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Research Article

Pollination Biology of *Potentilla recta* (Sulfur Cinquefoil) and Its Cooccurring Native Congener *Potentilla gracilis* in Northeastern Oregon

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Pollination biology of the invasive plant sulfur cinquefoil (*Potentilla recta* L.) and it's native cooccurring congener slender cinquefoil (*P. gracilis* Dougl. ex. Hook.) was studied from 2002–2004, at four sites in northeastern Oregon, USA The native cinquefoil flowered first for five weeks, followed by the invasive for five weeks, with two weeks overlap in mid-June. Invasive flowers attracted 74 species and 543 individuals; the native attracted 93 species and 619 individuals. The most important pollinators for the invasive, in order of importance, were: *Apis mellifera*, *Ceratina nanula*, *Halictus tripartitus*, *Lasioglossum sisymbrii*, and *Bombus rufocinctus*; for the native: *C. nanula*, *Trichodes ornatus*, *H. ligatus*, *L. sisymbrii*, and *L. olympiae*. The invasive produced higher numbers of seeds per plant, having greater mass per unit vegetation. Mean seed size was lower for the invasive when pollinators were allowed access to flowers, but seed size increased linearly with more complete exclusion of pollinators; the native showed no such response to pollinator exclusion. Compared to the native, nearly twice as many seeds germinated for sulfur cinquefoil (35.0% versus 19.5%), with seeds germinating over a longer period of time. Results are discussed as they relate to the invasiveness of sulfur cinquefoil relative to the native.

1. Introduction

Nonnative invasive plants are increasingly recognized as major threats to ecosystems worldwide, particularly in arid and semiarid regions [1]. In western North America, invasive plants have changed fire regimes [2], reduced livestock forage quality, damaged real estate and recreation values [3], and impacted biodiversity [2]. While their influence on biodiversity has been described well in terms of the structure of native plant communities, relatively less is known on their ecological relationships to other species, including those that play critical functional roles, such as pollinators.

Insects, especially bees, beetles, flies, and butterflies are known to pollinate a majority of vascular plant species worldwide; beetles alone have been observed to pollinate 211,935 species, or over 88% of the total species of vascular plants [4]. Insects also play a major role in crop reproduction: Williams [5] estimated that 84% of crop species in the European Union are pollinated by insects, and Buchmann and Nabhan [4] reported that 67 principal crop species are pollinated by insects worldwide, out of 84 listed (80%). The key to effective pollination service is diversity, since most native insect pollinator species visit only a small set of potential flowering plant species [6], and since many plant species are designed to be pollinated by only a small set of available pollinators [7]. As a result, most ecosystems require a diversity of both plants and pollinators in order for effective pollination to be carried out [8].

When exotic plants invade native communities, plant species diversity can decline, and this may lead to concomitant decreases in the diversity of native pollinator communities. Furthermore, the spread of invasive plants, especially those that reproduce only by seed [9], may be dependent on how successful they are at competing for the service of resident pollinators. Thus pollinators can act to exacerbate the spread of invasive plants, by providing a service that improves seed production and the colonization potential of these species [10, 11]. Unfortunately, basic

information on the pollination ecology of invasive plants is lacking for most species. This information is especially critical for those species that reproduce primarily by seed, particularly if seed viability depends on outcrossing [11].

This study describes the pollination biology of the invasive plant sulfur cinquefoil (*Potentilla recta* L; Rosaceae) and its native cooccurring congener slender cinquefoil (*P. gracilis* Dougl. ex. Hook.), in northeastern Oregon. Sulfur cinquefoil is native to Eurasia and was introduced into North America before 1900 [12]. It is now naturalized across much of the United States and southern Canada, occurring from British Columbia east to Newfoundland and Nova Scotia, south to Florida, and west to eastern Texas [12–15].

In northeastern Oregon, sulfur cinquefoil occurs in open grasslands, shrubby areas, and disturbed areas including old fields, roadsides, pastures, and fencerows [16]. Sulfur cinquefoil can be highly competitive and has been observed to invade bluebunch wheatgrass (*Pseudoroegneria spicata*) rangeland in good condition and to displace other invasive species at some sites [17]. Sulfur cinquefoil is unpalatable to most livestock and wildlife, primarily because of its high-tannin content [12, 18, 19]. In fact, cattle will selectively graze spotted knapweed, another unpalatable species, in preference to sulfur cinquefoil [19]. As a consequence, overgrazing, which reduces competition from grass and other competing vegetation, generally favors sulfur cinquefoil [20].

Like its native congeners [21], sulfur cinquefoil is a long-lived perennial forb, having one to several erect, stout stems 30–70 cm tall growing from a woody caudex [12, 17, 18]. Peak flowering generally occurs in late June, depending on locality [12, 18]. Sulfur cinquefoil reproduces primarily by seed, and although self-fertilization can occur, most seeds are produced by cross-fertilization [22]. Seeds do not have a special dispersal mechanism [22]. Seeds germinate naturally at anytime during the growing season [23], and most vegetative growth occurs early the following spring [19].

In northeastern Oregon, sulfur cinquefoil cooccurs with its native congener *P. graclis* at many localities [24], and this presented the opportunity to study its pollination biology relative to the native. In particular, a comparative study of plants of both species living side by side could shed light on the extent to which the invasive has evolved distinct strategies to attract and retain pollinators, relative to the native congener. The current study compares the pollination biology of *P. recta* and *P. gracilis* by investigating respective flowering phenology, pollinator community structure, pollinator preference, nectar rewards, fidelity of pollen transfer, and influence of pollinator exclusion on seed set, seed size and number, and germination timing and rate.

2. Study Sites and Methods

The study was conducted between May 2002 and July 2004, in northeastern Oregon, where cinquefoil grows in small meadows intermixed with trees and shrubs (Figure 1). The general area experiences a Pacific Maritime Climate, warm and dry from late June to October, and cool and wet from November through May. Between 1965 and 2005, annual mean daily high temperature in La Grande, OR was 16°C, annual mean low temperature was 3°, and annual precipitation was 43.5 cm. Four study sites were selected for this study (Figure 1): the "Foothill" site (800 m elevation), just south of and closest to the largest municipality (La Grande OR, USA), was also the most dominated by sulfur cinquefoil (>95% *P. recta*); the "Rice" site was at slightly higher elevation (1000 m) on Glass Hill Road, 5 km southwest of La Grande, and here *P. recta* represented about 70% of total *Potentilla* cover; the "Ham" site (elevation 900 m) was located on Hamburger Hill, between Imbler and Elgin, 15 km northeast of La Grande, at which *P. recta* represented 50% of total *Potentilla* cover and the "Morgan" site was located at Morgan Lake, 10 km west of La Grande (1200 m elevation), and here *P. recta* represented just 10% of the total *Potentilla* cover.

In May 2002, we established five circular 400 m^2 plots (11 m radius) at each of the four study sites, within which most subsequent fieldwork was undertaken. Plots were selected so as to represent the approximate invasive to native composition of *Potentilla* species at that site. To determine flower phenology, relative flower availability was assessed at weekly intervals throughout each flowering season at each site, by counting the number of open flowers of each species (invasive or native) within each 400 m^2 plot. To determine the structure of the pollinator community of each cinquefoil species through time (species composition and relative abundance), we collected and identified all flower visitors within each plot at weekly intervals throughout each flowering season (2002, 2003, and 2004). By combining data on pollinator community structure for the two plant species within each plot with the relative abundance of flowers for each species, we could determine pollinator preference, by calculating an "electivity" index [25] for each flowering species, with the use of the following equation:

$$\mathrm{EI}_a = \frac{R_a - P_a}{R_a + P_a}, \tag{1}$$

where EI_a is Electivity index for plant species a, R_a is proportion of total pollinator population visiting plant species a, and P_a is proportion of plant species a in total flowering population.

This index will range between (−1), indicating total avoidance by pollinators of that plant species, to nearly (+1), which would indicate total dominance by that plant species of the pollinator resource. A value of (0) would indicate no preference for flowers of the given species of plant.

To gain insight into the potential efficacy of insects for distributing cinquefoil pollen, we removed and identified pollen from at least ten individuals of the 20 most common flower visitor species. Pollen was brushed off the bodies of randomly selected pinned individuals onto glass slides and preserved with standard methods. Pollen was identified with the use of a reference collection obtained by extracting pollen from flowers curated in the plant collection at Eastern Oregon University. In June and July 2003, we measured nectar quality in flowers of *P. recta* and *P. gracilis*, using a hand-held refractometer. Flowers of both species were collected, centrifuged, and a capillary tube was used to extract and measure the quality of nectar (% solute).

