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ARTICLE

An assessment of the potential for pollination facilitation of a rare plant by common plants: *Symphyotrichum sericeum* (Asteraceae) as a case study

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Abstract: Pollination facilitation can occur when plant species share pollinators. Whether facilitation occurs depends on the flowering period overlap (synchrony), number of shared insect visitors (similarity), quantity and quality of insect visits, and the subsequent impact on seed production. Western Silvery Aster (*Symphyotrichum sericeum* (Vent.) G.L. Nesom) is a rare, self-incompatible plant visited by a wide range of generalist insect species. There are 22 common plant species that may facilitate insect visitation to the rare plant by supporting shared pollinators. Plant species with low synchrony and high similarity with *S. sericeum* are potential facilitators. In contrast, plant species with high synchrony and similarity likely act as competitors as the aggregative response to increasing plant density was saturating, suggesting that synchronously flowering species do not increase insect visitations. Hymenoptera responded more strongly than Diptera to increases in flowering stem density. These data suggest that facilitation of insect visitation between plant species via a numerical response that extends the flower season is possible but not likely via an aggregative response. Restoration of *S. sericeum* may therefore be more successful if potentially facilitating plants are grown with it; further testing of the impact of potential facilitators on seed production in *S. sericeum* is required.

Key words: facilitation, insect visitation, pollination, sequential mutualism.

Résumé : La pollinisation peut être facilitée lorsque des plantes partagent leurs pollinisateurs. L'expression de cette facilitation dépend de la période de recouvrement (synchronie), du nombre d'insectes visiteurs partagés, de la qualité et de la quantité des visites par les insectes et de l'impact subséquent sur la production de semences. L'aster argenté de l'ouest (Symphyotrichum sericeum (Vent.) Nesom est une plante rare autocompatible visitée par une large gamme d'espèces d'insectes généralistes. Il y a 22 espèces de plantes pouvant faciliter la visite des insectes cette plante rare en supportant une pollinisation partagée. La faible synchronisation des espèces de plantes et la grande similitude avec le *S. sericeum* pourraient faciliter la pollinisation. Au contraire, les espèces de plantes montrant de fortes synchronisations et similarités sont susceptibles d'agir comme des compétiteurs puisque la réaction agrégative pour augmenter la densité des plantes se trouve saturante, suggérant que les plantes à floraisons synchrones n'augmentent pas les visites des insectes. Les hyménoptères réagissent plus fortement que les diptères dans l'augmentation de la densité des tiges forales. Ces données suggèrent que la facilitation des visites d'insectes entre les espèces de plantes via une réaction numérique étalant la saison de floraison est possible, mais peu susceptible de survenir via une réaction agrégation. La restauration du *S. sericeum* pourrait conséquemment être plus efficace si des plantes capables de facilitation sont cultivées avec elle; on doit conduire d'autres essais sur l'impact des facilitateurs potentiels pour la production des gaines chez le *S. Sericeum*. [Traduit par la Rédaction]

Mots-clés : facilitation, visite des insectes, pollinisation, mutualisme séquentiel.

Introduction

Much of pollination research has focused on how plants compete with each other for the attention of pollinators (Levin and Anderson 1970; Knight et al. 2005). Less studied is the question of whether plants facilitate the persistence of other plant species via their mutual support of the same pollinators (Sargent and Ackerly 2008; Bruno et al. 2003). In fact, the possibility that facilitation and competition are simultaneously occurring has been suggested (Callaway and Walker 1997). One potential mechanism for facilitation is via a numerical response where populations of pollinators grow disproportionately larger when two plant species co-occur, via extension of the flowering season (Feldman 2006). Pollinators that are active throughout the flowering season, such as bumblebees (*Bombus* spp.) and hummingbirds, would be affected more positively by sequential flowering than species that complete their life cycles in a shorter period of time (Moeller 2004; Waser and Real 1979). Indeed, food shortages during droughts were found to negatively affect the abundance of bum-

blebees in mixed-grass prairie (Hobbs 1966). Waser and Real (1979), and Moeller (2004) presented evidence that plant species sharing pollinators can facilitate each other's persistence by flowering sequentially.

Another potential mechanism is an aggregative response that occurs when plants that share pollinators facilitate each other's visitation by increasing the floral density (Rathcke 1983; Feldman 2006). Facilitation among plant species sharing pollinators may occur at low densities as larger floral displays attract more insects, and competition may occur at higher densities (Rathcke 1983). Evidence for a facilitative effect would consist of a sigmoid, rather than a saturating or linear visitation response curve as flower density increases (Feldman et al. 2004). Data confirming this hypothesis is still lacking; Feldman (2006) found no evidence supporting this mechanism.

Symphyotrichum sericeum (Vent.) G.L. Nesom (Asteraceae) is a rare, protected vascular plant in Canada, as it is found only in the tallgrass prairies of southern Manitoba and western Ontario

(COSEWIC in press). *Symphyotrichum sericeum* is also rare in several northern and eastern US states (NatureServe 2010). It is restricted to areas of sandy and gravelly soil, which are being mined for road building and construction materials, resulting in habitat loss. Where it occurs it tends to be relatively sparse as opposed to locally abundant. In Canada, *S. sericeum* normally flowers from mid-August to mid-September. The insect visitors to this species, inability to self-pollinate, and presence of seed predators have already been documented in studies conducted in Manitoba (Robson 2010a, 2010b). Competition for some insect visitors between *S. sericeum* and *Solidago nemoralis* Ait. var. *longipetiolata* (Mack. & Bush) Pal. & Steyerm. (Asteraceae) was demonstrated (Robson 2010a). However, this competition was strongest during the period of highest synchrony and then largely disappeared when *S. sericeum* reached its flowering peak and the number of receptive *Solidago nemoralis* flowers declined (Robson 2010a). These results suggest that sequential flowering in this plant community reduced the competition for pollinators that would otherwise have occurred if both plants reached their flowering peaks at exactly the same time. However, the impact that plant species other than *Solidago nemoralis* have on *S. sericeum* was not examined.

Because it is unlikely that the generalist insect taxa visiting *S. sericeum* started becoming active at the precise time that it began flowering, I hypothesized that some of the insects were feeding on the pollen and (or) nectar of other plant species earlier in the year. If a link between rare and common plants via mutual insect visitors can be demonstrated, and if these plant species flower at different times during the season, a facilitative relationship via a numerical response may be occurring. The identification of facilitating plant species and insect taxa is important because conserving the rare plant would then require the conservation of a wider variety of organisms as well. This knowledge would also prove useful for habitat restoration of the rare plant. Plant species that support pollinators of the rare plant at a different time of the year would need to be grown along with it to increase the likelihood that their shared pollinators are attracted to, and adequately sustained by, the restored areas.

