

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

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Abstract A growing number of studies have reported 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, we investigate the effect of the invader Scotch broom (*Cytisus scoparius*) on the visitation, pollen deposition, and female reproductive output of three co-flowering species (two native, one exotic) of the critically endangered Garry oak grassland ecosystem on the Saanich peninsula of Vancouver Island. The presence of *C. scoparius* was largely neutral, with the exception of some facilitation of pollen deposition to the native *Camassia leichtlinii*, the one species exhibiting pollinator overlap with Scotch broom. Yet, this pattern occurred despite a decreased visitation rate from pollinators. **There was little observed effect of the invader on the native *Collinsia parviflora* or the exotic *Geranium molle*.** Because broom was not favoured by any of the observed pollinators, this study provides evidence that the spread of Scotch broom is not due to the reduction of pollination success of natives nor is *C. scoparius* likely to be

facilitating the pollination of other exotics in Garry oak ecosystem remnants.

Keywords *Cytisus scoparius* · Pollination · Seed set · Pollen delivery

Introduction

Invasives are widely acknowledged to threaten biodiversity and ecosystem services (Mack et al. 2000). In Canada, 24 % of vascular plants are exotic in origin, 12 % of which are known to be weedy or invasive, and billions of dollars are spent annually to control them (Government of Canada 2004). Scotch broom [*Cytisus scoparius* (L.) Link (Fabaceae)] is an invasive established in coastal North America that forms dense stands and displaces 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 2009). In Canada, showy yellow *C. scoparius* flowers often replace the diverse and colourful array of flowers characteristic of the critically imperilled Garry oak (*Quercus garryana*) grassland community (Fuchs 2001).

In general, the negative effects of invasive plants are thought to manifest through direct interactions with co-flowering species, such as competition for water, nutrients or light (Levine et al. 2003). However, recent attention has focussed on the potential effects of

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indirect interactions between invaders and their co-flowering associates, most notably the possibility of an effect of invasive plants on pollination and reproductive success (Burd 1994; Ollerton et al. 2011). If invasive plants share similar animal pollinators with natives and other co-flowering species, the potential exists for invaders to affect plant-pollinator interactions, yet the effect may not always be negative (Kearns et al. 1998; Da Silva and Sargent 2011). Pollen limitation (PL) of multiple community members are often examined with the use of pollen limitation indices (Wolowski et al. 2013) to evaluate whether they are responding similarly to common environmental changes (such as the presence of an invasive species), yet such methods have been criticised for confounding pollen quality and quantity delivery changes [i.e., whether it was due to poor quality conspecific pollen deposition caused by shifts in the pollinator community or increases in heterospecific pollen deposition caused by changed in pollinator behaviour (Aizen and Harder 2007; Arceo-Gómez and Ashman 2014)]. As well, dividing the individuals into pollen unsupplemented and supplemented subgroups may unwittingly confound results with differences in the underlying resource pools. While the limitations of PL to study population- and/or community-level effects have been studied before (Knight et al. 2005), rarely have alternate methods been investigated simultaneously in the same sites and species. Below we outline the sources of variation involved in measuring pollination success (summarized in Fig. 1).

Decreased deposition of compatible conspecific pollen can lead to pollen limitation of co-flowering species, whereby insufficient compatible pollen is received by natives to produce full seed set (Knight et al. 2005). However, invaders can potentially change the resource distribution (either because they compete for soil nutrients and light, or in the case of a nitrogen fixator, increase nutrients) and alter the number of seeds through routes that have little to do with pollinator visitation. Therefore, it is possible that pollen limitation can remain unchanged or even lessen in the presence of an invader because a greater proportion of flowers develop into fruit or a greater proportion of ovules develop into seeds despite a decline in pollinator visitation. Here, we attempt to tease apart these various alternate mechanisms of change in pollination and reproductive success in the native community (see Fig. 1).

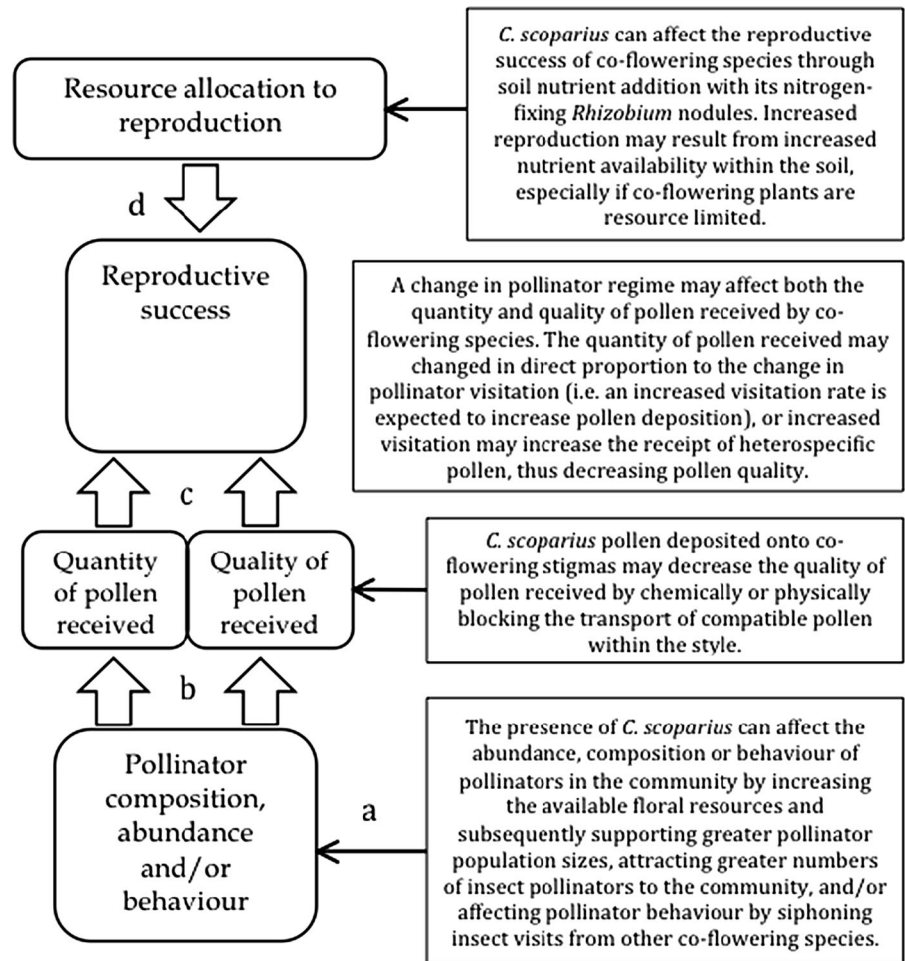
Changes to pollinator composition and abundance