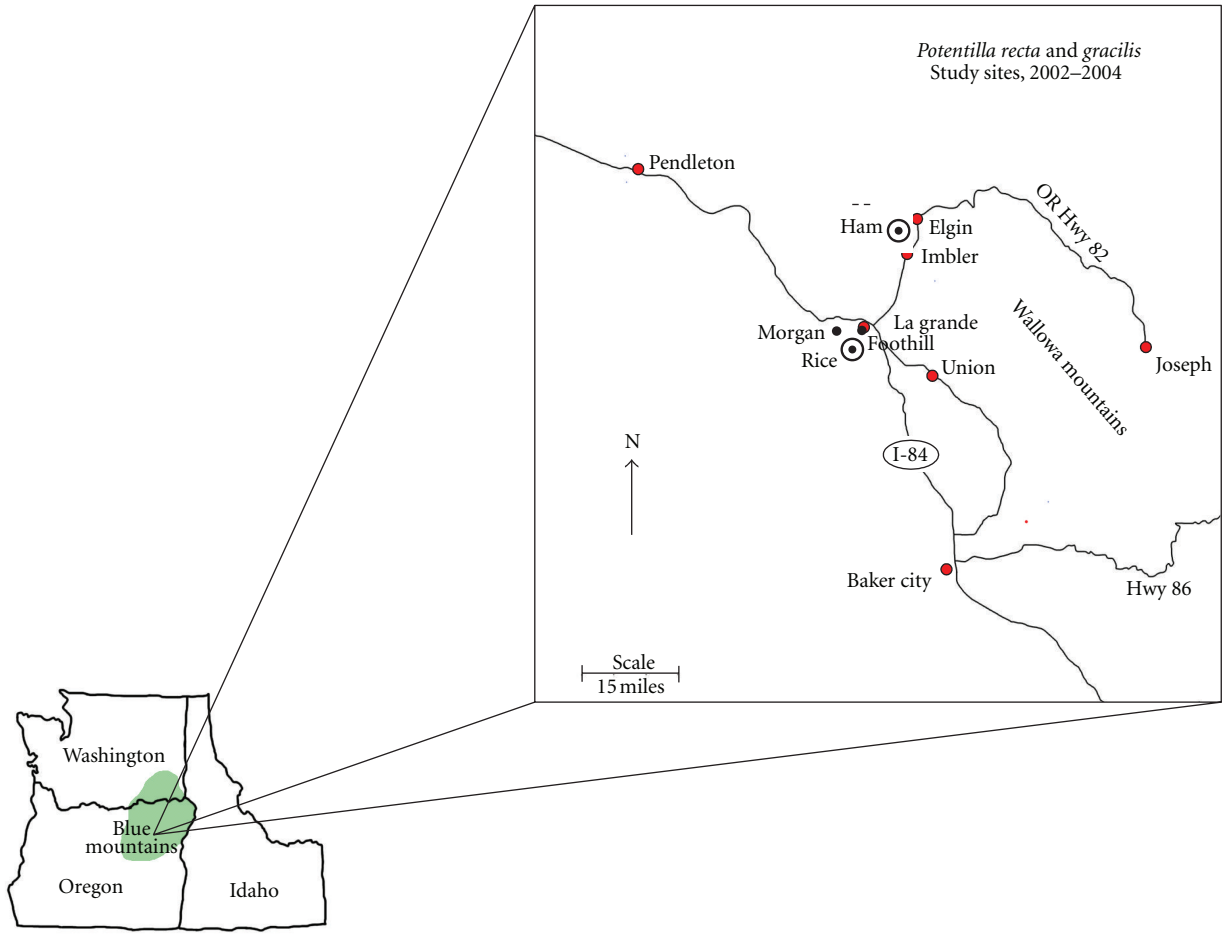


Figure 1: Map of *Potentilla* study sites, northeastern Oregon, 2002–2004.

Between late May and early July 2003, at two of the four study sites (Ham and Rice), we conducted a pollinator exclusion experiment designed to measure the potential influence of pollinators on seed set, seed size, and germination rate. Following the general protocol of Barthell et al. [11], five treatments were applied, four of which featured flower-head exclusion bags that varied in mesh size, designed to exclude pollinators of various sizes (Figure 2): (1) 1-mm mesh size: excluded all pollinators, regardless of size; (2) 3-mm mesh size: allowed access to the smallest pollinators, such as most Halictids and small Syrphid flies, but excluded medium and large pollinators such as most Apids, Megachilids, Andrenids, and large Syprhid and Bombyliid flies; (3) 5-mm mesh size: allowed access to small and medium-sized pollinators, but excluded the largest pollinators such as Bombids; (4) 10-mm mesh size: a "sham" cage, designed to test for bag effects *per se*: technically allowed access to all pollinators, regardless of size; and (5) no bag: flowerheads were left in the natural state, which allowed uninhibited access to all pollinators. One complete block of the five treatments was applied to a total of 240 flowerheads, 120 at each site, with each flowerhead representing an individual cinquefoil plant. At each site, we established four separate transects, separated by at least 100 m, along which we positioned 30 randomly selected plants, 15 of which were sulfur cinquefoil, alternating with 15 that were native cinquefoil. Bags were installed at least one week prior to flowering (late May to early June), and because flowerheads continued to expand during the experiment, bags had to be regularly re-positioned to accommodate new growth. Throughout the experiment, we visited bag installations on a weekly basis, to check for bag damage or other problems in installation, to record unexpected ingress of insects into the bags, and to count visitors on unbagged flowers of each species. Once flowering ceased, experimental bags were replaced with opaque cotton "seed bags," to insure that no seeds escaped from flowerheads as the seeds within them matured in the weeks following the cessation of flowering. After flowerheads had stopped growing and had clearly senesced (by the end of July), flowerheads were removed from plants and taken back to the lab for processing. In early August, flowerheads were oven-dried, dissected, and all seeds removed, counted, and weighed. To check for potential effects of seed predation on germination, a

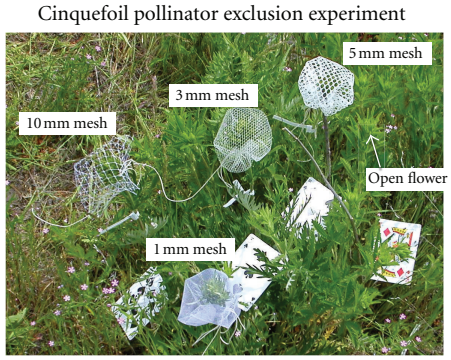


Figure 2: Photograph of a block of the five treatments deployed in the cinquefoil pollinator exclusion experiment: open flower (all access); 10 mm mesh size (sham cage, all access); 5 mm mesh (excludes large pollinators); 3 mm mesh (excludes large and medium pollinators); 1 mm mesh (excludes large, medium, and small pollinators).

total of 30 flowerheads of each species, 15 from both Rice and Ham sites, were dissected and checked for evidence of seed predation. To determine germination success over time, a subset of the total seeds (typically > 30) within each flowerhead were randomly selected, placed on moist filter paper within a covered petri dish, and monitored weekly for one year, and cumulative germination was determined.

Data on community structure are presented descriptively for all four study sites, as lists of species found through each of the three sampling seasons (2002, 2003, and 2004). The 20 most commonly collected pollinator species for each plant species are then compared descriptively. The ordination method "Nonmetric multi-dimension scaling" (NMS) [26] was used to characterize sites based on their composition and relative abundance of species, and then axes are correlated with site factors in an attempt to explain among-site and between-species patterns of community structure. NMS is ideal for ordination of most community data, because the technique is nonparametric, and thus does not assume any underlying distributional properties in the data set. Data on flower preference, using the electivity index were used to augment insights on the nature of patterns of pollinator use of the two plant species. For the bag experiment, we analyzed for the fixed effect of bag type on seed size, seed number per head, seed mass per head, and germination timing and rate with the use of a mixed general linear model, that included plant species, transect, and site as random factors.

3. Results

A total of 1,045 individual flower visitors were collected at the four sites over the three-year study period, comprising four orders, 36 families, and 111 species of insects (Table 7). Sulfur cinquefoil flowers attracted 74 species and 543 individuals, 16% of which were European honeybees (*A. mellifera* L.), while the native cinquefoil attracted a more diverse fauna of 93 species and 619 individuals, only 2% of which were honeybees. The 20 most commonly collected flower visitor species represented nearly 69% of the total individuals collected for each cinquefoil species (Table 1). Most pollinator species were "rare", reflected by the fact that 50 of 93 insect species observed on the native (53%) were represented by one or two individuals; for sulfur, 41 of 74 species were so represented (54%). Based on a combination of abundance and the presence of pollen on their bodies, the five most important pollinators for sulfur cinquefoil, in order of importance, were likely to be *A. mellifera, Ceratina nanula, Halictus tripartitus, Lasioglossum sisymbrii*, and *Bombus rufocinctus*; for the native, the most important pollinators were likely to be *C. nanula, Trichodes ornatus, H. ligatus, L. sisymbrii*, and *L. olympiae*. None of the 10 principle pollinators of each species were abundant throughout each respective flowering season, although for the native cinquefoil, most species were present throughout June, and for sulfur cinquefoil, most species were present from mid-June to mid-July (Table 2).

