence (square metres) has little effect (Jakobsson *et al.* 2009).

To my knowledge, the *Camassia* results provide is only one of two cases of increased conspecific pollen deposition in invaded areas (see also McKinney and Goodell 2011), and this is the first evidence of increased pollen deposition in the face lower floral visitation in the presence of an invasive plant. Although this increased pollen deposition did not significantly affect reproductive success during 2011, it could be much more meaningful to population persistence in years with low pollinator service. The cause of increased pollen deposition with lower visitation was not identified directly, but a variety of *Camassia* floral characters may be at play and future research would do well to tease apart the relation between pollinator visitation rates and pollinator efficiency in *Cytisus*-invaded *Camassia* populations and increase the pollinator observations so that differences of floral visitors might be more apparent. In addition, pollinator behavioural observations would inform the hypothesis of increased geitonogamy in *Cytisus*-invaded locations.

The results of this study must be interpreted in light of the fact that *Cytisus* is nearly ubiquitous in GOE habitat fragments on the Saanich Peninsula and thus it is no longer feasible to study ‘invaded’ and ‘uninvaded’ sites. That the invader has previously been removed from ‘uninvaded’ sites has great implications for interpretation. For example, Fiedler et al. (2012) found that immediately after the removal of the invader *Frangula alnus*, plant composition differed strongly between invader-present invader-removed and control plots for at least two years. In contrast, the pollinator community recovered to control levels after the first year (Fiedler *et al.* 2012). This delayed recovery may especially be true in the case of *Cytisus* invasions, because of the plant’s nitrogen-fixing abilities, and as a consequence control sites in this study may be influenced by ‘the ghost of *Cytisus*’ past’. In the long run, the effects of *Cytisus* invasion may not be reversible at all. Rook et al. (2011) observed that historical

proximity to *Cytisus scoparius* correlated strongly with a reduction in native species in prairie ecosystems of the Pacific Northwest (2011).

Cytisus invasion is a primary conservation priority in remaining Garry oak ecosystem habitat fragments on the Saanich peninsula (Fuchs 2001). Although the results of this study will not change ongoing *Cytisus* management efforts, they elucidate some indirect effects that the presence of *Cytisus* exerts on the pollination of co-flowering species. Restoration efforts should continue to focus on *Cytisus* invasion within the Garry oak habitat, while edge habitats and nearby residential or disturbed land uses seem to be less of a priority, as no indirect competitive effects of *Cytisus* were observed for the focal species studied here.

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**APPENDIX A: INSECTS COLLECTED BY PAN TRAP IN REMNANT FRAGMENTS OF
GARRY OAK ECOSYSTEM IN 2010.**

A star (*) indicates a Cytisus-invaded site. (BH = Bear Hill Park, XH = Christmas Hill Park, GO = Gore Park, HH = Horth Hill Park, KN = Knockan Hill Park, KO = Konukson Park, LA=Layritz Park, SU= Summit Park)

Floral Visitor	Family	<u>Early Bowls (May 25 to June 8, 2010)</u>							<u>Late Bowls (June 10 to June 25)</u>						
		BH*	XH*	GO	HO	KN*	KO	LA*	BH*	XH*	GO	HO	KN*	KO	LA*
<i>Adelidae</i>	Lepidoptera	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Agapostemon texanus</i>	Hymenoptera	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Andrena morphosp. 1</i>	Hymenoptera	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. 10</i>	Hymenoptera	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. 12</i>	Hymenoptera	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. 2</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	2	0
<i>Andrena morphosp. 3</i>	Hymenoptera	0	0	2	0	0	0	0	3	0	1	5	0	1	3
<i>Andrena morphosp. 4</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Andrena morphosp. 5</i>	Hymenoptera	0	0	1	0	0	0	0	0	0	0	2	0	0	1
<i>Andrena morphosp. 6</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	3	0
<i>Andrena morphosp. 8</i>	Hymenoptera	1	2	0	0	3	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. 9</i>	Hymenoptera	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. A</i>	Hymenoptera	0	0	0	0	0	0	0	0	2	1	8	0	0	6
<i>Andrena morphosp. B</i>	Hymenoptera	0	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Andrena morphosp. C</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	5	0	18	0
<i>Andrena morphosp. E</i>	Hymenoptera	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Andrena morphosp. F</i>	Hymenoptera	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Andrena nigrocaerulea</i>	Hymenoptera	49	5	0	0	10	1	1	0	3	0	0	1	0	4
<i>Andrena salicifloris</i>	Hymenoptera	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Andrena sola</i>	Hymenoptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anthidium manicatum</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anthomyiidae</i>	Diptera	4	1	0	3	2	0	1	0	0	0	1	1	0	1
<i>Apis mellifera</i>	Hymenoptera	2	0	2	0	0	0	0	5	3	4	0	1	1	0
<i>Bombus bifarius</i>	Hymenoptera	8	6	5	1	3	19	0	0	0	0	0	1	1	1