The presence of invasive plants within a community can affect the composition and abundance of visiting pollinators by increasing floral resource availability, consequently supporting larger pollinator populations (Graves and Shapiro 2003; Tepedino et al. 2008) or facilitating alternate pollinators (e.g. *Apis*; Parker et al. 2002). Changes in the functional groups of pollinators may change the quality of pollen deposition even if pollinator visitation rates remain unchanged (Adderley and Vamosi 2015). While a variety of effects have been observed, the majority of results point toward a positive (Carvalhiero et al. 2008; McKinney and Goodell 2011) to neutral (Bartomeus et al. 2008; Nienhuis et al. 2009) effect of invaders on pollinator populations. Floral visitation rates of co-flowering species is by far the most frequently studied aspect of native-invader pollination interactions, and results are nearly 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 may not otherwise visit (Grabas and Laverly 1999; Totland et al. 2006; Lopezaraiza-Mikel et al. 2007). Conversely, it is possible that the 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, the native *Lythrum alatum* received significantly fewer visits in the presence of the invader *Lythrum salicaria* (Brown et al. 2002), and *Stachys palustris* experienced a decrease in visitation in the presence of the invasive *Impatiens glandulifera* (Chittka and Schurkens 2001).

Influences of invasives on pollen receipt and reproductive success

Increased visitation caused by invader facilitation should subsequently result in increased pollen receipt. However, despite the number of studies observing increased visitation of co-flowering species in the presence of exotics, very few have observed a corresponding increase in conspecific pollen receipt (but see McKinney and Goodell 2011). This pattern would imply that pollinator preference for invader

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



flowers tends to change the composition of pollen increasing the proportion 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. 2012). Increased deposition of heterospecific pollen (especially allelopathic pollen) can have negative consequences on reproduction by mechanically or chemically blocking transport of conspecific pollen in the stigma or style (Thomson et al. 1982; Brown and Mitchell 2001; Montgomery 2009a; Da Silva and Sargent 2011 but see Flanagan et al. 2009; Montgomery 2009b; Tscheulin et al. 2009). The invader-induced changes in the deposition of conspecific and heterospecific pollen are generally observed to have negative consequences on fruit and seed production of co-flowering species (Grabas and Lavery 1999; Chittka and Schurkens 2001; Brown

et al. 2002; Totland et al. 2006; Takakura et al. 2009; Kandori et al. 2009; Flanagan et al. 2009; Thijs et al. 2012) yet can be largely neutral in effect (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).

Invading plants can have similar effects on the pollination success of resident exotics but this topic has received much less attention (Parker et al. 2002). Positive associations have been commonly observed wherein one exotic increases the success of another (Simberloff and Von Holle 1999; Traveset and Richardson 2006). Such “invasional meltdowns” have been observed in a number of different interactions among and between animal and plant species (Simberloff and Von Holle 1999), including plant-pollinator interactions (Morales and Aizen 2002; Liu et al.

2006; Molina-Montenegro et al. 2008; Yang et al. 2011; Thijs et al. 2012).

The above dynamics can be assessed with Scotch broom (*Cytisus scoparius* (L.) Link (Fabaceae), an extremely successful invader in temperate “Mediterranean-type” ecosystems (Fogarty and Facelli 1999) that has displaced 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), in addition to its establishment in 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). The current study aims to clarify the relationship between the invasive *Cytisus scoparius* and three co-flowering plant species characteristic of the endangered Garry oak grassland community by observing the sequence of events leading to their pollination and reproductive success (see Fig. 1). Two native species, *Camassia leichtlinii* and *Collinsia parviflora*, as well as one exotic naturalized species, *Geranium molle*, were observed during the spring of 2011 in four sites where *Cytisus scoparius* was present and four sites where *C. scoparius* was absent. The following hypotheses were addressed: (1) *Cytisus scoparius* affects site-level pollinator composition and abundance by fostering an increase in the abundance of *C. scoparius*—associated insect species within invaded areas. (2) *C. scoparius* acts as a pollinator vacuum, siphoning pollinators away from native species and subsequently reducing their visitation rate. (3) Decreased visitation in *C. scoparius*—invaded sites results in lower conspecific pollen deposition and an increased proportion of heterospecific pollen on native stigmas. (4) The pollination success (as measured by pollen limitation and seed production) of native focal plants is reduced in invaded sites when compared to uninvaded sites.

Methods

Focal plant species and sites

Cytisus scoparius is a woody shrub (1–3 m tall) that can shade out native forbs, and changes the soil

chemistry by increasing nitrogen content and in some cases decreasing soil pH (Wheeler et al. 1987; Fogarty and Facelli 1999; Haubensak and Parker 2004; Caldwell 2006). It is a prolific seed producer (9650 viable seeds/shrub/year, as estimated by Bossard and Rejmanek 1994) with a persistent seed bank, and it is able to resprout after being cut or burned (Zielke et al. 1992). Its multitudinous large (16–20 mm) yellow flowers (Stout 2000) (Fig. 2) exhibit an ‘explosive’ pollination mechanism, whereby a visit from a large enough pollinator ‘trips’ the flower, resulting in the discharge of the stamens and style and a subsequent release of pollen onto the insect (Darwin 1888; Stout 2000). The flower remains open after being tripped, displaying deceptive nectar guides in open flowers (Stout 2000). *Cytisus scoparius* 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).