Although the pollinator fauna of the native cinquefoil was more abundant and rich than the fauna of sulfur cinquefoil, temporal (among-year) variance to mean ratios for pollinator abundance and richness for the native were roughly fourfold higher than for sulfur, and the spatial (among-site) variance to mean ratios were more than tenfold higher for the native, compared to sulfur (Table 3). Thus, it was much easier to predict both counts and species richness at any give time and place for sulfur cinquefoil, compared to the native. For example, despite equivalent sampling efforts at all sites each year, the native cinquefoil had very low abundance and richness of pollinators at the Foothill site, where sulfur cinquefoil dominated in percent cover (>90% sulfur), but very high abundance and richness of pollinators at the Morgan site, where the native dominated (90% native). In addition, the native pollinator fauna was roughly twice as abundant and three times as rich in 2003, as it was in the other two years (2002 and 2004). As a consequence, the invasive sulfur cinquefoil had a much more constant community of flower visitors over space and time compared to the native.

NMS ordination demonstrated few clear patterns of among-site, or between-cinquefoil species differences in pollinator communities. The most apparent pattern was the significant difference in community structure among survey years (Figure 3). The distinctiveness of the fauna in 2002 was represented best by Axis 2, with *C. nanula* (Apidae) and *L. sisymbrii* (Halictidae) having the highest correlations with Axis 2. The species that most indicated the position of the 2004 site samples, also correlated closely with Axis 2, were *Panurginus* sp. (Andrenidae) and *Coenonympha tullia* (Satyridae), followed by *Eristalis hirta* (Syrphidae), *Hylaeus episcopalis* (Hylaeidae), and *H. ligatus* (Halictidae). Axis 1 best separated 2003 as a distinctive year, and its strongest indicators were *E. hirta*, *L. olympiae*, *C. acantha*, and *H. farinosus* (Table 1).

Under field conditions of equal flower dominance, we were able to acquire preference data for nine taxa of pollinators (Table 4). Of these, only the European honeybee and two *Megachile* speices exhibited preference for sulfur cinquefoil (electivity index > 0), while two bee genera (five species) showed no preference (*Halictus, Bombus*), and 11 species in

Table 1: List of most commonly observed pollinator species (total abundance ≥ 5) for sulfur and native cinquefoils, ordered by abundance for each species, at four study sites in northeastern Oregon, 2002, 2003, and 2004. KEY to abbreviations: MO: Morgan Lake; FH: Foothill; RI: Rice; HH: Ham; NAT: Native Cinquefoil; SULF: Sulfur Cinquefoil.

Pollinator species	2002	2003	2004	MO	FH	RI	HH	TOT NAT
Panurginus sp. (UID)	0	27	68	11	0	15	69	95
Eristalis hirta	0	32	9	21	9	8	3	41
Ceratina nanula	40	1	0	0	0	2	39	41
Trichodes ornatus	16	6	10	2	0	23	7	32
Lasioglossum sp. (UID)	3	6	17	5	0	15	6	26
Lasioglossum olympiae	0	21	0	7	0	2	12	21
Halictus ligatus	7	8	5	5	0	1	14	20
Lasioglossum sisymbrii	17	0	0	3	0	2	12	17
Hylaeus episcopalis	0	11	4	7	0	7	1	15
Apis mellifera	0	11	3	1	5	0	8	14
Andrena sp. (UID)	0	11	3	8	1	5	0	14
Coenonympha tullia	0	5	8	1	0	5	7	13
Halictus tripartitus	1	11	0	4	0	1	7	12
Evylaeus sp. (UID)	0	11	0	9	0	0	2	11
Halictus sp. (UID)	1	7	2	0	0	2	8	10
Ceratina sp. (UID)	0	0	10	0	0	0	1	10
Colias sp. (UID)	7	0	0	0	0	0	7	7
Ceratina acantha	0	7	0	2	0	2	3	7
Bombus rufocinctus	0	7	0	3	1	2	1	7
Speyeria sp. (UID)	6	0	0	0	0	3	3	6
Osmia sp. (UID)	0	2	4	2	0	2	2	6
Halictus farinosus	1	5	0	2	2	2	0	6
Epicauta puncticolis	0	3	2	1	0	3	1	5
Total abundance	144	299	176	153	25	164	268	619
Total richness	48	133	55	56	13	51	54	93
Pollinator species	2002	2003	2004	MO	FH	RI	HH	TOT SULF
Apis mellifera	41	28	16	0	42	3	4	85
Lasioglossum sp. (UID)	19	1	18	4	6	2	8	38
Eristalis hirta	0	13	17	12	1	6	2	30
Ceratina nanula	24	1	0	5	8	3	9	25
Halictus tripartitus	15	5	5	9	5	7	4	25
Hylaeus episcopalis	0	9	12	9	0	7	5	21
Bombus bifarius	8	10	1	5	5	5	4	19
Lasioglossum sisymbrii	17	2	0	0	4	8	7	19
Ceratina sp. (UID)	0	7	10	9	0	0	8	17
Bombus rufocinctus	4	5	5	4	1	8	1	14
Halictus ligatus	1	1	12	1	7	3	3	14
Andrena prunorum	5	4	2	2	2	5	2	11
Panurginus sp. (UID)	0	2	8	4	5	0	1	10
Halictus sp. (UID)	1	0	8	0	6	1	2	9
Andrena sp. (UID)	0	3	5	4	0	4	0	8
Trichodes ornatus	6	0	1	1	0	5	1	7
Lasioglossum titusi	4	3	0	1	1	3	2	7
Megachile perihirta	2	2	3	2	1	2	2	7
Total abundance	222	164	157	107	144	127	102	543
Total richness	63	88	70	40	30	44	41	74

Table 2: Phenology of ten most commonly observed flower visitors of *Potentilla gracilis* (native) and *P. recta* (exotic), at four sites in Northeastern Oregon, 2002–2004.

Pollinator species	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31
			P. gracilis		
Coenonympha tullia	46.2	38.5	15.4		
Trichodes ornatus	12.5	37.5	40.6	9.4	
Panurginus sp.	10.5	62.1	25.3	2.1	
Halictus ligatus	4.8	42.9	52.4		
Ceratina nanula		97.6		2.4	
Lasioglossum olympiae		85.7	14.3		
Lasioglossum sisymbrii		76.5	23.5		
Eristalis hirta		70.7	14.6	14.6	
Apis melifera		50.0	42.9	7.1	
Hylaeus episcopalis		6.7	66.7	26.7	
			P. recta		
Halictus ligatus		42.9	21.4	28.6	7.1
Bombus rufocinctus		7.1		92.9	
Bombus bifarius		5.3	47.4	47.4	
Eristalis hirta		3.3	76.7	20.0	
Apis melifera		1.2	64.7	32.9	1.2
Lasioglossum sisymbrii			42.1	57.9	
Hylaeus episcopalis			38.1	61.9	
Andrena pronorum			36.4	63.6	
Halictus tripartitus			12.0	64.0	24.0
Ceratina nanula				72.0	28.0

Table 3: Summary data for pollinator surveys for sulfur and native cinquefoil at four sites in northeastern Oregon, 2002, 2003, and 2004.

Sulfur cinquefoil			Native cinquefoil		
Year	Mean abundance per site	Mean richness per site	Year	Mean abundance per site	Mean richness per site
2002	55.5	15.8	2002	36.0	12.0
2003	41.0	22.0	2003	74.8	33.3
2004	39.3	17.5	2004	44.0	13.8
Mean/Year	45.3	18.4	Mean/Year	51.6	19.7
Var	79.6	10.4	Var	418.5	139.1
Var/Mean	1.8	0.6	Var/Mean	8.1	7.1
Site	Mean abundance per year	Mean richness per year	Site	Mean abundance per year	Mean richness per year
Morgan	107	40	Morgan	153	56
Foothill	144	30	Foothill	25	13
Rice	127	44	Rice	164	51
Ham	102	41	Ham	268	54
Total	543	74	Total	619	93
Mean/Site	120.0	38.8	Mean/Site	152.5	43.5
Var	372.7	36.9	Var	9909.7	417.7
Var/Mean	3.1	1.0	Var/Mean	65.0	9.6

5 taxonomic groups demonstrated preference for the native (*C. nanula*; *Andrena*—2 spp; *Hylaeus*—2 spp, Syrphidae—3 spp, Coleoptera—3 spp). These data roughly correspond to survey data, when pollinator species are ordered in terms of relative abundance for each of the cinquefoil species (Table 1).