The objectives of this study were as follows: (*i*) to document the plant species visited by insects known to visit *S. sericeum* to determine if a numerical facilitation mechanism is possible; (*ii*) to determine the synchrony between these plant species and *S. sericeum* to identify potential facilitators and competitors; and (*iii*) to test for an aggregative response by determining the impact of flowering stem density on insect visitation to *S. sericeum*.

Materials and methods

Study sites

Birds Hill Provincial Park, located north of Winnipeg, Manitoba (50°01′N, 96°53′W), is a 35 km² protected area that contains a variety of plant communities including tallgrass prairie and oak savannah. The park contains one of the largest populations of *S. sericeum* in Canada; an estimated 4400 genets are scattered throughout the park (Manitoba Conservation, personal communication). At least 492 other vascular plant species occur in the park (Manitoba Naturalists Society 1996).

Vegetation surveys

I established 16 plots throughout the park that contained at least five stems of *S. sericeum* to examine more closely during this study. The plots were 2.5 m² in size and ranged from 5 m to 2.91 km apart; on average, plots were 1.44 km apart. Sampling at this scale might not be sufficient for larger insect species with wide foraging ranges to distinguish between patches, particularly the social bees (Greenleaf et al. 2007; Waddington 1983). Sampling was conducted for 37 nonconsecutive days: 6 days in June (2011), 12 days in July (2010 and 2011), 11 days in August (2008 and 2010), and 8 days

in September (2008). I recorded the number of flowering stems of all plant species in the plots each sampling day. I calculated the total and individual flowering stem density by totaling the number per plot and dividing by the plot area (6.25 m²). I determined the mean density per plot by averaging the number of stems per day, and the mean density per day by averaging the number of stems per plot. From the flowering data I derived the following five phenological parameters: onset (date first flower opened or was first observed); end date (date last flower opened or was last observed); duration (difference between dates of first and last flowers); flowering peak (date when the largest number of stems in the plot were in flower); and synchrony (flowering overlap with *S. sericeum*). The flowering synchrony as defined here was calculated from a method modified from Primack (1980). The index of synchrony (*X*) for a plant species (*i*) and *S. sericeum* (*j*) is given by:

$$X_i = (1/f_i)e_{j \neq i}$$

where *f* is the total number of days individual *i* was in flower and e_j is the number of days individual *i* and *j* overlapped in their flowering. The index of synchrony was used to distinguish potential competitors from potential facilitators since species with a zero synchrony cannot compete for pollinators. The maximum index of synchrony (X_{max}) was the number of days of overlap when 50% of the stems at the flowering peak in the plots were blooming. *X* varies from 1 (plant flowering overlaps with that of all individuals of *S. sericeum*) and 0 (no overlap with any *S. sericeum* individuals). Maximum synchrony was used to help assess the intensity of the synchrony during the co-flowering period.

Floral visitor surveys

Flower-visiting insect sampling occurred for 37 nonconsecutive days from mid-June to mid-September (99 h total sampling time), thus covering the main period of insect activity. I sampled each plot for 10 min on each sampling day, the maximum amount of time that I could spend surveying. As foraging activity is generally low in the early morning when temperatures are cooler (Kevan and Baker 1983), surveys were conducted between 1000 and 1700. Surveys were never conducted when it was raining, as rain hampers insect activity (Kevan and Baker 1983). I varied the order in which the plots were visited each day by using a random number table to determine the visitation sequence. Some of the flower-visiting insects may have been predators or parasites on other flower-visiting insects. Regardless of whether insects were foraging for pollen, nectar, or other insects, all were considered potential pollinators.

A direct observation technique was used to sample the insects; the number of flowering stems each adult insect visited in each plot was recorded. The first time I observed an insect on a plant each sampling week at each plot, the specimen was netted or captured with an aspirator depending on the size of the insect, placed in a killing jar, and then transferred to a container with a unique reference number. When I observed the same (or very similar) species later that day on another plant, the reference number was used to link the insect visit to the plant. Although this technique does not allow for complete identification "on the wing" (resulting in an underestimate of insect taxa), it does enable evaluation of plant–insect visitation frequency (Parachnowitsch and Elle 2005). Capturing the insects may have altered the number of visits by some species. I calculated the visitation rate by dividing the number of visits recorded to each plant species by the amount of time in minutes spent in observation. The number of insect visits per flowering stem was also determined. All insect voucher specimens were identified by Heather Flynn, Robert Wrigley, or Sarah Semmler using reference specimens at The Manitoba Museum and the Wallis-Roughly Museum in Winnipeg,

Fig. 1. Flowering phenology of plant species that share insect visitors with *Symphyotrichum sericeum* over 87 calendar days. The line indicates the flowering duration and the square the day of the flowering peak in the research plots at Birds Hill Provincial Park, Manitoba.
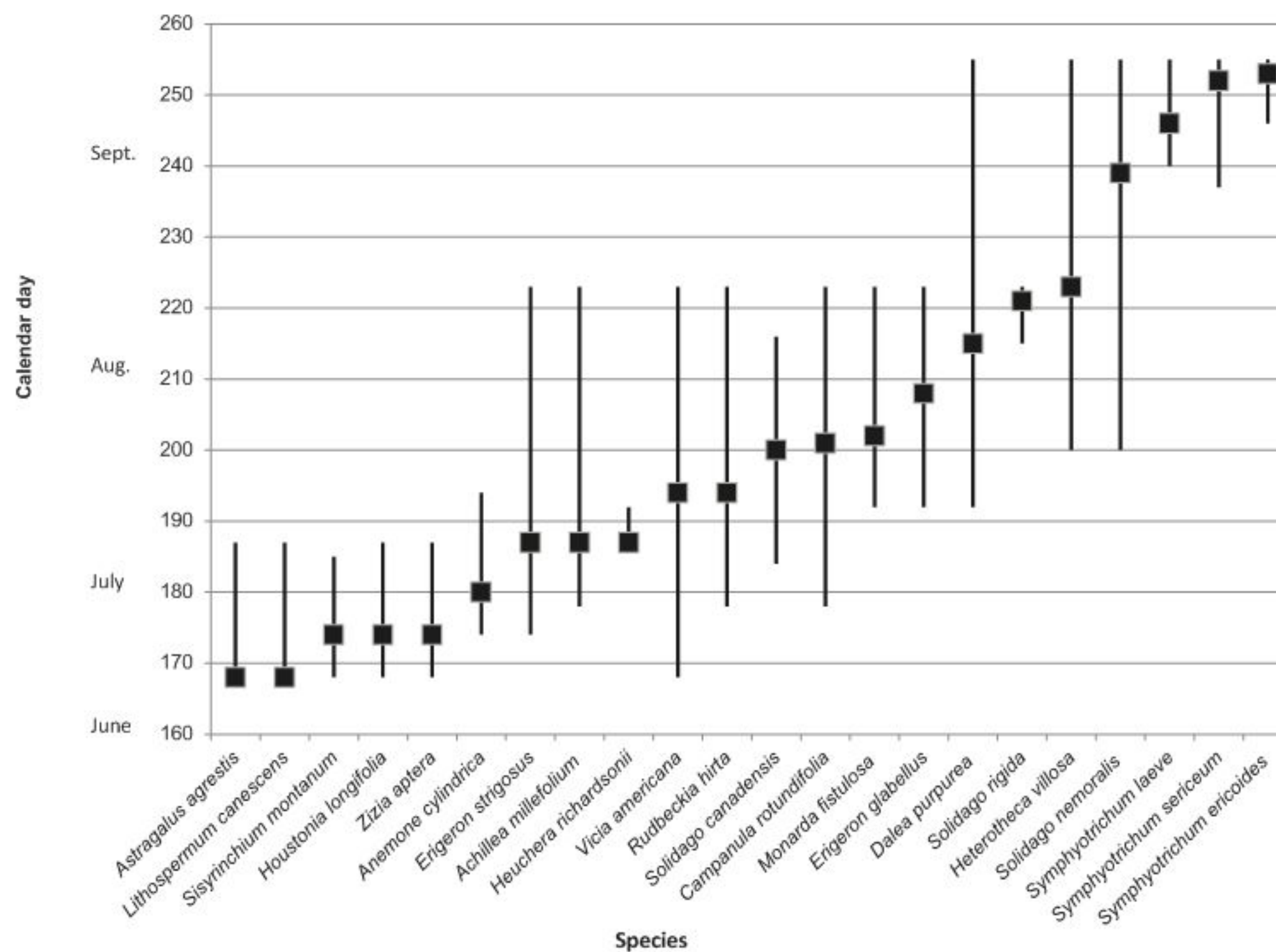
Manitoba, and digitally photographed; the images and specimens were deposited in The Manitoba Museum's zoology collection.