The Garry oak ecosystem (hereafter referred to as GOE), occupies a Mediterranean climate and is distributed from southwestern British Columbia southward along the coast to southern California (Fuchs 2001; Lea 2006). In Canada, the GOE is largely limited to British Columbia: southern Vancouver Island, the Gulf Islands (Fuchs 2001) and is currently 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 its natural unadulterated form (Lea 2006), the remaining fragments hosting over 100 provincially listed species at risk, including 61 provincially listed and 11 federally listed (COSEWIC) plant species (Fuchs 2001).

We identified four sites where flowering *C. scoparius* was present and four sites where flowering *Cytisus* was absent (“invaded” and “uninvaded” sites, respectively) on the Saanich peninsula of Vancouver Island in the spring of 2011 (Fig. 3). While adequate records of the initial *C. scoparius* invasion of the Saanich peninsula are not available, the scope of *C. scoparius* invasion is quite extensive and all sites presently devoid of *C. scoparius* had *C. scoparius* plants previously that were removed through outside effort. Due to the persistence of *C. scoparius* seeds in the seed bank, such removal efforts are ongoing at all “uninvaded” sites. As such, immediately preceding the flowering season, any remaining *C. scoparius*



Fig. 2 The focal plant species in the current study. Clockwise from *top to left*: maiden blue-eyed Mary, *Collinsia parviflora*; Great Camas, *Camassia leichtlinii*; Scotch broom, *Cytisus scoparius* (an open “tripped” flower); and dovesfoot geranium, *Geranium molle*

plants were removed from the “uninvaded” sites. To avoid the possibility that pollinators were foraging on *C. scoparius* just outside the confines of the GOE remnant in “uninvaded” sites, effort was taken to remove *C. scoparius* from the local surrounding area. Within each site, three focal species were identified that were (1) consistently co-flowering with Scotch broom, (2) found in moderate abundance at all sites,

and (3) preliminary observations indicated that they shared similar pollinators with *C. scoparius*: great camas (native, *Camassia leichtlinii* ssp. *suksdorfii*), maiden blue-eyed Mary (native, *Collinsia parviflora*), and dovesfoot geranium (exotic, *Geranium molle*) (Fig. 2).

Camassia leichtlinii Baker (S. Watson) subsp. *suksdorfii* (Greenman) Gould (Liliaceae) is a bulbous

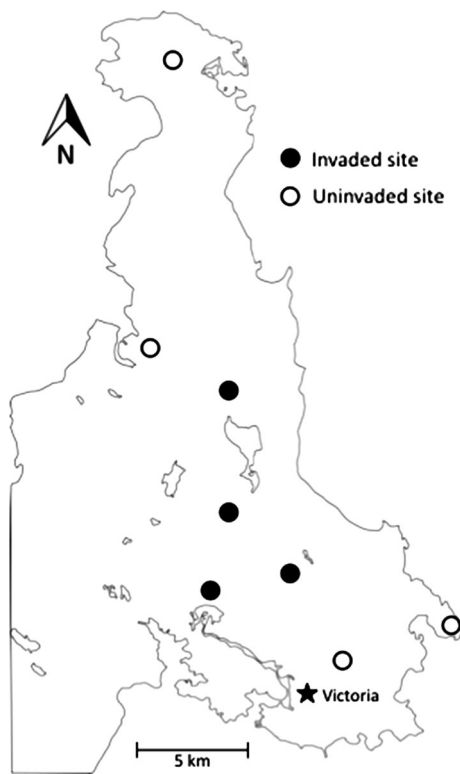


Fig. 3 Study locations on the Saanich peninsula of Vancouver Island. Empty circles represent sites where *Cytisus* was removed, and Filled-in circles represent sites where *Cytisus* was present

perennial lily native to wet meadows of western North America with showy blue to bluish-violet actinomorphic flowers (Mathew 2004) and blooms in late-spring from May to June (Turner and Kuhnlein 1983; Ranker and Hogan 2002). *C. leichtlinii* produces 6–12 seeds per locule and 3 locules per fruit (Gould 1942; Ranker and Hogan 2002). *Collinsia parviflora* Dougl. ex Lindl. *C. parviflora* is a winter annual common in western North America (Elle and Carney 2003) with small bluish-purple zygomorphic flowers (Elle et al. 2010). On Vancouver Island, *C. parviflora* blooms from March to June, and ripe capsules open and passively disperse 3–8 seeds (Elle and Carney 2003; Parachnowitsch and Elle 2004). *C. parviflora*'s main pollinators have previously been observed to include a number of *Bombus* species, *Osmia*, and “several species of hover flies”, and visitation rate has been dependent on *C. parviflora* population size (Elle and Carney 2003). This species is known to be primarily outcrossing but also able to produce seeds through

autonomous selfing for reproductive assurance (Elle and Carney 2003; Kennedy and Elle 2008). *Geranium molle* L. is an herbaceous annual plant with bright pink to purple actinomorphic flowers (Aedo et al. 1998) that is primarily autogamously selfing (Fiz et al. 2008). Each ovary has 10 ovules (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 GOE, but is not thought to be as large of a threat or as destructive as invasive grasses or shrubs (Fuchs 2001).

We assessed site characteristics in terms of plant and insect composition. Plant diversity within each site was observed at peak flowering of *C. scoparius* (mid- to late-May). This was done by walking transects 10 m apart throughout the entirety of each site, and undertaking floristic surveys where all observed flowering plant species were recorded, as well as whether these plants were flowering or not at the time of census (and thus co-flowering with *C. scoparius*). In 2010, pan trap transects were used to obtain an estimate of 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 a.m. to 5 p.m., after which the pollinators were collected from the pans and stored in 95 % ethanol until they were able to be processed and identified. The pan traps were set out in each site twice during the period in which *C. scoparius* 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 transects. This analysis was carried out three separate times: on the set of early-season bowls (May 25–June 8), on the set of later-season bowls (June 10–June 25), and on the total sets of bowls.

Presence/absence of species was analyzed using a PERMANOVA analysis, part of the PRIMER-E v.6 package (Anderson 2001; Clarke and Gorley 2006). Unless otherwise noted, all statistical analysis was carried out using SAS 9.3 (SAS Institute 2011). PERMANOVA analysis 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). We used Bray-Curtis similarities (that incorporate differences in pairwise abundance into composition similarities) and ran 9999 permutations for each of the analyses to examine differences in composition between invaded and uninvaded sites.