Estimates of percent sugar concentration in nectar were more than six-fold higher for sulfur cinquefoil than for

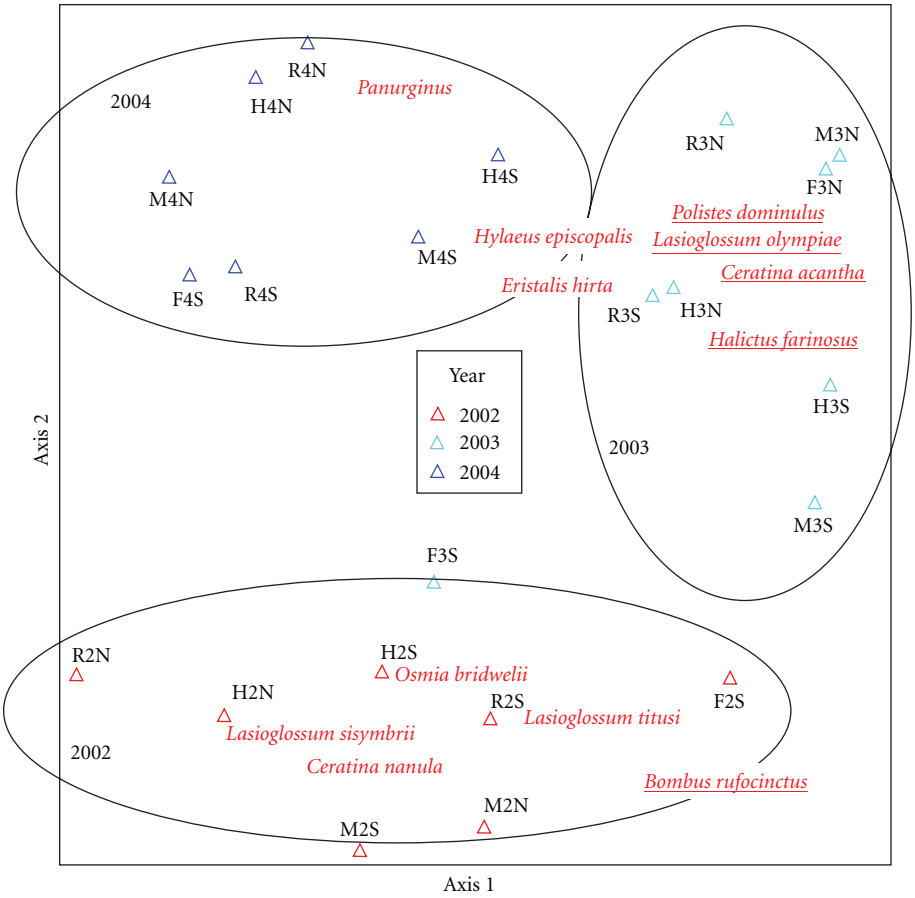


FIGURE 3: Ordination of sites by species for sulfur and slender cinquefoil pollinator communities at four sites in northeastern Oregon, 2002–2004. Key to sample acronyms (upright font): M = Morgan; F = Foothill; R = Rice; H = Ham; 2 = 2002; 3 = 2003; 4 = 2004; S = Sulfur; N = Native. Indicator species indicated in italicized font (Axis 2 correlates) and underlined font (Axis 1 correlates).

TABLE 4: Electivity indices for pollinator taxa under conditions of equal flower abundance. *R*: proportion of total pollinator population visiting plant sulfur cinquefoil; *P*: proportion of sulfur flowers among all cinquefoil flowers; *E*: electivity index = $(R_{\text{sulfur}} - P_{\text{sulfur}})/(R_{\text{sulfur}} + P_{\text{sulfur}})$.

Pollinator	Tot obs	No. of sulfur	No. of native	*R*	*P*	*E*
Apis mellifera	11	10	1	0.91	0.5	**0.29**
Megachile—2 spp.	5	4	1	0.80	0.5	**0.23**
Bombus—3 spp.	7	4	3	0.57	0.5	0.07
Halictus—3 spp.	21	9	12	0.43	0.5	−0.08
Andrena—2 spp.	13	3	10	0.23	0.5	**−0.37**
Ceratina nanula	19	4	15	0.21	0.5	**−0.41**
Hylaeus—2 spp.	5	1	4	0.20	0.5	**−0.43**
Syrphidae—3 spp.	6	1	5	0.17	0.5	**−0.50**
Coleoptera—3 spp.	10	0	10	0.00	0.5	**−1.00**

the native cinquefoil (59.0 ± 0.8 S.E. versus 9.6 ± 0.3 S.E.). These estimates correspond to observations indicating that honeybees were much more attracted to invasive flowers compared to the native.

When seed parameters are compared between the two species for the unmanipulated (open) treatment, several differences were observed. First, mean individual seed mass was significantly higher for the native compared to sulfur cinquefoil (0.207 mg mean seed mass ± 0.003 S.E. for the native, versus 0.172 mg ± 0.003 S.E. for sulfur), and these differences were consistent for both the Ham and Rice sites. Second, the native cinquefoil produced significantly fewer seeds per head than did sulfur (1202 seeds per head ± 103 S.E. for the native versus 1817 ± 104 S.E. for sulfur), although seed production by the native was significantly lower at the Rice site. Despite having significantly smaller

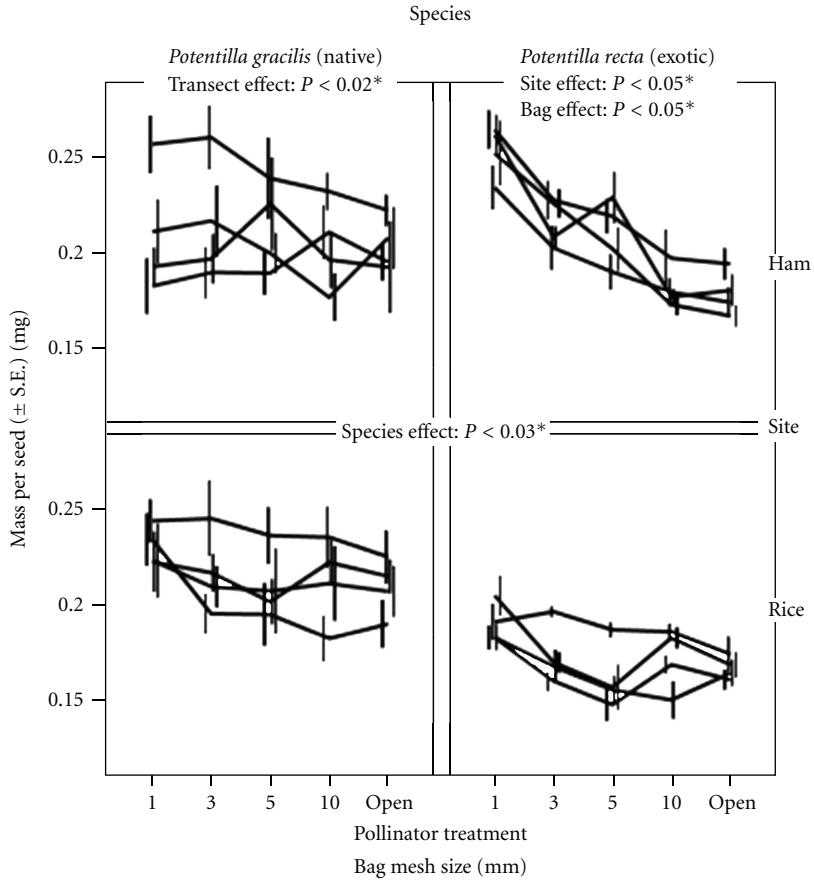


Figure 4: Mass per individual seed (mg) for *Potentilla gracilis* and *P. recta* seeds produced by flower heads exclosed by bags having mesh sizes designed to exclude various sizes of pollinators, along four transects at both Ham and Rice sites, northeastern Oregon, June-July 2003.

seeds, overall differences in seed number per head translated into significantly higher total seed mass per head for sulfur, compare to the native (0.31 g mass per head ± 0.02 S.E. for sulfur, versus 0.23 g ± 0.02 S.E. for the native). Once again however, native production was lower at the Rice site.