I obtained additional data on insect interactions from previous research in Manitoba published in Robson (2008), and as part of a general literature search (Reed 1993; Robertson 1929; Petersen 1996; Hilty 2002; Patenaude 2007). I used insect collection data from the Wallis-Roughly Museum at the University of Manitoba to help determine the active period for each insect taxon in Manitoba.

Similarity assessment

To determine the relationship between other plant species and *S. sericeum* total and maximum floral synchrony were considered. Species with total and maximum synchronies of zero were considered potential facilitators, as they can't compete with *S. sericeum* because their flowering periods do not overlap at all. In contrast, plants with a total and maximum synchrony of one were considered potential competitors due to perfect flowering overlap. However, as noted by Ghazoul (2006), facilitation may occur between co-flowering plants that have morphologically distinct flowers. Therefore, plant species with a total synchrony between one and zero were considered potential competitors or facilitators (or possibly both). Whether a species was considered a potential competitor–facilitator (e.g., more likely a competitor) or a potential facilitator–competitor (e.g., more likely a facilitator) depended on the maximum synchrony; if it was zero (indicating that the flowering peaks were not overlapping) the plant was considered a potential facilitator–competitor and if it was greater than zero it was considered a potential competitor–facilitator.

To determine which of the potential facilitator/competitor and facilitating plant species were likely most important in maintaining shared insect visitors (and therefore useful to include in future research), I ranked the species according to the number of shared total and high quality insect visitors, and the average number of insect visits per flowering stem (indicating their relative attractiveness to insects); these ranks were then averaged. High quality insect visitors included all species in the Bombyliidae, Apidae, and Halictidae as taxa in these families were frequent visitors to

S. sericeum (Robson 2010a), and more likely to transfer pollen owing to their behavioural characteristics and body size (Waddington 1983; Kwak and Bekker 2006). Some of the potential facilitators were visited by insect taxa that have been recorded as visiting the plant species outside of Birds Hill Provincial Park but not inside.

Data analysis

I used linear and nonlinear regression analyses to determine the relationship between the insect visitation rate and the flowering stem density, and selected the best fit shape to describe the data pattern. The distribution of residuals from the linear regression examining the impact of flowering stem density on insect visits per stem was used to determine the breakpoint (i.e., the point at which the linear relationship changes direction) (Ghazoul 2006). These statistical tests were done using Analyze-It software (Analyze-It).

Results

Flower density

The onset and flowering duration of each plant species in the research plots that share at least one insect visitor with *S. sericeum* are graphed in Fig. 1. The plants may have been in flower before or past the indicated duration period outside of the research plots. The surveys started on calendar day 168 (17 June) and ended on day 255 (12 September). The mean onset date of all species was calendar day 190 (9 July), the mean flowering peak was day 202 (21 July), and the mean end day 220 (8 August).

The total synchrony (X) with *S. sericeum* of all but five plant species was zero, indicating no flowering overlap at all (Table 1). Two species, *Symphyotrichum ericoides* (L.) Nesom var. *pansum* (Blake) Nesom and *Symphyotrichum laeve* (L.) A. & D. Love var. *geyeri* (Gray) Nesom, were considered potential competitors due to their total and maximum synchronies of one. However, since *S. ericoides* still flowered for several days after *S. sericeum*'s end date, the synchrony is likely slightly lower than indicated. The total synchrony of *Solidago nemoralis* was one but since its maximum synchrony was less than one it was considered a potential competitor–

Table 1. Data on plant phenology and insect visits to 22 plant species that share or likely share insect visitors with *Symphyotrichum sericeum* in Manitoba.

Plant species	Total synchrony (X)	Maximum synchrony (X_{max})	Flowering peak (month)	Shared insect visitor taxa (#)	Shared high quality taxa (#)[a]	Visits per flowering stem (mean #/m²)	Interaction type (importance rank)[b]
Symphyotrichum ericoides	1	1	Sept.	11	6	0.08	Potential competitor
Symphyotrichum laeve	1	1	Sept.	12	7	0.41	Potential competitor
Solidago nemoralis	0.34	0.88	Aug.	17	11	0.69	Potential competitor–facilitator
Dalea purpurea	0.29	0	Aug.	17	12	0.22	Potential facilitator–competitor (1)
Heterotheca villosa	0.34	0	Aug.	6	4	0.21	Potential facilitator–competitor (2)
Solidago rigida	0	0	Aug.	12	9	0.42	Potential facilitator (1)
Rudbeckia hirta	0	0	July	14	6	0.26	Potential facilitator (2)
Solidago canadensis	0	0	July	13	7	0.18	Potential facilitator (3)
Monarda fistulosa	0	0	July	9	6	0.27	Potential facilitator (4)
Erigeron glabellus	0	0	July	4	2	0.21	Potential facilitator (5)
Achillea millefolium	0	0	July	8	2	0.11	Potential facilitator (6)
Zizia aptera	0	0	June	5	2	0.13	Potential facilitator (7)
Erigeron strigosus	0	0	July	5	1	0.18	Potential facilitator (8)
Campanula rotundifolia	0	0	July	4	3	0.07	Potential facilitator (9)
Sisyrinchium montanum	0	0	June	2	1	0.01	Potential facilitator (10)
Melilotus alba[c]	0	0	July	1	1	0.50	Potential facilitator (11)
Astragalus agrestis	0	0	June	1	1	0.15	Potential facilitator (12)[d]
Vicia americana	0	0	June	1	1	0.13	Potential facilitator (13)[d]
Anemone cylindrica	0	0	June	1	0	0.01	Potential facilitator (14)
Lithospermum canescens	0	0	June	1	1	<0.01	Potential facilitator (15)[d]
Houstonia longifolia	0	0	June	1	1	<0.01	Potential facilitator (16)[d]
Heuchera richardsonii	0	0	July	1	1	<0.01	Potential facilitator (17)[d]
Mean	0.14	0.13	—	6.6	3.9	0.19	—