Pollen limitation

To determine whether **pollen limitation** exists in the focal GOE species and if the presence of *C. scoparius* affects pollination success, pollen supplementation experiments were carried out. In each site, each species was subdivided into pollen-supplemented and control groups, with 25 individuals of each species in each group. *C. scoparius* was also pollen-supplemented in three of the four invaded sites. The pollen-supplemented group was pollinated by hand using pollen from at least 2–3 conspecific individuals (mixed prior to application) acquired from between one metre and 15 m away from the experimental plants to increase the probability of using outcross donors and minimize the possibility of outbreeding depression. An attempt was made to supplement all flowers on herbaceous plants, due to the potential for resource reallocation within inflorescences when only a portion of flowers are supplemented (Zimmerman and Pyke 1988). However, due to time constraints this was often not possible, so the proportion of flowers supplemented was recorded. In *C. scoparius* the flowers on only one branch were supplemented due to its shrubby growth habit (Parker 1997; Wesselingh 2007).

After the flowering period, **fruits** from the pollen-supplemented and control groups were collected and seeds, aborted seeds and ovules were counted for each fruit in each focal species except for *C. scoparius*, for which fruit set was the only measure of reproductive success due to early harvest of **seed pods**. Fruit set was calculated for all sampled plants and seed set was calculated for a random subset of approximately one quarter of the collected plants. To compare the pollen limitation among plant species, pollen limitation for seed and fruit set for each species in each site were calculated using the log response ratio (Knight et al. 2005; Burd et al. 2009) as follows:

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

Pollen limitation for *C. scoparius* was only calculated via fruit set, as seed set was not measured. A log-response ratio of 0 indicates that naturally pollinated flowers are receiving sufficient pollen to produce full seed set [i.e., no pollen limitation (PL)]. A positive log-response ratio indicates pollen limitation, and a negative log-response ratio is indicative of increased fecundity of naturally pollinated plants as compared to the pollen-supplemented group. We compared the PL among species and determined whether there is a relationship between PL and floral visitation (number of visits per minute per flower) for each focal species. This was done for pollen limitation indices for both fruits and seeds, and these analyses were done in PROC GLM with a type three error and invasion as a covariate. We examined the relationship between *C. scoparius* invasion and pollen limitation metrics for both fruits and seeds in similar fashion. Significant differences among plant species were determined with the use of the Tukey HSD test.

We addressed whether a pollen supplementation strategy was an effective means to assess pollination success by contrasting the standard PL methods with plant-level reproductive success analyzed using generalized linear mixed models in PROC GLIMMIX. We tested whether the number of seeds per plant, and the number of fruits per flower depended upon invader presence and/or supplementation treatment. All analyses were blocked by the random factor of site nested within site type (invader present or invader absent), and a spatial block nested within site (this was an unplanned factor, but due to potential microclimatic, genetic or other similarities, each perceived ‘stand’ of plants observed in the field was recorded as a separate “spatial block” within each site). This random ‘block within site’ factor was omitted within analyses where it precluded the calculation of a covariance estimate for site nested within site type.

For each focal plant the number seeds per plant was approximated with a negative binomial distribution and its associated canonical 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 *C. leichtlinii* and *C. scoparius*-supplemented *Camassia* (number of ripe fruits as response variable and the total

number of flowers as a covariate) and a binomial distribution for *G. molle* and *C. parviflora*, with their respective canonical link functions (log and logit, respectively).

We performed analyses on the total number of ovules (defined as the sum of seeds, aborted seeds and unripened ovules) produced per plant and the total number of flowers produced per plant as a function of *C. scoparius* presence, supplementation treatment, or their interaction. This was done separately for each plant species using a generalized linear mixed model (PROC GLIMMIX) with negative binomial errors with the log link function and site nested within *C. scoparius* invasion as a random factor. Total number of flowers per plant was used as an additional covariate when ovule number per plant was used as a response variable.

Floral visitation

Observational periods were conducted two to six times for each focal plant species in each site between the hours of 09:00 and 17:00 h during days with clear weather and a temperature above 14 °C. Due to the vagaries of weather, observational periods (20 min) and total number of observation periods (40–130 min) had to be occasionally curtailed and so was included as a covariate in the analysis. The number of pollinator visits to each species was counted and when possible the visitors were collected and brought back to the lab to be identified to as fine of a scale as possible. A “pollinator” was defined as a floral visitor observed contacting the reproductive surfaces of the flower. Observational periods were conducted in patches of flowers representative of each site, and the number of focal flowers observed was counted to determine the local floral abundance in the observed patch. Using PROC GLIMMIX and site nested within invasion as a random factor, the number of pollinators during each observation period was fitted with a Poisson distribution for *C. leichtlinii* and *C. parviflora* and a negative binomial distribution for *G. molle* visitors. The associated canonical link functions (log for both) were used in addition to the following covariates: length of observation period, number of flowers observed, and ambient temperature. A comparison of floral visitation rates among focal plants was carried out by calculating the mean visitation rate (number of visits per minute per flower) for each focal plant in each site, and using

PROC GLM to compare these values with a type three error rate and invasion as a covariate. 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), we examined whether the visitor community of each focal plant changed with *C. scoparius* invasion (as in Tonietto et al. 2011). Using all pollinators identified for each species, Pianka’s niche overlap index (hereafter NOI) was calculated per site to determine the degree of pollinator sharing each GOE resident focal species had with *C. scoparius*:

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

where p_i is the frequency of occurrence of each pollinator taxa i of plant species j and k . This index takes into account the identity and frequency of pollinators of each plant, and gives values between 0 and 1, where 0 indicates total separation and 1 indicates complete overlap (Pianka 1973).