Pollinator exclusion at the Rice and Ham sites caused significant changes in seed parameters for both species of cinquefoils, but effects were much more pronounced for sulfur cinquefoil and were generally of greater magnitude at the Ham site. At both sites, sulfur cinquefoil plants produced progressively larger seeds as bag treatments became limiting to progressively smaller pollinators (Figure 4). This effect; however, was somewhat site-specific, with the Ham site exhibiting a more pronounced effect ($P < 0.0001$), compared to the Rice site ($P < 0.05$). This is reflected by the magnitude of increases in mean seed mass for sulfur cinquefoil between the open treatment and the most exclusive 1 mm bag treatment: at the Rice site, mean seed mass increased just 14% from 0.17 mg (± 0.003 S.E.) to 0.19 mg (± 0.004 S.E.), while at the Ham site, mean seed mass increased 41% from a mean of 0.18 mg (± 0.004 S.E.) to a mean of 0.25 mg (± 0.006 S.E.). For the native, mean seed mass did not generally increase with progressive decreases in bag mesh size, though at the Rice site, mean size mass increased slightly from 0.21 mg (± 0.004 S.E.) to 0.23 mg (± 0.008 S.E.). For the number of seeds per exclosed head, significant effects were observed only at the Ham site. For the native, although there was no significant bag effect overall for seed number, plants at the Ham site that had received the most exclusive bag treatment (1 mm) produced seed heads having significantly fewer seeds compared to the open treatment (928 seeds/head ± 85 S.E. versus 1538 ± 161 S.E.). For sulfur, the experimental results at the Ham site were also distinctively different than for the Rice site in terms of seed number per head. In particular, flower heads that were exclosed by the 1 mm bag produced only 1/2 of the total seeds per head compared to the open treatment (949 seeds/head ± 61 S.E. versus 1892 seeds/head ± 179 S.E.). In contrast, at the Rice site, plants of neither species responded significantly to treatments in terms of seed number per head. Overall however, for sulfur cinquefoil, the larger seeds observed in the 1 mm bag were produced at the expense of a significantly lower seed number per head, although this effect was much more pronounced at the Ham site. For total seed mass per head, effects were not obviously progressive when comparing all bag treatments, and also tended to vary with site, in much the same way as for the number of seeds per head. For the native, while there were no significant treatment effects on seed mass per head when all bag treatments were analyzed together, seed mass at the Ham site decreased significantly ($P < 0.01$) from 0.28 g per head (± 0.02 S.E.) in the open treatment to 0.18 g per head

(± 0.01 S.E.) for the 1 mm bag, representing a 36% decrease. At the Rice site; however, the decrease was only 9% and was not significant. For sulfur cinquefoil, once again seed mass per head decreased significantly only at the Ham site, from 0.33 g (± 0.03 S.E.) for the open treatment to 0.24 g (± 0.01 S.E.) for the 1 mm bag treatment, representing a 27% decrease; at the Rice site, both treatments produced a mean seed mass per head of 0.29 g. Finally, note that the among-site variation presented above was augmented by within-site variation, as reflected by the four transects located at each experimental site (Figure 4). In particular, note that variation among transects was substantial, both in mean seed mass, and in the pattern of response across treatments, especially for the native cinquefoil. Clearly, while pollinator exclusion had clear effects in some cases, the magnitude of spatial variation at two scales makes it risky to predict what might happen with a similar experiment at other sites.

There is no obvious explanation for the observed differences in treatment effects between the Rice and Ham sites. These two sites were similar in elevation, aspect, and general landscape conditions, and while seed productivity was much higher at Ham for the native, sulfur cinquefoil plants produced roughly similar seed numbers and seed mass at the two sites in the open condition. To assess whether the greater magnitude of effects at the Ham site could have been due to higher numbers of pollinators or a more diverse pollinator community there, we observed patterns of flower visitation during the experiment. These data indicate that site differences cannot be explained by either the number or community structure (Table 5) of pollinators that may have been excluded: the richness and species composition of pollinators observed at flowers of plants neighboring those that had received treatments were roughly similar for the Rice and Ham sites (Table 5), and there were actually more pollinators available at the Rice site compared to the Ham site, during the experiment. Moreover, if the more subtle effects of treatment at the Rice site was due to a lower level of pollinator service, we would expect that seed numbers and mass per head would be equally high for the open versus 1 mm bags, instead of equally low, as we observed. For example, at the Rice site, mean seed mass per head for the native in the open treatment was only 0.16 g (± 0.02 S.E.), compared to 0.28 g (± 0.02 S.E.) in the open condition at the Ham site. If differences in pollinator community structure or overall abundance were responsible for the lack of effect at Rice, then we would have expected both the open and 1 mm treatment to have seed mass equally high, and more similar to the Ham site. Clearly, some other factor or set of factors was responsible for the difference in treatment effects between the Rice and Ham sites.

When other aspects of seed biology for the two plant species was compared, there were three distinct differences observed. First, the proportion of buds within which evidence of seed predation was observed was 0.22 for the native, compared to just 0.01 for the invasive (Table 6). Second, the invasive *P. recta* invested proportionally greater resources in seed production compared to the native cinquefoil, with total seed mass per head three times that observed for the native (Figure 5). Third, less than 20% of native cinquefoil

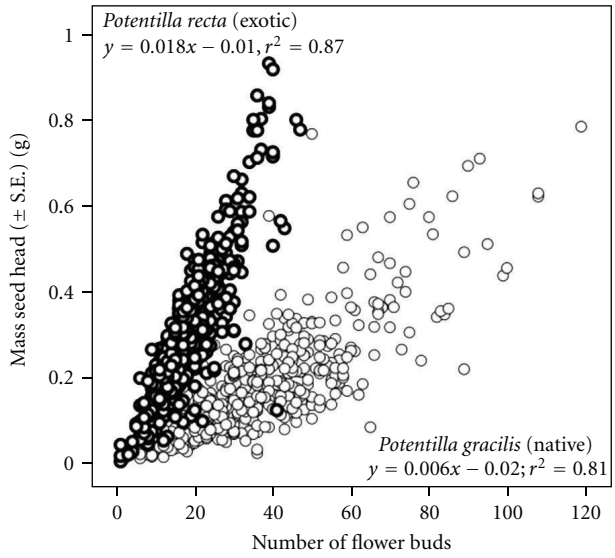


Figure 5: Mass of seed head (grams) as function of the number of buds in a head for *Potentilla gracilis* (native) and *P. recta* (invasive), at Rice and Ham sites, northeastern Oregon, June-July, 2003.

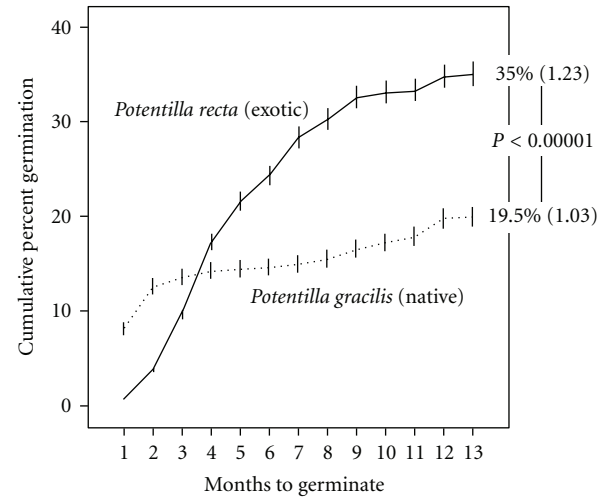


Figure 6: Cumulative percent germination by month for *Potentilla gracilis* (native) and *P. recta* (invasive), from seeds collected from plants at Ham and Rice sites, northeastern OR, July 2003–June 2004.

seeds germinated, and most germination occurred within two months after wetting, while 35% of sulfur cinquefoil seeds germinated, with germination occurring consistently for more than eight months after wetting (Figure 6). Finally, none of these germination parameters were significantly influenced by the pollinator exclusion treatment.

4. Discussion

Collectively, the flowers of cinquefoil attracted 111 insect species at four sites in northeast Oregon, but just 26 insect species comprised roughly 70% of total flower visitors observed. Although "pollinator quality" cannot be conclusively demonstrated in terms of plant fitness after Herrera [27], judging by the combination of relative abundance and

Table 5: List of pollinator species observed more than once, in order of abundance, for the 2003 flowering season at Ham and Rice sites, at *Potentilla recta* (exotic) and *Potentilla gracilis* (native) flowers, throughout the duration of the pollinator exclusion experiment conducted at these two sites, in June and early July 2003. Bold face refers to large bodied individuals, underline refers to medium bodied individuals, and light face refers to small bodied individuals.