[a]High quality taxa include all Bombyliidae, Apidae, and Halictidae, as they are likely provide superior pollination services to *S. sericeum* over other taxa (Robson 2010a).

[b]The number in brackets, where present, indicates the importance rank of the potential facilitator–competitor or potential facilitator relative to the other plants in the category, calculated by ranking the plant species using shared insect visitor and visits–flowering stem data and averaging the value.

[c]Indicates the species is exotic to Canada.

[d]The interaction between the insect visitor of these plants and *S. sericeum* is unconfirmed in Manitoba.

facilitator since it may contribute to facilitation via a numerical response. Two species, *Dalea purpurea* Vent. var. *purpurea* and *Heterotheca villosa* (Pursh) Shin. var. *villosa*, had a maximum synchrony of zero indicating even less flowering overlap; for this reason these species may contribute to a numerical response and were considered potential facilitator–competitors. A total of 17 species were considered potential facilitators as their total and maximum synchronies with *S. sericeum* were zero. Based on visitation rates, *Solidago rigida* L., *Rudbeckia hirta* L., *Solidago canadensis* L., and *Monarda fistulosa* L. are likely the most important of the potential facilitators, as they have a high number of shared insect visitors and a large number of insect visits per stem. Whether five of these plant species are indeed potential facilitators requires confirmation that *Bombus vagans* Say, *Eristalis dimidiatus* (Wied.), and *Megachile relativa* Cresson do indeed visit *S. sericeum* in Canada. To confirm that these species facilitate the actual seed production of *S. sericeum*, an experiment assessing the impact on seed set when *S. sericeum* is grown in a mixture with them is still required.

Six species reached their flowering peak in June, nine in July, four in August, and three in September. The mean number of shared visitors per plant species was 6.6 and the mean number of high quality visitors (defined as insects in the Bombyliidae, Apidae, and Halictidae) was 3.9. The mean number of insect visits per flowering stem was 0.19 visits per minute. *Solidago nemoralis*, *Melilotus alba*, and *S. rigida* had the greatest number of insect visits per flowering stem, indicating that they are highly attractive to insects.

To assess floral resource production throughout the season, the cumulative flowering stem density of *S. sericeum* and its potential facilitators, facilitator–competitors, competitor–facilitator, and competitors using data from all 3 years was produced (Fig. 2a). The mean stem density was 6.5 stems/m²; the lowest density was on day 187 (6 July) and the highest density was on day 241 (30 August).

If only *S. sericeum* and its potential facilitators (grey dotted line) grew in the plots about two flowering stems/m² would have been available for pollinators throughout spring and early summer (calendar days 168–219), but there would be fewer than two flowering stems/m² for a period of about 18 days in mid- to late-August. As Fig. 2b indicates, insect visitation is normally quite high in August. A greater abundance of flowers would likely be required to supply enough food to sustain late summer insects. When potential facilitator–competitor species are included (black dashed line), the late summer floral deficit is largely eliminated.

Flower visitors

During the study, I observed 21 insect taxa visiting *S. sericeum* in the research plots; 14 of these taxa also visited at least one other species of plant (Table 2). All taxa were considered potential pollinators, although the quality of their pollination may vary considerably (Robson 2010a). When additional visitation data from Robertson (1929), Reed (1993), Petersen (1996), Hilty (2002), and Robson (2008) are added, the total number of insect taxa recorded as visiting *S. sericeum* increases to 24, and the number of insect taxa visiting other plant species increases to 22. The bumblebee, *Bombus bifarius* Cresson, made the most visits to all plant species and to *S. sericeum*. Almost 30% of all insect visits observed were to *S. sericeum*. The syrphid fly, *Toxomerus marginatus* Say, visited the greatest number of plant species. Only two taxa were observed only visiting *S. sericeum*. Four insect taxa have been observed as early as May in Manitoba, whereas seven others have not been observed until September. The taxa were active for a mean of 2.8 months.

The best fit shape to explain the relationship between the insect visitation rate to *S. sericeum* and the total flowering stem density ($R^2 = 0.641$, $P < 0.05$, $n = 16$), and with its own flowering stem density ($R^2 = 0.715$, $P < 0.001$, $n = 16$), are saturating (logarithmic)