<i>Bombus californicus</i>	Hymenoptera	0	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bombus flavifrons</i>	Hymenoptera	1	2	1	4	4	1	0	1	2	4	1	2	4	3
<i>Bombus melanopygus</i>	Hymenoptera	53	8	6	12	16	10	7	1	1	3	8	2	2	2
<i>Bombus mixtus</i>	Hymenoptera	4	9	4	5	11	10	6	0	3	4	1	3	4	2
<i>Bombus occidentalis</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Bombus sitkensis</i>	Hymenoptera	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Bombus sp.</i>	Hymenoptera	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Bombus vosnesenskii</i>	Hymenoptera	0	7	0	0	2	3	1	0	1	0	0	1	2	1
<i>Calliphoridae</i>	Diptera	20	5	0	12	53	16	2	0	6	0	0	7	0	0
<i>Calliphoridae (Opsodexiinae)</i>	Diptera	0	1	0	0	2	0	0	0	0	0	0	0	0	0
<i>Calliphoridae (Pollenia)</i>	Diptera	1	0	1	1	4	5	0	0	1	6	0	0	0	0
<i>Ceratina acantha</i>	Hymenoptera	0	24	1	6	7	0	61	5	10	0	19	1	4	23
<i>Ceratina nanula</i>	Hymenoptera	0	5	0	0	1	0	0	0	0	0	0	1	0	0
<i>Chalcididae</i>	Hymenoptera	1	1	0	0	0	0	0	0	2	0	0	1	2	0
<i>Chrysididae</i>	Hymenoptera	0	7	0	0	1	1	9	0	8	0	0	1	1	3
<i>Coelioxys morphosp. A</i>	Hymenoptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coelioxys sodalis</i>	Hymenoptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coelioxys sp.</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	3	0
<i>Coccinellidae</i>	Coleoptera	1	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Coleoptera morphosp. A</i>	Coleoptera	8	27	0	0	7	0	14	2	0	0	0	8	1	2
<i>Coleoptera morphosp. B</i>	Coleoptera	0	0	1	0	3	0	5	1	0	0	0	0	1	1
<i>Coleoptera morphosp. C</i>	Coleoptera	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Coleoptera morphosp. D</i>	Coleoptera	1	0	0	0	0	0	0	5	0	0	0	0	0	0
<i>Coleoptera morphosp. E</i>	Coleoptera	1	1	0	0	0	1	0	1	0	0	0	0	2	0
<i>Coleoptera morphosp. F</i>	Coleoptera	0	0	2	1	1	0	0	0	0	0	0	0	0	1
<i>Coleoptera morphosp. G</i>	Coleoptera	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Coleoptera morphosp. H</i>	Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Coleoptera morphosp. I</i>	Coleoptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coleoptera morphosp. J</i>	Coleoptera	0	0	0	0	0	0	0	2	0	0	0	0	0	0
<i>Coleoptera morphosp. K</i>	Coleoptera	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Colletes kincaidii</i>	Hymenoptera	0	0	0	0	0	0	0	0	1	0	0	0	1	0

<i>Conophorus</i>	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Cynipidae</i>	Hymenoptera	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Diptera sp.</i>	Diptera	7	9	3	2	4	1	2	0	2	6	1	8	5	3
<i>Dolichopodidae</i>	Diptera	0	0	0	5	2	2	0	1	0	2	0	0	0	2
<i>Empididae</i>	Hymenoptera	1	0	0	2	1	0	0	0	0	0	0	0	0	0
<i>Eristalis tenax</i>	Diptera	4	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Eumerus funeralis</i>	Diptera	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Evylaeus morphosp. 1</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Evylaeus morphosp. 2</i>	Hymenoptera	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Evylaeus morphosp. 3</i>	Hymenoptera	0	0	1	0	0	0	0	0	0	2	1	0	0	0
<i>Evylaeus morphosp. 4</i>	Hymenoptera	1	1	1	3	5	0	2	5	2	2	9	0	1	1
<i>Evylaeus morphosp. 6</i>	Hymenoptera	0	1	0	0	0	0	2	0	1	0	0	0	4	0
<i>Evylaeus morphosp. 7</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	1	3	0
<i>Halictus confusus</i>	Hymenoptera	0	0	0	0	0	0	1	0	0	0	1	0	0	0
<i>Halictus rubicundus</i>	Hymenoptera	0	2	1	1	9	1	1	0	1	0	0	3	2	4
<i>Halictus tripartitus</i>	Hymenoptera	0	0	0	0	2	0	1	0	0	1	1	0	0	7
<i>Hemaris diffinis</i>	Lepidoptera	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Hemipenthes</i>	Diptera	0	0	0	0	0	0	0	0	3	0	0	0	0	0
<i>Hylaeus modistus</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	2	0
<i>Hymenoptera sp.</i>	Hymenoptera	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ichneumonidae</i>	Hymenoptera	3	0	0	2	1	2	0	0	1	0	1	1	2	0
<i>Lasioglossum cressonii</i>	Hymenoptera	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Lasioglossum egrigium</i>	Hymenoptera	1	0	0	0	1	0	0	0	0	0	1	1	0	0
<i>Lasioglossum incompletum</i>	Hymenoptera	5	3	4	1	7	0	7	2	5	2	5	6	7	3
<i>Lasioglossum knereri</i>	Hymenoptera	0	2	1	11	9	11	14	2	0	4	43	3	33	19
<i>Lasioglossum nevadense</i>	Hymenoptera	0	1	1	0	1	0	0	1	0	0	8	0	2	0
<i>Lasioglossum olympiae</i>	Hymenoptera	2	2	7	1	6	1	22	2	10	7	2	11	3	50
<i>Lasioglossum pacificum</i>	Hymenoptera	12	0	0	1	4	2	1	0	0	4	0	1	1	0
<i>Lasioglossum sisymbrii</i>	Hymenoptera	0	0	0	1	0	0	0	0	2	0	0	0	0	0
<i>Lasioglossum zonulum</i>	Hymenoptera	0	0	1	0	0	1	1	0	0	0	0	0	7	0
<i>Lycaenidae</i>	Lepidoptera	10	1	0	0	0	0	0	0	0	0	0	0	0	0