Pollen deposition

To relate visitation to the quantity and quality of pollen deposition, styles were collected from 10 to 12 senescing flowers per focal species in all sites, and stored in 0.5 µl microfuge 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 dye. Dyed styles were mounted onto slides with a drop of glycerine and the numbers of both conspecific and heterospecific pollen grains present on the stigmatic surface(s) were then counted with the use of a light microscope at 1000× magnification. Conspecific pollen grain identity was checked against a pollen library prepared from pollen samples collected from all co-flowering species in the community at the time of stigma collection. Pollen deposition was analyzed using generalized linear mixed models in PROC GLIMMIX, with site nested within invader presence as a random factor. For each focal plant the number of pollen grains (conspecific, heterospecific, and total) as well as the proportion of conspecific pollen deposited on each stigma was tested against the null hypothesis that there is no significant difference in pollen deposition when invaders present or absent. All

models were fitted with a negative binomial distribution and its associated canonical log link function. The number of conspecific pollen grains and the proportion of conspecific pollen grains deposited on floral stigmas were also compared among focal plant species by calculating the mean value for each focal plant species in each site and using PROC GLM to compare each plant species with a type three error and invasion as a covariate in the model. Significant differences among plant species were determined with the use of a Tukey HSD test.

Results

Plant and pollinator diversity

Using the presence/absence of plant species as a metric of community composition, **there was no significant difference between *C. scoparius*-invaded and uninvaded sites when looking at either total plant presence** (PERMANOVA: pseudo- $F_{1,6} = 0.712$; $p = 0.78$) or flowering plant presence (PERMANOVA: pseudo- $F_{1,6} = 0.337$; $p = 1.00$). *C. scoparius* was observed for 380 min total, wherein 50 pollinators were observed of which 34 were collected and identified to be within 21 taxa. Full lists of pollinators to all four species are provided in Appendix S1-4. The most common pollinators of *C. scoparius* were *Bombus melanopygus* (10), *Lasioglossum pacificum* (4), and *Lasioglossum olympiae* (4). A total of 709 observation minutes were carried out on *Collinsia parviflora*, and within this time period 38 visitors were observed, 22 of which were collected and identified to be within 12 taxa. Of those visitors collected, the most common were the bee fly *Bombyllius major* (4), and the solitary bees *Ceratina acantha* (4) and *Osmia odontogaster* (4). *Geranium molle* was observed for a total of 717 min, within which 85 pollinators were observed (63 collected) and identified to be within 24 taxa. Of the collected insects the most common pollinators of *G. molle* were *Ceratina acantha* (25), the bee fly *Bombyllius major* (5), and *Osmia pusilla* (5). *C. leichtlinii* was observed for 590 min total, within which 165 floral visits were observed. 123 visitors were collected and determined to be within 26 taxa. The most common pollinators collected were *Bombus mixtus* (41), *Apis mellifera* (22), and *Lasioglossum olympiae* (19). When sites with and without *C.*

scoparius were compared, there was no significant change in the composition of pollinators for any of the focal plant species (Table 1). There was also no effect of *C. scoparius* presence on the insects collected in the pan traps for either the early set (PERMANOVA: pseudo- $F_{1,5} = 1.349$; $p = 0.1726$), late set (PERMANOVA: pseudo- $F_{1,5} = 0.881$; $p = 0.5984$), or overall (PERMANOVA: pseudo- $F_{1,6} = 1.372$; $p = 0.085$; also see Appendix S5 for list). Using the niche overlap index, the degree of pollinator sharing between *C. scoparius* and *C. parviflora*, *G. molle*, and *C. leichtlinii* in the invaded sites were found to be 0.06, 0.08, and 0.42, respectively. Despite the trend for higher niche overlaps between *C. leichtlinii* with *C. scoparius* at every site, they were not significantly higher than that observed with *G. molle* or *C. parviflora* ($F_{2,6} = 4.09$; $p = 0.056$).

Pollen limitation and quantity of floral visitation

There was no difference in pollen limitation among species when pollen limitation was measured with seeds as reproductive output, but there were differences in pollen limitation when fruit set was used as reproductive output (Fig. 4a). In particular, *G. molle* had the lowest pollen limitation (-0.50 ± 0.16), *C. scoparius* (0.52 ± 0.28) and *C. parviflora* (0.33 ± 0.16) had the highest pollen limitation, and *C. leichtlinii* had an intermediate PL value (-0.12 ± 0.16). Pollen limitation did not follow intuitively from visitation rates, however, as we find that *C. leichtlinii* had the highest visitation but moderate PL (Fig. 4b). Similarly, conspecific pollen deposition did not relate as expected to per-flower visitation rates (Fig. 4c). PL was not significantly affected by invasion for either seed set or fruit set in *C. leichtlinii* or *C. parviflora* (Table 2). *G. molle* fruit set in invaded sites was more pollen-limited than in uninvaded sites, but seed set was not different between site types (Table 2).

We find that floral visitation in the presence of Scotch broom exhibited a trend to be lower than where the invader was absent for *C. leichtlinii*, yet not for either *G. molle* or *C. parviflora* (Table 3). Generally, *C. leichtlinii* was favoured by pollinators (Fig. 4) whereby *C. leichtlinii* had a higher visitation rate (0.013 ± 0.002 visits/min/flower) than *C. scoparius* (0.0015 ± 0.003 visits/min/flower), *C. parviflora* (0.0003 ± 0.002 visits/min/flower) or *G. molle* (0.0036 ± 0.002 visits/min/flower). Surprisingly, there was no observed

Table 1 The effect of *Cytisus* invasion and associated covariates on the composition of observed pollinators 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. <i>p</i>	MS	Pseudo-F	Perm. <i>p</i>	MS	Pseudo-F	Perm. <i>p</i>
Pollinator 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	–	–