Fig. 2. Cumulative flowering stem density (*a*) and insect visitation rate (*b*) to *Symphyotrichum sericeum* and its potentially facilitating and competing plant species over 87 calendar days.
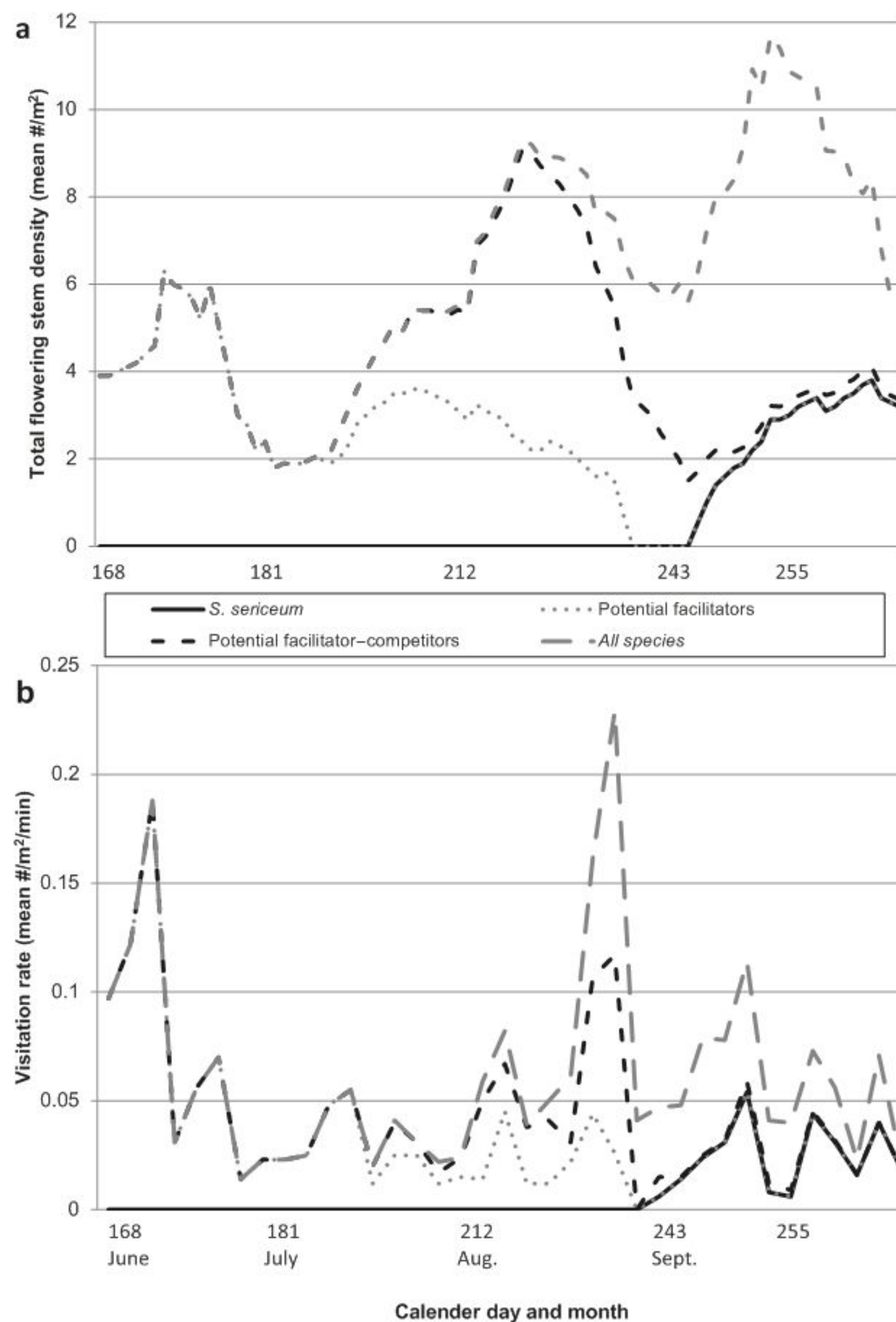
rather than linear (total stem density $R^2 = 0.363$, $P < 0.05$, $n = 16$; *S. sericeum* stem density $R^2 = 0.593$, $P < 0.001$, $n = 16$) (Fig. 3). The best fit polynomial curves determined using nonlinear regression were inverse sigmoid-shaped, not sigmoid; this means that pollinator response does not accelerate when density increases. When the insect visits are split according to Hymenoptera and Diptera, the best fit curves are also saturating (Hymenoptera, $R^2 = 0.786$, $P < 0.001$, $n = 16$; Diptera, $R^2 = 0.192$, $P = 0.179$, $n = 16$) rather than linear (Hymenoptera, $R^2 = 0.618$, $P < 0.001$, $n = 16$; Diptera, $R^2 = 0.030$, $P = 0.515$, $n = 16$) (Fig. 4). Again, the best fit polynomial curves were inverse-sigmoid shaped indicating that some insect visits occur even at very low densities. Only Hymenoptera visits increase significantly with density.

The number of insect visits to each individual *S. sericeum* flowering stem did not significantly increase with the total flowering stem density (Fig. 5*a*). Instead, the number of visits to *S. sericeum* increased and then declined once stem densities surpassed 1.25/m², the value determined to be the breakpoint as it resulted in the least residual deviance (Fig. 5*b*). At low densities (i.e., densities less than the breakpoint), insect visits to *S. sericeum* in-

creased with the abundance of flowering stems. At high densities (i.e., densities greater than the breakpoint), insect visits to *S. sericeum* decreased with the abundance of flowering stems. This indicates that individual flowers received the maximum number of visits when the flowering stem density of the community was 1–2/m².

Discussion

The results of this research demonstrate that the rare *S. sericeum* plant directly shares insect visitors with plant species that have little or no flowering overlap with it. About 70% of all shared insect visits observed were to plant species other than *S. sericeum*, indicating that most taxa are generalists that rely on many plants for sustenance. Because most plant-pollinator communities are highly nested (Waser et al. 1996; Olesen et al. 2007), this pattern is not unexpected. Most of the insect visitors observed are typically active for several months prior to the onset of *S. sericeum* flowering, indicating that these organisms require floral resources for an extended period of time to survive. If two plants share pollina-

Table 2. Activity and plant visitation data for insect taxa observed visiting *Symphyotrichum sericeum* plants.

Insect taxon	Visits to *S. sericeum* (#)	Visits to all species (#)	Visits to *S. sericeum* (%)	Plant species visited (#)[a]	Active period[b]
Bombus bifarius	103	319	32.3	5 (5)	July–Sept.
Anastoechus sp.	53	117	45.3	7 (7)	July–Sept.
Lasioglossum pruinosum	24	30	80.0	2 (13)	May–Sept.
Allograpta oblique	23	30	76.7	3 (7)	June–Sept.
Agapostemon texanus texanus	18	23	78.3	3 (6)	May–Sept.
Toxomerus marginatus	15	151	9.9	14 (17)	May–Sept.
Megachile latimanus	14	102	13.7	7 (11)	June–Sept.
Sphaerophoria contiqua	12	81	14.8	9 (14)	June–Sept.
Lasioglossum leucozonium	9	14	64.3	2 (3)	May–Sept.
Coelioxys rufitarsis	8	8	100	2 (4)	Sept.
Archytas sp.	8	40	20	3 (7)	Aug.–Sept.
Augochloropsis metallica fulgida	6	6	100	1 (7)	Sept.
Melissoides rustica	6	6	100	1 (6)	July–Sept.
Bembix sp.	6	6	100	1 (2)	Sept.
Pipiza sp.	5	5	100	1 (1)	Sept.
Lasioglossum coriaceum	3	4	75	3 (7)	Aug.–Sept.
Poecilanthrax sp.	2	2	100	1 (2)	Aug.–Sept.
Lasioglossum sp.	1	2	50	1 (12)	Sept.
Zodion sp.	1	1	100	1 (4)	Sept.
Hesperia comma assiniboia	1	1	100	1 (1)	Sept.
Bombus vagans[c]	—	70	—	2 (12)	May–Sept.
Eristalis dimidiatus[c]	—	57	—	3 (10)	June–Sept.
Megachile relativa[c]	—	3	—	1 (4)	June–July
Total	318	1078	29.5	—	—

[a]Indicates the number of plant species including *S. sericeum* observed being visited by each insect taxon in Birds Hill Provincial Park, Manitoba, and, in brackets, the number of additional plant species visited by the taxon outside of the park, as documented in Robertson (1929), Reed (1993), Petersen (1996), Hilty (2002), and Robson (2008).