Pollinator species	Rice native	Pollinator species	Ham native
Hylaeus episcopalis	6	*Panurginus sp.*	23
Lasioglossum sp.	5	*Lasioglossum olympiae*	12
Trichodes ornatus	4	*Halictus ligatus*	7
Eristalis hirta	4	*Halictus tripartitus*	7
Panurginus sp.	2	*Halictus sp.*	7
Lasioglossum olympiae	2	*Apis melifera*	6
Bombus rufocinctus	2	Bombyliidae 2	6
Andrena sp.	2	*Eristalis hirta*	3
Ceratina acantha	2	***Coenonympha tullia***	3
Andrena candida	2	*Ceratina acantha*	3
Bombyliidae UID	2	*Osmia sp. A*	3
Halictus farinosus	2	*Andrena augustitarsata*	2
Chlosyne paulla	2	***Aporinellus yucatanchsis***	2
Pollenia pseudorudis	2	*Lasioglossum (Evylaeus)*	2
		Melissodes bimatris	2
17 species Seen Once	17	20 Species seen once	20
Total richness	31	Total richness	35
Total abundance	56	Total abundance	108
Pollinator species	Rice sulfur	Pollinator species	Ham sulfur
Hylaeus episcopalis	6	*Apis melifera*	27
Eristalis hirta	6	*Hylaeus episcopalis*	3
Bombus rufocinctus	2	***Bombus bifarius***	3
Bombus bifarius	2	*Eristalis hirta*	2
Andrena sp.	2	*Andrena candida*	2
Andrena prunorum	2	*Colletes sp.*	2
Ceratina acantha	2	*Osmia pusilla*	2
Megachile perhirta	2	*Andrena thaspii*	2
14 species seen once	14	16 Species seen once	16
Total richness	22	Total richness	25
Total abundance	38	Total abundance	84

the presence of cinquefoil pollen on their bodies, perhaps just seven species performed most of the pollination service during the three-year study period. Although two abundant insect species served both species of flowers (the apid *C. nanula* and the halictid *L. sisymbrii*), the European honey bee was clearly the dominant pollinator in the mix, but only for the invasive sulfur cinquefoil. Moreover, the consistent dominance of the honey bee as the principle pollinator for sulfur cinquefoil was a primary factor explaining the much higher constancy of flower visitation by potential pollinators for sulfur cinquefoil than for its native congener.

Compared to most other studies, our collection of potential pollinators was very diverse. For example, we collected 60 species of bees over the three-year study period, compared to an average of just 19.6 (± 2.5 S.E.) species of bees in pollinator surveys of single species of plants [28]. Two of these studies are worth noting here. Richards [29] found a total of only 24 species (mostly *Megachile* and *Bombus* spp.) visiting cicer milkvetch (*Astragalus cicer* L.: Fabaceae) in southern Alberta, Canada, in a similar landscape setting, with a similar sampling effort, and over a similar time period (1978 to 1981). Richards and Edwards [30] found that just six species of bees (alfalfa leafcutting bee, honey bee, and four species of *Bombus*) served as pollinators of the forage legume sainfoin (*Onobrychis viciaefolia* Scop.) in southern Alberta from June to August 1986. Interestingly, sainfoin flower-handling time was inversely correlated with pollinator body size, with bumble bees able to extract nectar at a higher rate than honey bees or leafcutting bees, and thus it is possible that glossa length, which is also correlated with body size [31], might determine whether an individual bee can successfully extract nectar from zygomorphic flowers like legumes. However, nectar within simple, open flowers like cinquefoils, can be extracted by a wide variety of insect species, including not only bees, but flies, beetles, butterflies, and wasps. The only study we could find that reported a

Table 6: Proportion of cinquefoil buds ($N = 10$) within which evidence of insect activity was observed, for 15 paired samples of *Potentilla gracilis* and *P. recta*, at Ham and Rice sites, June, 2004.

Pair no.	Site	Species	Prop. buds infested	Type of insect activity	Species	Prop. buds infested	Type of insect activity
1	Ham	*P. gracilils*	0.1	Lepidoptera exuvia	*P. recta*	0	
1	Rice	*P. gracilils*	0.4	Diptera pupae	*P. recta*	0	
2	Ham	*P. gracilils*	0.0		*P. recta*	0	
2	Rice	*P. gracilils*	0.1	Diptera pupa	*P. recta*	0	
3	Ham	*P. gracilils*	0.1	Diptera pupa	*P. recta*	0	
3	Rice	*P. gracilils*	0.0		*P. recta*	0.1	Diptera pupa
4	Ham	*P. gracilils*	0.0		*P. recta*	0	
4	Rice	*P. gracilils*	0.2	Excrement	*P. recta*	0	
5	Ham	*P. gracilils*	0.1	Unknown insect parts	*P. recta*	0	
5	Rice	*P. gracilils*	0.2	Diptera pupae	*P. recta*	0	
6	Ham	*P. gracilils*	0.0		*P. recta*	0	
6	Rice	*P. gracilils*	0.1	Unknown insect parts	*P. recta*	0	
7	Ham	*P. gracilils*	0.0		*P. recta*	0	
7	Rice	*P. gracilils*	0.5	Unknown insect parts, Diptera pupae	*P. recta*	0	
8	Ham	*P. gracilils*	0.0		*P. recta*	0	
8	Rice	*P. gracilils*	0.4	Unknown insect parts, Diptera pupae	*P. recta*	0	
9	Ham	*P. gracilils*	0.1	Unknown insect parts	*P. recta*	0	
9	Rice	*P. gracilils*	0.7	Unknown insect parts, Diptera pupae	*P. recta*	0	
10	Ham	*P. gracilils*	0.2	Unknown insect parts	*P. recta*	0	
10	Rice	*P. gracilils*	0.6	Unknown insect parts, Diptera pupae	*P. recta*	0	
11	Ham	*P. gracilils*	0.2	Unknown insect parts	*P. recta*	0	
11	Rice	*P. gracilils*	0.4	Unknown insect parts, Diptera pupae	*P. recta*	0	
12	Ham	*P. gracilils*	0.0		*P. recta*	0	
12	Rice	*P. gracilils*	0.5	Unknown insect parts	*P. recta*	0	
13	Ham	*P. gracilils*	0.0		*P. recta*	0	
13	Rice	*P. gracilils*	0.6	Unknown insect parts, Diptera pupae	*P. recta*	0	
14	Ham	*P. gracilils*	0.0		*P. recta*	0.1	Diptera pupa
14	Rice	*P. gracilils*	0.7	Unknown insect parts, Diptera pupae	*P. recta*	0	
15	Ham	*P. gracilils*	0.1	Unknown insect parts	*P. recta*	0	
15	Rice	*P. gracilils*	0.2	Unknown insect parts, Diptera pupae	*P. recta*	0.1	Diptera pupa
Mean proportion		*P. gracilils*	0.22		*P. recta*	0.01	

more diverse pollinator fauna was our own study on the flower visitors of the invasive plant yellow starthistle (*Centaurea solstitialis* L.: Asteraceae), also conducted in northeast Oregon [32], over a similar time period (2000–2002). In that study, flowers of starthistle attracted 1923 individuals and an astonishing 203 species of insects, including 87 species of bees. Compared to the present study, this is 84% more individuals, 83% more total species, and 45% more bee species, observed with a similar sampling effort. The flowers of yellow starthistle are also relatively easy to access, and are also well known to produce copious quantities of rich nectar [33], so it is likely that the combination of rich nectar and easy access explains to a large extent the richness and abundance of the pollinator fauna of yellow starthistle.

It is interesting that between 2002 and 2004, the dominant pollinator of sulfur cinquefoil in northeastern Oregon was likely to be the European honey bee. This observation lends support to the idea that sulfur cinquefoil, like yellow starthistle [11], is part of an "invasive mutualism", in which the pollinator and the plant benefit from their relationship

Table 7: List of species observed visiting flowers of native (*Potentialla gracilis*) and sulfur (*Potentilla recta*) cinquefoil species at four sites in northeastern Oregon, 2002, 2003, and 2004. Site Codes: MO: Morgan Lake; FH: Foothill; RI: Rice; HH: Hamburger Hill.