<i>Megachile genula</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Merodon equestris</i>	Diptera	1	0	1	0	3	0	0	0	0	2	0	5	0	0
<i>Muscidae</i>	Diptera	14	5	3	5	10	9	2	0	4	1	2	6	1	1
<i>Nematocera</i>	Diptera	1	4	0	1	3	4	0	0	28	3	1	2	1	2
<i>Nomada morphosp. 1</i>	Hymenoptera	0	1	0	1	0	0	0	0	0	0	1	0	0	1
<i>Nomada morphosp. 3</i>	Hymenoptera	0	0	0	12	1	0	1	0	0	0	4	0	2	0
<i>Nomada morphosp. A</i>	Hymenoptera	2	1	1	8	0	0	1	1	0	0	1	0	0	0
<i>Osmia bucephala</i>	Hymenoptera	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Osmia coloradensis</i>	Hymenoptera	1	2	5	0	2	0	2	1	2	2	0	0	0	0
<i>Osmia cyanella</i>	Hymenoptera	0	1	0	0	0	0	0	2	0	0	1	0	0	0
<i>Osmia dolerosa</i>	Hymenoptera	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Osmia lignaria</i>	Hymenoptera	1	1	0	0	3	1	0	0	0	0	0	0	0	0
<i>Osmia morphosp. 1</i>	Hymenoptera	3	0	1	0	1	0	1	0	0	0	1	0	0	0
<i>Osmia morphosp. 2</i>	Hymenoptera	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Osmia morphosp. 4</i>	Hymenoptera	1	0	1	0	0	0	1	0	0	0	0	0	0	0
<i>Osmia morphosp. 5</i>	Hymenoptera	2	0	0	0	3	0	0	0	0	0	0	1	0	0
<i>Osmia morphosp. 6</i>	Hymenoptera	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Osmia morphosp. 7</i>	Hymenoptera	2	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Osmia morphosp. 8</i>	Hymenoptera	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Osmia morphosp. A</i>	Hymenoptera	0	1	0	0	4	0	0	2	0	0	0	1	1	0
<i>Osmia odontogaster</i>	Hymenoptera	2	7	0	0	4	0	1	1	3	0	0	0	0	1
<i>Osmia pusilla</i>	Hymenoptera	0	3	0	0	0	0	1	0	0	0	0	0	0	2
<i>Phoridae</i>	Diptera	1	5	1	16	2	1	0	1	5	0	0	1	2	0
<i>Pieridae</i>	Lepidoptera	0	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pompilidae</i>	Hymenoptera	0	4	1	7	0	1	0	5	5	1	9	5	9	11
<i>Sarcophagidae</i>	Diptera	90	80	15	29	159	69	30	1	51	27	7	107	24	19
<i>Sericomyia chalcopyga</i>	Diptera	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sphecidae</i>	Hymenoptera	0	1	0	0	3	0	0	3	0	2	2	0	7	0
<i>Sphecodes morphosp. 1</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sphecodes morphosp. A</i>	Hymenoptera	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Sphecodes morphosp. B</i>	Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1

<i>Sphecodes morphosp. C</i>	Hymenoptera	0	0	1	0	0	0	1	0	0	0	0	0	1
<i>Sphecodes morphosp. D</i>	Hymenoptera	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Sphecodes morphosp. E</i>	Hymenoptera	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Sphecodes morphosp. F</i>	Hymenoptera	0	0	1	1	0	0	1	0	0	0	0	0	0
<i>Stelis albosignata</i>	Hymenoptera	0	1	0	0	0	0	0	0	1	0	0	0	1
<i>Systoechus vulgaris</i>	Diptera	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Tachinidae</i>	Diptera	2	6	0	7	22	3	0	0	2	0	0	5	2
<i>Tenthredinidae</i>	Hymenoptera	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tipulidae</i>	Diptera	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Toxomerus occidentalis</i>	Diptera	1	0	0	0	0	0	0	0	0	2	0	0	0
<i>Trichoceridae</i>	Diptera	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Vespidae</i>	Hymenoptera	0	0	0	0	4	2	2	1	2	0	3	1	1
<i>Volucella bombylans</i>	Diptera	7	2	0	0	2	2	0	0	0	0	0	0	0