[b]Months when insect taxa have been observed in Manitoba were based on field observations, Wallis-Roughly Museum, University of Manitoba collection records, and Patenaude (2007).

[c]These insect species were observed visiting *S. sericeum* in Illinois (Hilty 2002) but not in Birds Hill Provincial Park, Manitoba. However, since the insect species was observed visiting other plant species in the park, they were included in the dataset.

Fig. 3. Relationship between the visits to *Symphyotrichum sericeum*, and the total and *S. sericeum* flowering stem density ($n = 16$). The curves indicate saturating responses to increasing plant density.
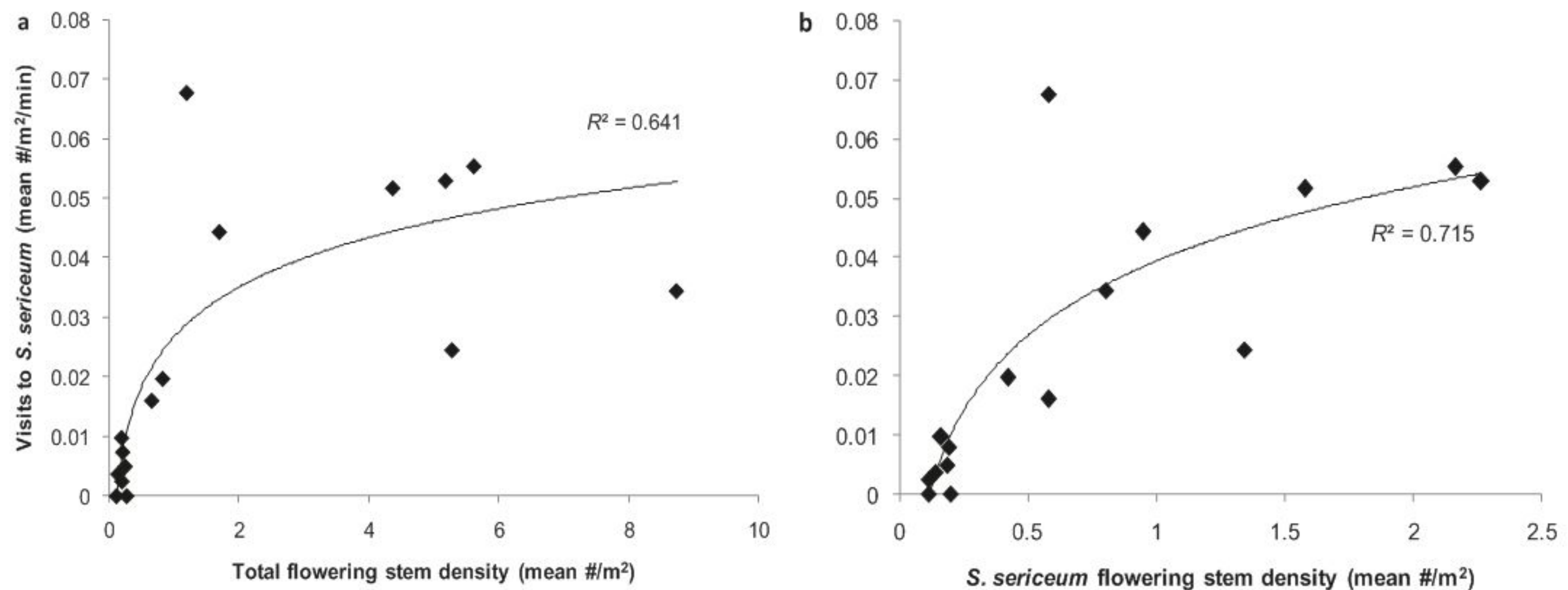

tors, this could lead to a numerical response in the pollinator populations. Essentially, insect populations may not be as high in the areas where *S. sericeum* grows if no other plant species are present to sustain them. By using a similar network analysis, the rare plant *Trinia glauca* (L.) Dumort was also found to depend on other plant species to support shared pollinators (Carvalheiro et al. 2008). To confirm a numerical response, a study where *S. sericeum* is grown in isolation and with combinations of potential facilitators is needed to assess the impact on the pollinator population. Facilitation via a numerical response would be con-

firmed if growing plants in mixes increases the reproductive success of the plants. Treatment plots would have to be large enough to ensure that pollinator populations are responding to the treatments.

The other component examined in this research project was the impact that flowering plant density had on insect visitation to the rare plant. As in many other studies (Kunin 1997; Fausto et al. 2001; Mustajärvi et al. 2001; Waites and Ågren 2004), the number of insect visits observed in the plots increased as flowering stem density increased. Essentially, patches with lots of flowers receive