Order/Family/Species	Native																	Sulfur															
	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT NAT	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT SULF
Coleoptera	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Buprestidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Cerambycidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Cerambycidae 1	0	2	0	0	0	0	0	0	0	0	0	1	2	0	0	1	**3**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Cerambycidae 2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	0	0	0	0	1	1	1	0	2	0	0	0	3	2	**5**
Chrysomelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Chrysochus cobaltinus	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Chrysomelidae 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	2	0	0	0	1	0	0	1	0	0	0	2	1	1	0	**4**
Cleridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Trichodes ornatus	1	1	0	0	0	0	13	4	6	2	1	4	2	0	23	7	**32**	0	0	1	0	0	0	5	0	0	1	0	0	1	0	5	1	**7**
Meloidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Epicauta oregana	0	0	0	0	0	0	0	1	3	0	0	0	0	0	4	0	**4**	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	**2**
Epicauta puncticolis	0	1	0	0	0	0	0	1	2	0	1	0	1	0	3	1	**5**	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	**2**
Lytta morenes	0	0	0	0	0	0	2	1	0	0	0	0	0	0	3	0	**3**	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	**2**
Coleoptera 1	0	1	0	0	0	0	0	2	5	0	0	0	1	0	7	0	**8**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Asilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Geron argatus	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	**3**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Bombyliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Anastoechus barbatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	1	0	0	0	0	0	2	0	0	0	1	0	2	0	**3**
10 Unidentified Spp.	1	0	0	0	0	0	2	2	0	3	7	0	1	0	4	1	**15**	0	1	1	4	2	0	1	1	1	6	1	2	2	6	12	9	**29**
Calliphoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Pollenia pseudorudis	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Nemestrinidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Sarcophagidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Blaesoxipha sp.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	**2**	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	**2**
Sarcophagidae 1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Syrphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Chrysotoxum fasciatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**
Eristalis hirta	0	17	4	0	8	1	0	4	4	0	3	0	21	9	8	3	**41**	0	0	12	0	5	5	0	6	0	0	2	0	12	1	6	2	**30**
Parasyrphus relictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	**2**
Platycheirus obscurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	**1**
Spaerophoria sulphuripes	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	**3**	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	**2**
Syrphus opinator	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	**2**
6 Unidentified Spp.	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	**2**	0	2	0	17	4	0	2	0	0	0	1	0	2	21	2	1	**26**
Tabanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
4 Unidentified Spp.	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	**2**	0	0	0	3	0	0	1	0	0	0	0	0	0	3	1	0	**4**

Table 7: Continued.

Order/Family/Species	Native																	Sulfur															
	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT NAT	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT SULF
Tachinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Peleteria malleola	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Tachinidae 1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Diptera 1	0	4	2	0	3	0	0	0	5	0	1	4	6	3	5	5	**19**	0	0	0	0	0	3	0	0	0	0	0	1	0	3	0	1	**4**
Heteroptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Miridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Irbisia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**
Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrena augustitarsata	0	2	0	0	0	0	0	0	0	0	2	0	2	0	0	2	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrena candida	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	**2**	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	**2**
Andrena miranda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**
Andrena nigrocaerulea	0	3	0	0	0	0	0	1	0	0	0	0	3	0	1	0	**4**	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	**2**
Andrena pensilis	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrena prunorum	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	**3**	0	1	1	2	0	0	3	2	0	0	1	1	2	2	5	2	**11**
Andrena quintiliformis	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrena scurra	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	**1**	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	**2**
Andrena thaspii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	2	**0**
Andrena sp. 1	0	8	0	0	1	0	0	2	3	0	0	0	8	1	5	0	**14**	0	1	3	0	0	0	0	2	2	0	0	0	4	0	4	0	**8**
Andrena sp. 2	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	**3**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**
Andrena sp. 3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Andrena sp. 4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Panurginus sp.	0	2	9	0	0	0	0	2	13	0	23	46	11	0	15	69	**95**	0	2	2	0	0	5	0	0	0	0	0	1	4	5	0	1	**10**
Apidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Anthophora urbana	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	**2**	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	**2**
Apis melifera	0	0	1	0	5	0	0	0	0	0	6	2	1	5	0	8	**14**	0	0	0	29	0	13	2	1	0	1	27	3	0	42	3	4	**76**
Bombus bifarius	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	5	0	4	0	1	3	2	0	1	3	0	5	5	5	4	**19**
Bombus californicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	**0**
Bombus huntii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Bombus insularis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	**2**
Bombus nevadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	3	0	0	1	0	0	0	0	0	0	3	1	0	**4**
Bombus rufocinctus	0	3	0	0	1	0	0	2	0	0	1	0	3	1	2	1	**7**	0	2	2	1	0	0	3	2	3	0	1	0	4	1	8	1	**14**
Ceratina acantha	0	2	0	0	0	0	0	2	0	0	3	0	2	0	2	3	**7**	0	1	0	0	0	0	0	2	0	0	1	0	1	0	2	1	**4**
Ceratina nanula	0	0	0	0	0	0	1	1	0	39	0	0	0	0	2	39	**41**	4	1	0	8	0	0	3	0	0	9	0	0	5	8	3	9	**25**
Ceratina sequoiae	3	0	0	0	0	0	1	0	0	0	0	0	3	0	1	0	**4**	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**
Ceratina sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	**1**	0	7	2	0	0	0	0	0	0	0	0	8	9	0	0	8	**17**
Melissodes bimatris	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Melissodes lutulenta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	**5**
Melissodes sp. 1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	**2**	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	**1**

Table 7: Continued.

Order/Family/Species	Native																	Sulfur															
	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT NAT	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT SULF
Chrysididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Chrysididae 1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Colletidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Colletes gypscolenes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	**1**
Colletes simulans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**
Colletes sp. 1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	**2**	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	**2**
Hylaeinae	2	2	0	0	0	0	0	0	0	0	0	0	4	0	0	0	**4**	1	0	0	4	0	0	5	0	0	0	0	0	1	4	5	0	**10**
Hylaeus episcopalis	0	5	2	0	0	0	0	6	1	0	0	1	7	0	7	1	**15**	0	0	9	0	0	0	0	6	1	0	3	2	9	0	7	5	**21**
Hylaeus nunemacheri	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Crabronidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Crabronidae 1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Eumenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Eumenidae 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	**2**
Halictidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Agapostemon virescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	**2**
Halictus farinosus	1	1	0	0	2	0	0	2	0	0	0	0	2	2	2	0	**6**	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	**2**
Halictus ligatus	0	1	4	0	0	0	0	0	1	7	7	0	5	0	1	14	**20**	0	0	1	0	0	7	0	0	3	1	1	1	1	7	3	3	**14**
Halictus sp.	0	0	0	0	0	0	0	0	2	1	7	0	0	0	2	8	**10**	0	0	0	0	0	6	1	0	0	0	0	2	0	6	1	2	**9**
Halictus tripartitus	1	3	0	0	0	0	0	1	0	0	7	0	4	0	1	7	**0**	2	3	4	5	0	0	5	1	1	3	1	0	9	5	7	4	**0**
Lasioglossum olympiae	0	7	0	0	0	0	0	2	0	0	12	0	7	0	2	12	**0**	0	2	0	0	0	0	0	1	0	0	0	0	2	0	1	0	**4**
Lasioglossum sisymbrii	3	0	0	0	0	0	2	0	0	12	0	0	3	0	2	12	**0**	0	0	0	2	2	0	8	0	0	7	0	0	0	4	8	7	**0**
Lasioglossum titusi	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**32**	1	0	0	0	1	0	2	1	0	1	1	0	1	1	3	2	**7**
Lasioglossum (Dialictus)	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Lasioglossum (Evylaeus)	0	9	0	0	0	0	0	0	0	0	2	0	9	0	0	2	**4**	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**2**
Lasioglossum sp. 1	0	1	4	0	0	0	3	5	7	0	0	6	5	0	15	6	**8**	1	0	3	4	1	1	9	0	11	5	0	3	4	6	2	8	**0**
Sphecodes sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Ichnuemonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Ichnuemonid 1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Megachillidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Hoplitis sp.	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	**2**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**
Hoplitis albifrons	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Megachile brevis	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Megachile melanophaea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Megachile perihirta	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**	0	0	2	1	0	0	0	2	0	1	0	1	2	1	2	2	**7**
Megachile sp. 1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**
Osmia atrocyanea	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Osmia bridwelii	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	**0**	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	**0**
Osmia coloradensis	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	**2**	0	0	0	1	0	0	3	0	0	0	0	0	0	1	3	0	**4**
Osmia marginipennis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Osmia pusilla	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	**2**
Osmia (Chenosmia)	0	2	0	0	0	0	0	0	1	0	0	1	2	0	1	1	**4**	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**

Table 7: Continued.