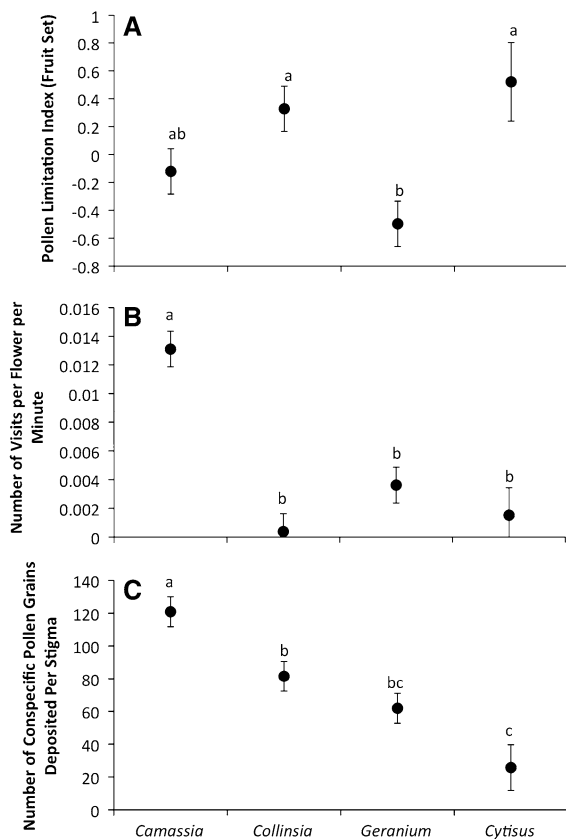


Fig. 4 Relative success of focal plant species as measured by **a** pollen limitation ($\ln R \pm SE$), **b** floral visitation and **c** conspecific pollen deposition. All relationships include invader presence as a covariate in the model and differences between plants determined with a Tukey test

relationship between PL (as measured as $\ln R$) and visitation rate in either seed set or fruit set for *C. leichtlinii* (seeds: $F_{1,6} = 0.00$, $p = 0.994$; fruit: $F_{1,6} = 0.96$, $p = 0.365$), *G. molle* (seeds: $F_{1,6} = 3.67$, $p = 0.104$; fruit: $F_{1,6} = 0.47$, $p = 0.518$), or *C. parviflora* (seeds: $F_{1,6} = 0.23$, $p = 0.652$; fruit:

$F_{1,6} = 1.70$, $p = 0.240$). Further, there was also no relationship seen between visitation and fruit set in *C. scoparius* ($F_{1,6} = 0.0$, $p = 0.975$).

Overall, our results suggest that the magnitude of PL was species-specific (Table 4). In *C. leichtlinii*, there was no effect of invader presence, supplementation treatment, or their interaction on the seed production per plant or per fruit (Table 5), yet we do find a significant interaction between supplementation treatment and invasion in *C. leichtlinii* fruit production and the effect suggests facilitation of pollination when *C. scoparius* is present (Fig. 5). There was no effect of treatment, invasion, or their interaction on the number of seeds produced per plant for *G. molle* or *C. parviflora* (Table 5; Fig. 5). The fruit set per flower of *C. parviflora* did indicate an increased proportion fruit set in supplemented plants (0.863 ± 0.02) than in control plants (0.82 ± 0.02) (Table 4; Fig. 5). Finally, *C. scoparius* branches that received conspecific pollen supplementation produced more fruits than naturally-pollinated control branches ($F_{1,109,2} = 4.48$, $p = 0.037$).

Confounding effects of resource differences were observed between pollen supplemented and naturally-pollinated groups. There were significant differences in the number of flowers produced among treatment groups for both *C. leichtlinii* and *G. molle*. In particular, plants in the unsupplemented treatment had higher numbers of flowers per plant than their pollen-supplemented counterparts (Table 5). *C. leichtlinii* plants additionally exhibited increased numbers of ovules per plant in the pollen-supplemented group than the control group (Table 5). Despite differences in flower and ovule number, we could find no consistent evidence that *C. scoparius* invasion altered resource allocation (i.e., ovules per flower) of any of the focal species (Table S1).

Table 2 The effect of *Cytisus* invasion on the overall pollen limitation ($\ln R = \ln(\text{mean output from supplementation/mean output from control})$) of each focal species

Source of variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
		MS	F	<i>p</i>	MS	<i>F</i>	<i>p</i>	MS	F	<i>p</i>
<i>Pollen limitation (seeds)</i>										
Invasion	1	0.024	0.20	0.669	0.019	0.23	0.650	0.064	0.31	0.596
Error	6	0.118	–	–	0.082	–	–	0.205	–	–
<i>Pollen limitation (fruits)</i>										
Invasion	1	0.354	1.33	0.293	0.909	7.57	0.033	0.036	0.19	0.675
Error	6	0.267	–	–	0.120	–	–	0.185	–	–

Table 3 The effect of *Cytisus* invasion and associated covariates on floral visitation for each focal plant

Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
		Den.	df	p	Den	df	p	Den	df	p
<i>Visitation</i>										
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

Generalized linear mixed model analysis of the site nested within *Cytisus* invasion was used as a random effect within each model. Bold type indicates $p < 0.05$, asterisk indicates a trend

Pollen deposition

Despite lowered visitation rate, we observed that there was a significant increase in both total pollen deposition and conspecific pollen deposition to *C. leichtlinii* stigmas, in invaded sites as compared to non-invaded sites (Table 4; Fig. 5) potentially due to changes in absolute number of flowers (and therefore the number of pollen grains) in the site types. There was no significant difference in the number of conspecific, heterospecific, or total pollen grains on *G. molle* or *C. parviflora* stigmas between sites where *C. scoparius* was present versus absent (Table 4; Fig. 5). In short, *C. scoparius* has weak effects on the pollination success of these three species (summarize in Table 6 with standardized effect sizes to streamline comparisons).

Discussion

While our results would suggest that the presence of *Cytisus scoparius* changes the pollination and

reproductive success of GOE associated species, the effects are species-dependent and not necessarily negative. *Camassia leichtlinii* displayed the highest pollinator overlap with *C. scoparius* and was the only species to exhibit invader-associated effects on pollinator visitation, pollen deposition and seed set. While a putative facilitative effect was seen in *C. leichtlinii*, *C. parviflora* and the exotic *G. molle* were relatively unaffected despite *C. parviflora*'s fruit set being pollen limited overall. The variable effect of *C. scoparius* presence on the pollination of co-flowering GOE species was 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) but also the highlight the need to concentrate on the patterns observed in naturally-pollinated plants (rather than the differences between naturally-pollinated and pollen-supplementation treatments). These results suggest that pollination dynamics are having little effect on these particular co-flowering GOE-associated species over and above the previously acknowledged direct negative effects of competition for space and other resources. Further, *C. scoparius* was not