Fig. 4. Relationship between *Symphyotrichum sericeum* flowering stem density and the visits to *S. sericeum* by Hymenoptera and Diptera (*n* = 16). The curves indicate saturating responses to increasing plant density.
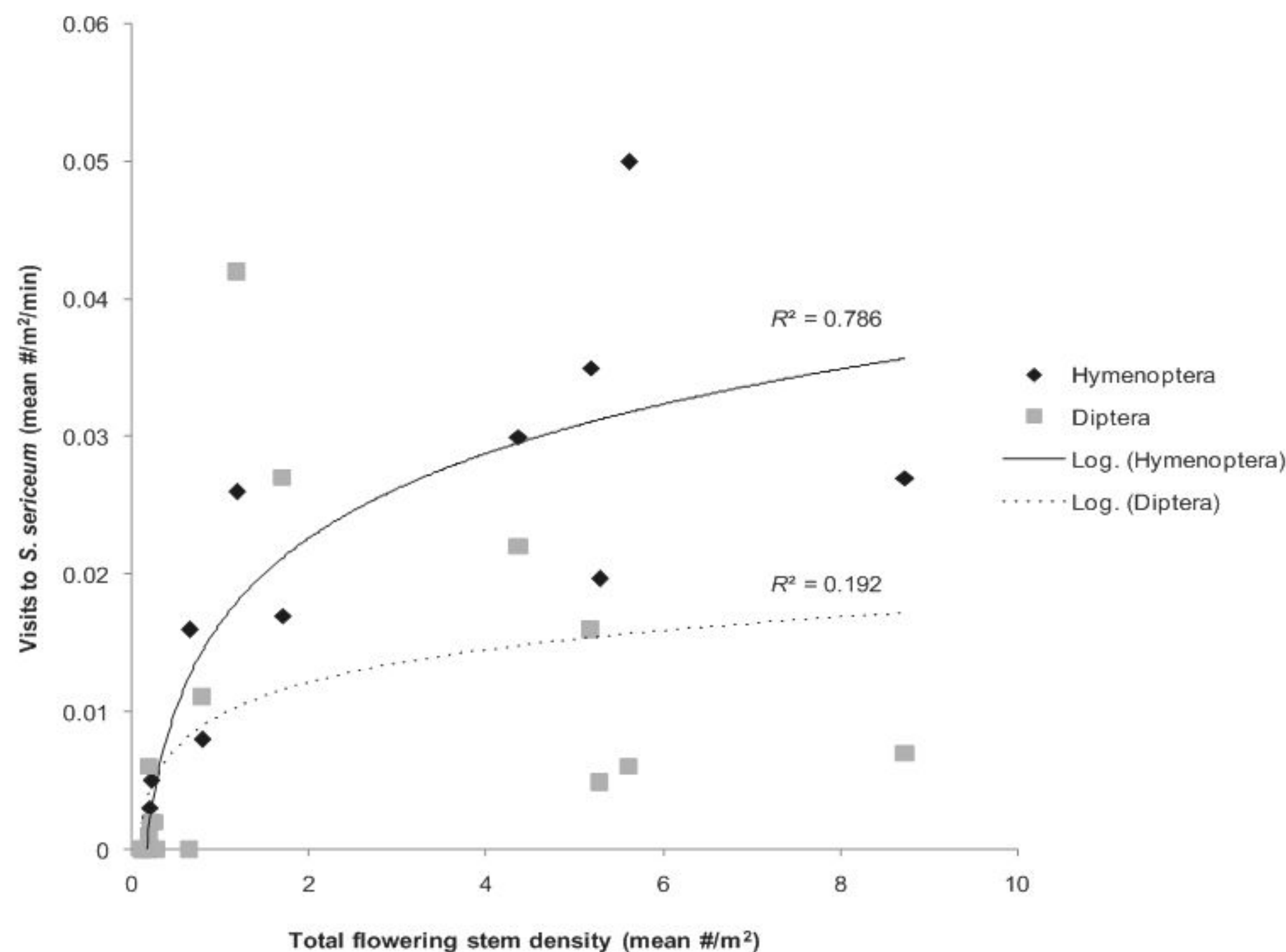
more visits than those with fewer (Stout et al. 1998; Thomson 1981). However, to prove that a facilitative effect is occurring via an aggregative response, the best fit to the data would have had to have been a sigmoid response curve with few visits occurring at low densities. In this study a saturating curve was the best fit, a similar result as that noted by Feldman (2006). This saturating curve likely occurs because insect visitors are not completely ignoring the very low density patches, and that the insect visitors in the area are not visiting flowers at more than a certain maximum rate (Feldman 2006); in this community about 0.07 flowering stems/m²/min. The species responsible for most visits was *Bombus bifarius*, a taxon that has a fairly large foraging range (Greenleaf et al. 2007). It is possible that this species did not discriminate among some of the plots at the scale measured in this study. Future studies should ensure that the distance between plots is large enough to allow for discrimination by this important visitor.

In this study, the number of visits per stem increased to a breakpoint (1.25 flowering stems/m²) then decreased. Thus, each individual flower would receive the highest quantity of visits when the density approximately equals the breakpoint. At densities higher than the breakpoint, competition begins occurring between plant species (resulting in fewer visits per stem) possibly due to handling time limitations or a limited number of available pollinators (Feldman 2006; Schmitt 1983). However, some research has noted that most seed production occurs when the plant in question reaches its flowering peak as the quality of visitations is highest at this point due to greater constancy of the insect visitors (Campbell 1985; Bishop and Schemske 1998; Hegland and Totland 2005). Low constancy may result in heterospecific pollen transfer (Feinsinger 1987) and stigmatic clogging (Morales and Traveset 2008), which may reduce the quality of the visit. Mixed pollen loads on insects, such as what we would see at low densities in multi-species mixes, may reduce the effective pollination of the rarer species (Levin and Anderson 1970; Campbell and Motten 1985). Previous research (Robson 2008) suggests that pollen limitation occurs when *S. sericeum* stem density is 1/m² but not when it is 3/m², a value that is indeed close to *S. sericeum*'s flowering peak of 3.8 stems/m². Thus,

to adequately attract insect visitors and ensure maximum seed production in *S. sericeum*, a desirable flowering stem density is likely between 2 and 4/m².

In a study by Thomson (1981), both Hymenoptera and Diptera responded in the same way to changes in density. However, in this study the Hymenoptera that visited *S. sericeum* responded more strongly to the increase in flowering stem density than Diptera, a result also observed in Feldman (2006). The number of Hymenoptera visitations to *S. sericeum* per m² increased significantly with increasing density. This may be because the higher energy requirements of bees resulted in more thorough exploitation of the resources in the plots (Waddington 1983). Diptera visits did not increase significantly as the density increased. This suggests that Diptera populations were relatively low and (or) did not need the additional resources.

Management recommendations

This research has implications for the conservation and restoration of *S. sericeum* and other rare plants with similar characteristics. Recovery plans for rare plant species may involve the establishment of new populations or restoration of extirpated ones, to increase the species' survivability (Demauro 1994). Mitigation measures for the destruction of a rare plants' habitat may involve the establishment of new populations in alternate locations, such as on mine spoil. However, this research suggests that planting just the rare species alone may not result in the establishment of a self-sustaining population, especially if the plant is incapable of self-pollinating. Rather, several facilitating plant species may need to be grown with the rare plant to attract and encourage the establishment of permanent populations of pollinating insects (Handel 1997; Winfree 2010). A consistent supply of diverse, pollen- and nectar-rich plants was found to be beneficial in attracting bees to restored arable field margins (Kells et al. 2001; Pywell et al. 2006; Carvell et al. 2004, 2007; Potts et al. 2009). As insects have different energy requirements and ranges over which they will forage (Greenleaf et al. 2007; Waddington 1983), the optimal density of a restored system will vary depending on the relative importance of