Order/Family/Species	Native																		Sulfur															
	MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT NAT		MO '02	MO '03	MO '04	FH '02	FH '03	FH '04	RI '02	RI '03	RI '04	HH '02	HH '03	HH '04	MO TOT	FH TOT	RI TOT	HH TOT	TOT SULF
Osmia sp. 1	0	0	2	0	0	0	0	1	1	0	1	1	2	0	2	2	**6**		0	0	2	0	0	0	0	1	0	0	0	1	2	0	1	1	**4**
Osmia sp. 2	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	**3**		0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**
Pompilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Aporinellus yucatanchsis	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	**2**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Sphecidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Sphex pensylvanicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	**7**
Sphecidae sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Vespidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Polistes dominulus	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	**2**		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**
Stenodynerus canus	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Vespula germanica	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	**2**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Vespula pennsylvanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	**1**
Hymenoptera 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	**3**
Hymenoptera 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	**1**
Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Hesperiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Icaricia acmon	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	**1**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Lycaenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Plebejus saepiolus	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**		2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	**3**
Lycaenidae 1	3	0	0	0	0	0	8	0	0	2	0	1	3	0	8	3	**14**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Nymphalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Chlosyne paulla	1	0	0	0	0	0	0	2	0	0	0	0	1	0	2	0	**3**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Speyeria sp.	0	0	0	0	0	0	3	0	0	3	0	0	0	0	3	3	**6**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Pieridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Colias sp.	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	7	**7**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Satyridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Coenonympha tullia	0	1	0	0	0	0	0	1	4	0	3	4	1	0	5	7	**13**		0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	**2**
Lepidoptera 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**1**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Lepidoptera 2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	**2**		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**

in an exotic location. For sulfur cinquefoil however, it is clear that a host of native insect species offer pollination service, and thus contribute to its success as an invading species. In particular, even though honeybees dominated the pollinator fauna of sulfur cinquefoil, more than 80% of flower visiting individuals were native, including more than 70 native insect species, and 46 native species of bees. Overall, the importance of native pollinators to sulfur cinquefoil indicate that this invasive is well-integrated into the ecosystem of northeastern Oregon. Moreover, although populations of sulfur cinquefoil flower for only about 45% as much time as do populations of yellow starthistle [32], this invasive cinquefoil, like starthistle, is likely to play an important role in the life histories of at least some native insect flower-visiting species.

Pollinator community constancy, reflected by temporal and spatial variance to mean ratios, was much higher for sulfur cinquefoil than for its native congener. Much of the temporal and spatial variation in flower visitors of the native cinquefoil was due to highly variable counts of some of the common bee species that frequented the native, particularly species of the smaller-bodied apid genera *Ceratina* and *Panurginus* and species of the halictid genus *Lasioglossum*. It is widely known through longer term monitoring work, that bee species such as these typically experience wide fluctuations in abundance from year to year, and from site to site within years [34, 35]. Williams et al. [28] highlighted data from several studies demonstrating that the number of "singletons" (just one observation of a species in a given study), coupled with the magnitude of spatial and temporal variation in native bee count data at the species level is typically so high that sampling efforts must be very robust to capture meaningful shifts in actual population numbers over time. However, this does not explain why sulfur cinquefoil did not tend to be serviced by so many highly variable native species during the study period, but rather tended to attract species belonging to populations that experienced much less temporal and spatial variation. In any case, this observation suggests that sulfur cinquefoil attracts a very stable pollinator fauna where it occurs in northeastern Oregon and did not seem to be limited by pollination service at any site or at any time during the study period.

Our evidence suggests that while most native insect species do not prefer sulfur cinquefoil relative to its native congener, the invasive may be a partner in an "invasive mutualism", together with the European honey bee. The honey bee was by far the most common insect observed at flowers of sulfur cinquefoil during the study period, and clearly preferred the invasive when flowers of the two cinquefoils were of equal abundance. These data are supported by the work of Barthell et al. [11], working with yellow starthistle, in which the honey bee has been implicated as an important partner in the establishment and spread of that invasive in California. Although sulfur cinquefoil can clearly reproduce by selfing (unlike yellow starthistle), the distinct response of plants to pollinator exclusion suggests that there may be a fitness consequence of selfing. In any case, this relationship of sulfur to the honey bee, and the fact that native bees, flies, and beetles did not clearly prefer sulfur cinquefoil, but visited it in accordance with its relative abundance, is consistent with observations in other systems [36, 37]. In terms of mechanisms that may explain our data on preference, it is possible that the higher sugar concentration of nectar in sulfur cinquefoil served as an attractant to honey bees. However, other qualities of nectar that we did not measure, including the ratio of sucrose to hexose [38, 39], and the presence of key amino acids [40] may be attractants as well, and may be more important for explaining why native pollinators in northeastern Oregon do not generally prefer sulfur over its native congener.

Pollinator exclusion produced a greater response in seed parameters in the invasive sulfur cinquefoil, compared to the native slender cinquefoil. The most pronounced effect was that mean seed size increased with increasingly aggressive exclusion of pollinators, at the expense of a lower seed number as pollinator exclusion became more pronounced. This supports the finding of Werner and Soule [12], who worked on the biology of sulfur cinquefoil in Michigan. However, while mean seed mass under exclosed conditions increased by only 30% in our study (two sites combined), mean mass increased by 60% in the Michigan study. The difference between the studies was even more pronounced with seed number: in northeastern Oregon, flowers produced 68% as many seeds as did open flowers, compared to just 13% for the study by Werner and Soule [12]. It seems that the kind of variation observed within and between sites in northeastern Oregon is also present when this species is studied at other geographically distant sites. Actually, variation of this kind may be more the rule than the exception, as other studies have reported similar variation and inferred its adaptive significance. For example, Kasagi and Kudo [41] reported substantial temporal variation in self-compatibility in *Phyllodoce aleutica* (Ericaceae), with high self-compatibility corresponding with periods of pollinator limitation. Werner and Soule [12] did not discuss whether the production of larger seeds had any adaptive significance for sulfur cinquefoil, or whether seed size increase is merely a consequence of a change in the rate of seed production, induced by the lack of pollen at a critical time in development. In any case, we observed no difference in germination rate for the larger seeds produced in the bagged treatment. Additional research on the fate of fertilized seedlings, versus those produced by selfing, would be needed to establish the conditions under which selfing might be advantageous.

Compared to pollinator exclusion studies on more self-incompatible plant species (e.g., yellow starthistle; [11]), the magnitude of our results were subtle. Yellow starthistle responded to pollinator exclusion by producing very few seeds in the exclosed condition, lending support to the idea that pollinators such as honey bees are indeed "invasive mutualists" and tend to facilitate invasion of some exotic species. While it is clear that sulfur cinquefoil can produce viable seeds without fertilization, it is interesting nonetheless that this invasive species is markedly more responsive to pollinator exclusion than is its native congener.

In terms of seed biology, we observed three differences between sulfur cinquefoil and its native congener: for sulfur, the general lack of evidence of seed predation, the greater

allocation to seed production relative to vegetative biomass, and a much more prolonged germination sequence, lasting nearly a year. First, one of the best documented observations on invasive species is the lack of effective natural enemies in the first decades of invasion [42]. Our observations on seed predation support the idea that native seed predators have not had sufficient time to adapt to the smaller sulfur cinquefoil seeds since introduction occurred a little more than 100 years ago. Indeed, although we did not establish a causal connection between the magnitude of seed predation and germination rates, it is noteworthy that proportionally nearly twice as many sulfur seeds germinated as did the native. Second, sulfur cinquefoil dedicated three times as much energy to reproduction each year during the three-year study period as did the native cinquefoil. It has long been observed that ruderal plant species tend to allocate proportionally greater resources to reproduction, even under relatively stressful environmental conditions [43, 44]. This strategy seems to balance the increased risk of mortality in the parent, with the increased opportunity for survival of the offspring. Similarly, the much longer germination "window" observed in sulfur cinquefoil, relative to the native, may be a strategy for retaining opportunity to take advantage of disturbed habitats over a longer period of time. Sulfur cinquefoil is highly successful at "filling in" suitable habitat once it arrives on the scene [45]. A longer germination window may be one mechanism this invasive species uses to gradually occupy an area once it colonizes. The native cinquefoil species on the other hand, can only respond to disturbance in a previously colonized area within a short period of time each year (~2 months), and thus may be at a competitive disadvantage over the long run, where it cooccurs with sulfur cinquefoil.

In general, our comparative data indicate that the invasive sulfur cinquefoil and the native slender cinquefoil employ different adaptive strategies, with the invasive using more of a "ruderal" strategy, as opposed to a "stress-tolerant" strategy used by the native [44]. Sulfur cinquefoil is clearly preferred as a nectar source by honey bees, utilizes a suite of native pollinators as well, invests relatively more energy in seed production, and enhances its chances to seize opportunities for disturbed conditions over a much longer period of time relative to the native cinquefoil. While our observations underline key differences in life history between sulfur cinquefoil and its native congener, additional work is required to understand exactly how these differences may translate into fitness differentials in the long run.

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