Table 4 Relative analysis of floral visitation rate (number of visits per minute per flower), pollen limitation [$\ln R = \ln(\text{mean output from supplementation/mean output from control})$] and pollen deposition among focal plant species using general linear model analysis, with invasion as a covariate

Response variable	Source of variation	df	MS	F	p
Visitation	Focal species	3	0.00025	26.94	<0.0001
	Invasion	1	0.00002	2.14	0.1580
	Species \times invasion	2	0.00004	4.94	0.0175
	Error	21	0.00001	–	–
Pollen limitation (seeds)	Focal species	2	0.04427	0.33	0.7245
	Invasion	1	0.02448	0.18	0.6752
	Species \times invasion	2	0.04112	0.30	0.7411
	Error	18	0.13491	–	–
Pollen limitation (fruits)	Focal species	2	1.36197	7.14	0.0052
	Invasion	1	0.10020	0.53	0.4778
	Species \times invasion	2	0.59950	3.14	0.0674*
	Error	18	0.19066	–	–
Pollen deposition (total heterospecific)	Focal Species	3	490.71	6.45	0.0029
	Invasion	1	27.647	0.36	0.5530
	Species \times invasion	2	68.580	0.90	0.4210
	Error	21	75.059	–	–
Pollen deposition (proportion conspecific)	Focal Species	3	0.00199	0.21	0.8865
	Invasion	1	0.00245	0.26	0.6144
	Species \times invasion	2	0.00456	0.49	0.6212
	Error	21	0.00937	–	–
Pollen deposition (total conspecific)	Focal species	3	8710.20	16.62	<0.0001
	Invasion	1	2507.35	4.78	0.0402
	Species \times invasion	2	2152.74	4.11	0.0312
	Error	21	524.09	–	–

As seed set was not quantified in *Cytisus*, only 3 focal species were compared when pollen limitation was quantified using seed set. $p < 0.05$ is indicated in bold type, and trends are indicated with an asterisk

observed to foster an ‘invasional meltdown’ nor ‘invasional interference’ with respect to the exotic *G. molle* within GOE remnants in this study.

Plant and pollinator community diversity

Perhaps due to the recent nature of the broom removal, there was no significant effect of the presence of *C. scoparius* on plant community diversity as measured by presence/absence of species, for either total plant species or species co-flowering with *C. scoparius*, generally corroborating previous studies in the GOE (Shaben and Myers 2009; Parker et al. 1997) and other ecosystems (Bartomeus et al. 2008, but see Moron et al. 2009). Generally, the local presence of *C. scoparius* is not a strong influence on the composition of pollinators for any of the focal GOE associated plant species, nor affecting the composition of insects collected with pan traps. Unlike previous studies in other systems (Nielsen et al. 2008; Flanagan et al.

2010), we found no evidence of a change in pollinator abundance or composition where *C. scoparius* was present.

Dissecting the effect of *Cytisus scoparius* on GOE focal plants

In teasing apart the different influences *Cytisus scoparius* could be having on reproductive success of three common co-flowering species (Fig. 1), we find, like previous studies (Thijs et al. 2012), that the species with greater pollinator overlap between the invader and native exhibit the larger effects on conspecific pollen deposition (Bjerknes et al. 2007). The fact that there was no corresponding increase in heterospecific pollen deposition in invaded sites suggests that while visitation rate in the presence of *C. scoparius* declined, the remaining floral visits to *Camassia* were more efficient at delivering conspecific pollen. It is possible that the observed increased

Table 5 Generalized linear mixed model analysis of the effect of treatment (pollen supplemented or control), invasion (*Cytisus scoparius* present or absent), and associated covariates

on the seeds per plant, fruits per flower and seeds per flower produced by each focal species

Source of Variation	df	<i>Camassia leichtlinii</i>			<i>Geranium molle</i>			<i>Collinsia parviflora</i>		
		Den. df	F	<i>p</i>	Den. df	F	<i>p</i>	Den. df	F	<i>p</i>
<i>Seeds/plant</i>										
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 × 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
<i>Fruits/flower</i>										
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 × 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

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

conspecific pollen deposition has been caused by changes in pollinator behaviour brought on by the presence of a new coflowering species (see Hegland and Totland 2008). In particular, pollinators may be visiting more flowers on the same plant, leading to increased geitonogamy and a subsequent increase in the receipt of self pollen (Yang et al. 2011). As we find that *C. leichtlinii* exhibits a mixed mating system with increased self-pollen deposition having a minimal effect on fruit and seed set (Table S2), the lack of increased seed production is more likely due to pollen deposition being well in excess of ovule number at all sites. Finally, as there was no allelopathic effect of *C. scoparius* pollen detected on *C. leichtlinii* stigmas (J. Muir, unpublished data), there is unlikely to be any direct effect of *C. scoparius* pollen on reproduction of native species (Montgomery 2009a, b; Jakobsson et al. 2008; Moragues and Traveset 2005).

Cytisus scoparius invasion is thought to affect soil nutrient and mineral composition through its nitrogen-fixing *Rhizobium* root nodules (Wheeler et al. 1987). There are conflicting results of the presence of *C. scoparius* on the growth and reproduction of co-occurring species: *Achillea millefolium* experienced a 30 % reduction in the growth in the presence of *C. scoparius* (Haubensak and Parker 2004), yet grasses *Dactylis glomerata* and *Festuca idahoensis* produced

greater numbers of inflorescences (Shaben and Myers 2009). We observed few consistent effects of *C. scoparius* on our focal species in terms of resource allocation, and the total seed production on the plant level indicates that *C. scoparius* only increases the population-level reproductive success of our focal plants of *G. molle* but *C. parviflora* or *C. leichtlinii* (results not show). Furthermore, pollen-supplemented flowers exhibited an increased number of aborted seeds than their naturally pollinated counterparts, even in invaded sites suggest that resource limitation is a factor in reproductive success even when *C. scoparius* was in the vicinity (Haig and Westoby 1988; Ashman et al. 2004). In sum, our results indicate that even though pollination success is modestly affected, our focal species generally make equivalent (or more) seeds when broom is present. However, considering broom is a prolific seed disperser, these modest increases in reproductive success are likely to be insufficient to overcome the increased competition for seed germination sites, leading to the spread of broom. In short, while broom does not gain ground by usurping pollinators, it does not facilitate pollination or seed production enough to become a naturalized member of the community. We advocate that future studies investigating pollination and seed production examine competition with this whole life cycle perspective.