Fig. 5. Relationship between the total flowering stem density and the number of insect visits to each *Symphyotrichum sericeum* flowering stem with the (*a*) linear regression line, and (*b*) breakpoint (= 1.25 flowering stems/m²) regression line (*n* = 16).
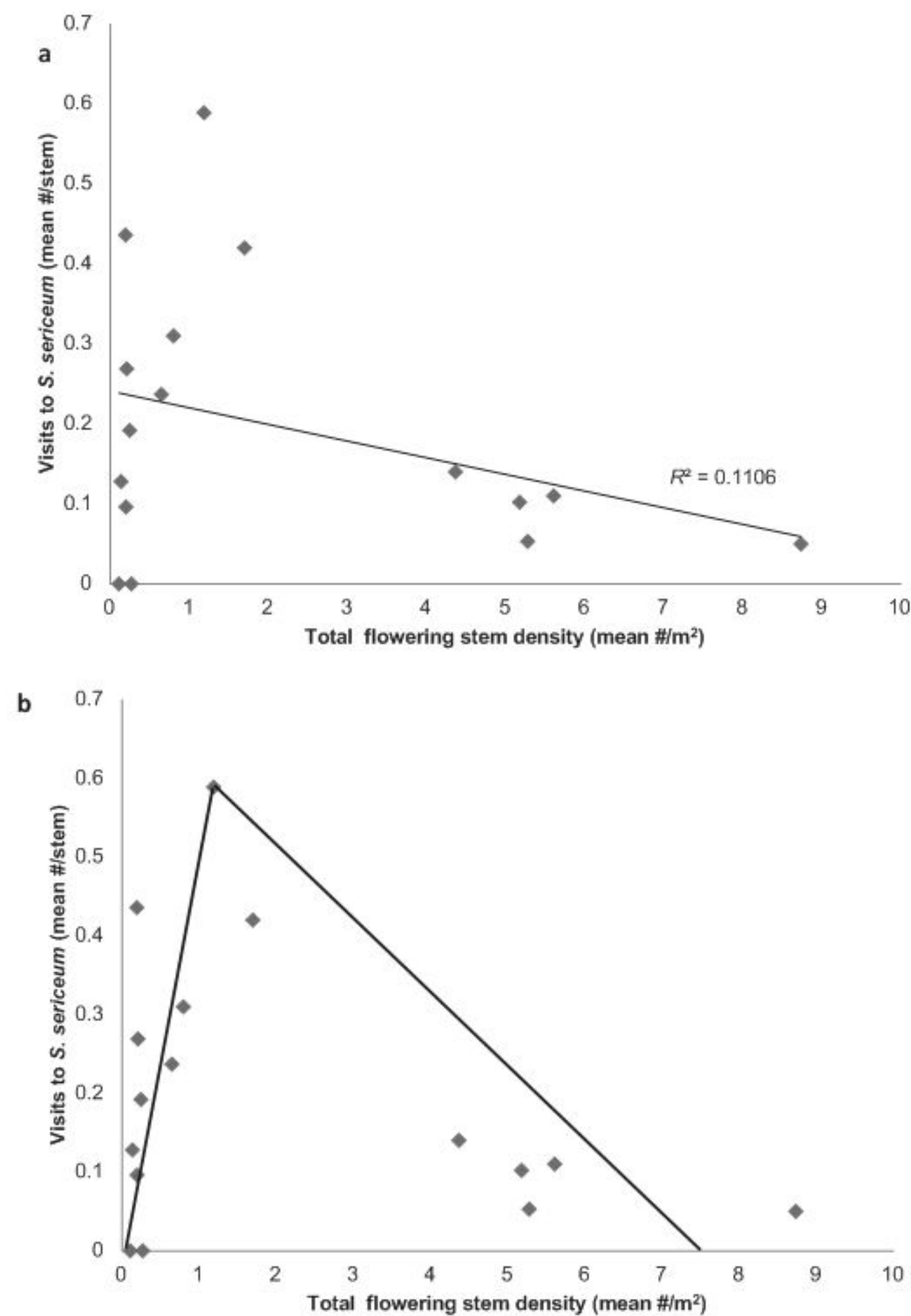
the pollinator. The optimal density must provide enough resources for the most important pollinator but not so high as to reduce the number of visits per plant stem.

Creating a plant–insect visitor interaction matrix and documenting the flowering phenology of a rare plants' community can aid in the selection of species for inclusion in restoration plans (Carvalheiro et al. 2008; Gibson et al. 2006). However, some caution is needed when interpreting these matrices, as previous research has indicated that the similarity of insect taxa from year to year is normally quite low, possibly due in part to insect responses to normal climate variability (Robson 2008; Herrera 1988; McCall and Primack 1992). Further, some species are normally rare in spring but more common in late summer (or vice versa) and may be difficult to observe, resulting in missing links (Foster et al. 2004; Oertli et al. 2005). In fact, Herrera (1988) found that only 21% of all taxa were present throughout the entire growing season. Gibson et al. (2006) also found substantial differences in the pollinator communities among sites, an observation also made in other tallgrass prairies in Manitoba (Robson 2008). Unless extensive surveys are conducted over multiple years at different sites, many interactions may not be detected. Nonetheless, monitoring the number of insect visits to the rare and most common plant species and recording even the family of each insect visitor would provide some information about potential facilitative interactions within the community that could be used to create better restoration plans.

Handel (1997) suggested that a restoration should be designed so that flowering is sequential. Based on the results of this research, I would recommend that a minimum of the following nine plant species be grown along with *S. sericeum* in any restoration plan to ensure sequential flowering: *Astragalus agrestis*, *Sisyrinchium montanum* Greene, *Zizia aptera* (L.) Koch (June), *Monarda fistulosa*, *Rudbeckia hirta*, *Solidago canadensis* (July), *Dalea purpurea*, *Heterotheca villosa*, and *Solidago rigida* (August). Together, these nine species provided about half of the total flowering stem density observed in the plots. Menz et al. (2011) suggested that "bridging" species (i.e., plant species that provide nectar and pollen resource during otherwise resource limited times) be included in pollinator restoration plans. As queen bees (*Bombus* spp.) need to create a honey pot to raise their first broods (Hobbs 1966), the presence of some plants that bloom in early spring are essential for the establishment of bumblebee colonies (Handel 1997). Plants that occur in the research plots at Birds Hill Provincial Park that may act as early season bridging plants for *S. sericeum* visitors include the following: *Allium stellatum* Nutt. ex Ker-Gawl., *Anemone patens* L., and *Geum triflorum* Pursh. Species of *Prunus* in the bluffs surrounding the research plots were also observed being visited by queen bees in April and May, and may be ultimately beneficial to *S. sericeum*. Thus the inclusion of several of these bridging plants in a restoration would likely improve the habitat for vital pollinators.

The quality of visits to a rare plant may be reduced when insects are carrying foreign pollen (Lewis 1961; Campbell 1985; Morales and Traveset 2008). Removal of the flowers of a competing plant species was found to increase insect visits and seed set in a target species, suggesting that existing populations of rare plants may benefit from lower densities of competing species (Campbell 1985). Thus, the potential competitor species of the rare plant should probably be avoided, or, at the very least, not planted in high densities in the immediate vicinity of restored populations, in order to minimize the negative effects of competition.

Conclusions

This research has established several key points as follows: (*i*) the rare *S. sericeum* plant shares insect visitors with at least 17 species of common plants; (*ii*) many of the shared insect visitors are active in the months prior to the onset of flowering in the rare plant; (*iii*) plant species sharing visitors may be facilitating visitation to the rare plant via a numerical response; (*iv*) facilitation via an aggregative response does not appear to be occurring; and (*v*) Hymenoptera respond more strongly to density affects in this ecosystem than Diptera. Successful conservation and restoration of rare plants likely requires consideration of the nature of the pollinator community structure to design plans that will ensure long-term persistence of the species.

Acknowledgments

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