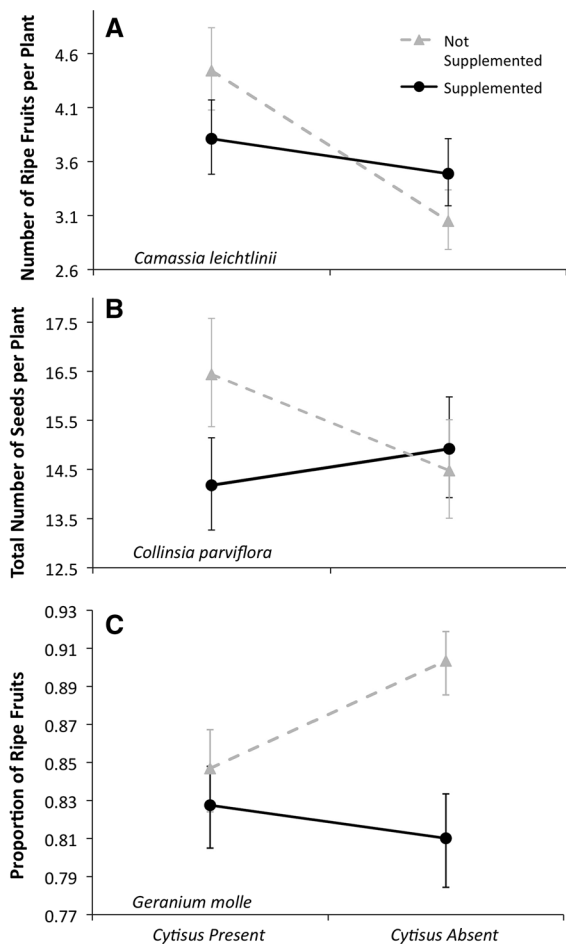


Fig. 5 The interactive effects of invader presence and supplementation treatments in fruits set per plant in *Camassia* (a), total seed production in *Collinsia* (b) and the proportion of ripe fruits set in *Geranium* (c). All values are back-transformed estimates. The figure highlights how PL indices can obscure important patterns of reproductive success as pollen-supplemented individuals often had lower reproductive success than naturally-pollinated individuals

Cytisus scoparius success in GOE remnants

Some have postulated that exotic plants become invasive when they are highly autogamous or have similar visitation rates to their native community members (Harmon-Threatt et al. 2009). In this study, *C. scoparius* had the lowest visitation rates of all species observed in addition to being obligately outcrossing, contrasting with other invasive species observed to have very high floral visitation within their novel habitats (Kandori et al. 2009; Vanparys et al. 2011; Bartomeus et al. 2008; Woods et al. 2012). This evidence is consistent with

other GOE sites sampled in the Washington prairies (Parker 1997), on the Marin peninsula of California (Parker and Haubensak 2002), and Fukuoka, Japan (Suzuki 2008). The ample seed production of *C. scoparius* is thus due to the sheer floral numbers of this shrub, like other prolific invaders [*Carpobrotus* affine *acinaciformis*, (Bartomeus and Vila 2009) and *Lonicera mackii* (Goodell et al. 2010)], suggesting that seed production is a more relevant metric than pollen limitation data for how invasion proceeds, as native plants are likely losing seed competitions more so than they are losing pollinator competitions (Vamosi et al. 2007).

Relative pollination of focal plants in the study

The results presented here showcase the diversity of ways that interactions with pollinators within a community influence reproductive success. Surprisingly, there was not a consistent relationship between pollen limitation and visitation rates, in agreement with that previously observed in other systems (Hegland and Totland 2008). While previous studies have shown that pollen limitation as measured through both fruit set and seed set is significantly correlated (Knight et al. 2005), this trend is not seen in the current study. Pollen-supplementation can cause plants to shift resources to well pollinated developing fruits, such that fewer fruits are produced, yet the mean seed production is equivalent or higher (Knight et al. 2005). The potential for resource allocation towards fewer heavily-seeded fruit was higher in our pollen supplemented plants that were observed to produce higher numbers of flowers than plants in the control treatment in both *C. leichtlinii* and *G. molle* and this may have influenced our results of fruit and seed set (J. Muir, unpublished data).

Cytisus scoparius is now widespread in GOE habitat fragments on the Saanich peninsula. Our choices of focal species was determined by presence in all eight sites and species that were susceptible to *C. scoparius* invasion through shading or decreases in reproductive success may have already been extirpated from most GOE sites, such that only the common species that are unaffected (through have low pollinator overlap) or facilitated remain. The historical proximity to *C. scoparius* is highly correlated to the reduction in native species in prairie ecosystems of the Pacific Northwest (Rook et al. 2011). Restoration efforts should continue to focus on *C. scoparius*

Table 6 A summary table of observed effects of *C. scoparius* invasion on various pollination metrics of co-occurring species

Metric	Interaction	Focal plant		
		<i>Collinsia parviflora</i>	<i>Camassia leichtlinii</i>	<i>Geranium molle</i>
Pollinator composition	a	0.23	0.44	0.33
Pollinator visitation	b	0.04	0.86	0.11
Pollen limitation (seeds)	c	0.02	0.20	0.07
Pollen limitation (fruits)	c	0.10	0.21*	0.08
Conspecific pollen deposition	c	0.04	0.34*	0.13
Total pollen deposition	c	0.06	0.42	0.22
Ovule number	d	0.12	0.0	0.24

Values presented are Cohen's *d* effect sizes (with the exception of the nonparametric analysis for pollinator composition where the analogous Cohen's f^2 was calculated). Bold values indicate a negative effect, and asterisks indicate $p < 0.05$. Interactions are illustrated in Fig. 1

invasion within the Garry oak habitat itself, while edge habitats and nearby residential or disturbed land uses seem to be less of a priority as no indirect competitive effects of *C. scoparius* were observed for the focal species studied here.

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